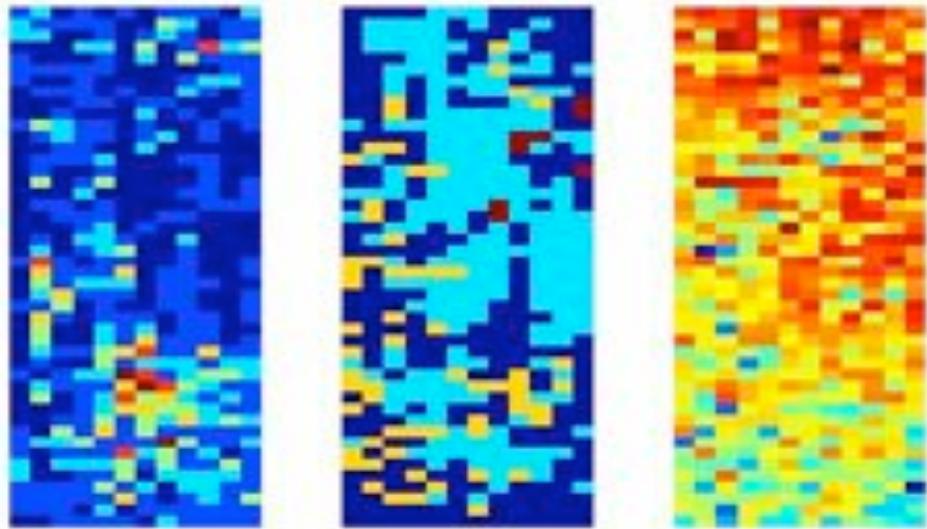


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CLUMP SIZE DISTRIBUTION OF ANTS AS A SIGNAL OF SELF-ORGANIZATION WITH SPATIALLY CONSTRAINED LOCAL EXPANSION

DOUG JACKSON, DAVE ALLEN, HUIJIE GAN, RACHEL HESSLER, IVETTE PERFECTO, COLIBRÍ SANFIORENZO-BARNHARD, SENAY YITBAREK, JOHN VANDERMEER

ABSTRACT

The spatial distribution of three dominant ant species, *Monomorium minimum*, *Solenopsis molesta*, and *Tetramorium caespitum*, in a 96 m by 22 m plot in a relatively homogenous environment, was mapped on two consecutive days. *S. molesta* and *T. caespitum* competitively excluded each other, exhibiting spatial distributions with very little overlap. *M. minimum* was distributed widely in the plot without any clear relationship to *S. molesta* or *T. caespitum*. The clump size distribution of *S. solenopsis* was characterized by a power law, suggesting self-organization with spatially constrained local expansion. The clump size distribution of *T. caespitum* deviated from a power law at large clump sizes, possibly because the large (2 m) spacing between samples artificially merged two or more smaller clumps into a single large clump. The clump size distribution of *M. minimum* also deviated from a power law, with excess small clumps, perhaps due to *M. minimum* employing a scramble competition foraging strategy.

INTRODUCTION

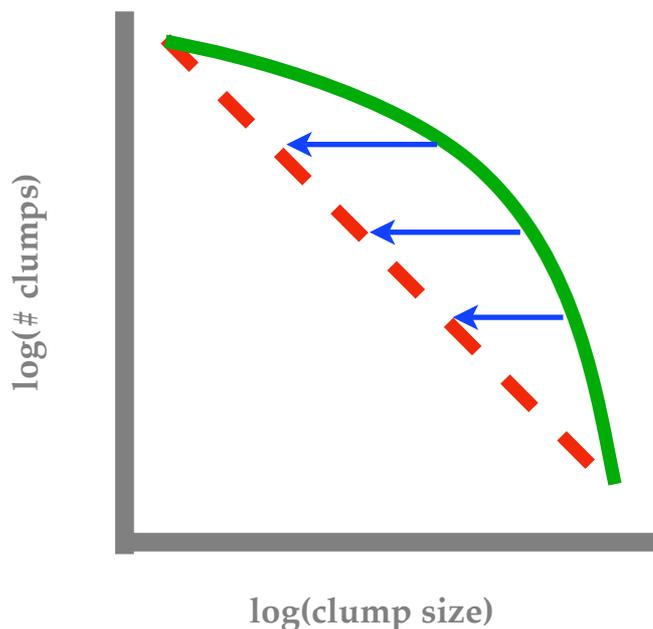
Spatial distributions of sessile organisms are often assumed to arise as a result of underlying environmental heterogeneity, e.g., edaphic variation or microclimatic differences. However, a growing body of research has demonstrated that spatial pattern can arise through endogenous, biotic processes through a phenomenon known as self-organization (Solé and Manrubia 1995, Maron and Harrison 1997, Gurney and Veitch 2000, Wootton 2001, Reitkerk et al. 2004). Self-organization occurs when microscale interactions between individuals lead to the emergence of spatial patterns at the macro scale. For example, local interactions between individual colonies of an arboreal-nesting ant and a phorid fly that parasitizes it have been shown to generate a low-density, clumped distribution of ant nests in a tropical coffee agroecosystem, even though the underlying environment is relatively homogeneous (Vandermeer et al. 2008).

When a spatial pattern generated by self-organization is identified in nature, an obvious question to ask is whether or not it is possible to infer anything about the underlying self-organization process by analyzing the resultant pattern, i.e., can process be inferred from pattern? In cases where the self-organization process involves local expansion, the clump size distribution may provide information about whether expansion is spatially unconstrained or spatially constrained. Spatially unconstrained expansion would generate an exponential relationship between clump frequency and clump size, while spatially constrained expansion would result in a power law distribution, as described in the following.

Spatially unconstrained expansion refers to the case when new individuals are free to disperse locally in any direction from their parent. For example, consider an area of habitat represented by a two-dimensional grid of cells. Spatially unconstrained expansion would imply that a clump of size one would be able to expand into all of its neighboring 8 cells, meaning that a clump of size one would grow to be a clump of size 9 in the next time step. Similarly, a clump of size two would be free to expand to a clump of size 18. In the spatially constrained case, in contrast, a clump cannot expand into a previously occupied cell. In this case, a clump of size two would only expand to a clump of size 12; each cell of the original two-cell clump would be able to expand into the five cells away from the other cell in the original clump, but would be prevented from expanding in the direction of the other original cell.

If the frequency of clumps is plotted versus clump size on a log-log scale for a pattern generated through spatially unconstrained expansion, a curved line results (Figure 1). If expansion is spatially constrained, clumps are smaller than they would have been in the unconstrained case, and the curve is shifted to the left, as shown by the arrows in Figure 1. The result is a straight line on the log-log plot, a relationship which is known as a power law. Thus, a power law distribution implies spatially constrained expansion, while an exponential distribution implies spatially unconstrained expansion.

Figure 1: The solid line represents an exponential curve resulting from spatially unconstrained expansion; the dashed line is a power law resulting from spatially constrained expansion. Arrows represent how clump sizes decrease due to spatial constraint.



We applied this concept — that the signal of spatially unconstrained or spatially constrained expansion can be detected by analyzing a spatial pattern — to the spatial distribution of ants in a field located at the Edwin S. George Reserve. In addition to revealing the presence or absence of spatial constraint, we expected that the pattern of clumps of the dominant ant species would reflect interspecific competition, with species that occupy a similar foraging niche excluding each other from certain areas of the plot.

METHODS

Study Site

This study took place at the E.S. George Reserve in Livingston County, Michigan. The site was located in a field where the topsoil had been removed in 1988. This site is a relative homogenous environment with sparse vegetation, grasses, and shrubs. The temperature remained high (> 20 °C) throughout the day, thereby providing optimal conditions for ant foraging.

Field Experiment

We established 10 transects in a grid-like structure that covered 92 X 22 meters. We placed tuna-baits every 2 meters and then waited 20-30 minutes for foraging ants to arrive at the baits. At each bait, we identified foraging ants to genus. We were interested in presence/absence of ants, so we did not record the numbers of individuals.

We plotted the spatial distribution of the three dominant ant species and counted the number of clumps of each size. Sample points of a given species were considered to be part of the same clump if they were touching in any of the four cardinal directions, i.e., clumps were defined by the von Neumann neighborhood (the four nearest neighbors).

RESULTS

There were 12 ant species observed on the baits in our two-hour survey in addition to the three dominant species (*Monomorium minimum*, *Solenopsis molesta*, and *Tetramorium caespitum*.) These dominant species exhibited distinct clustered distributions (Figure 2). While *M. minimum* was widely distributed with many isolated points, *S. molesta* and *T. caespitum* tend to have few overlaps within our study plot (Figure 3). When we repeated the survey on the second day, *S. molesta* was found to occupy more baits, but the exclusive pattern between *S. molesta* and *T. caespitum* remained (Figure 3).

Figure 2. Distribution of dominant ant species on the first day.

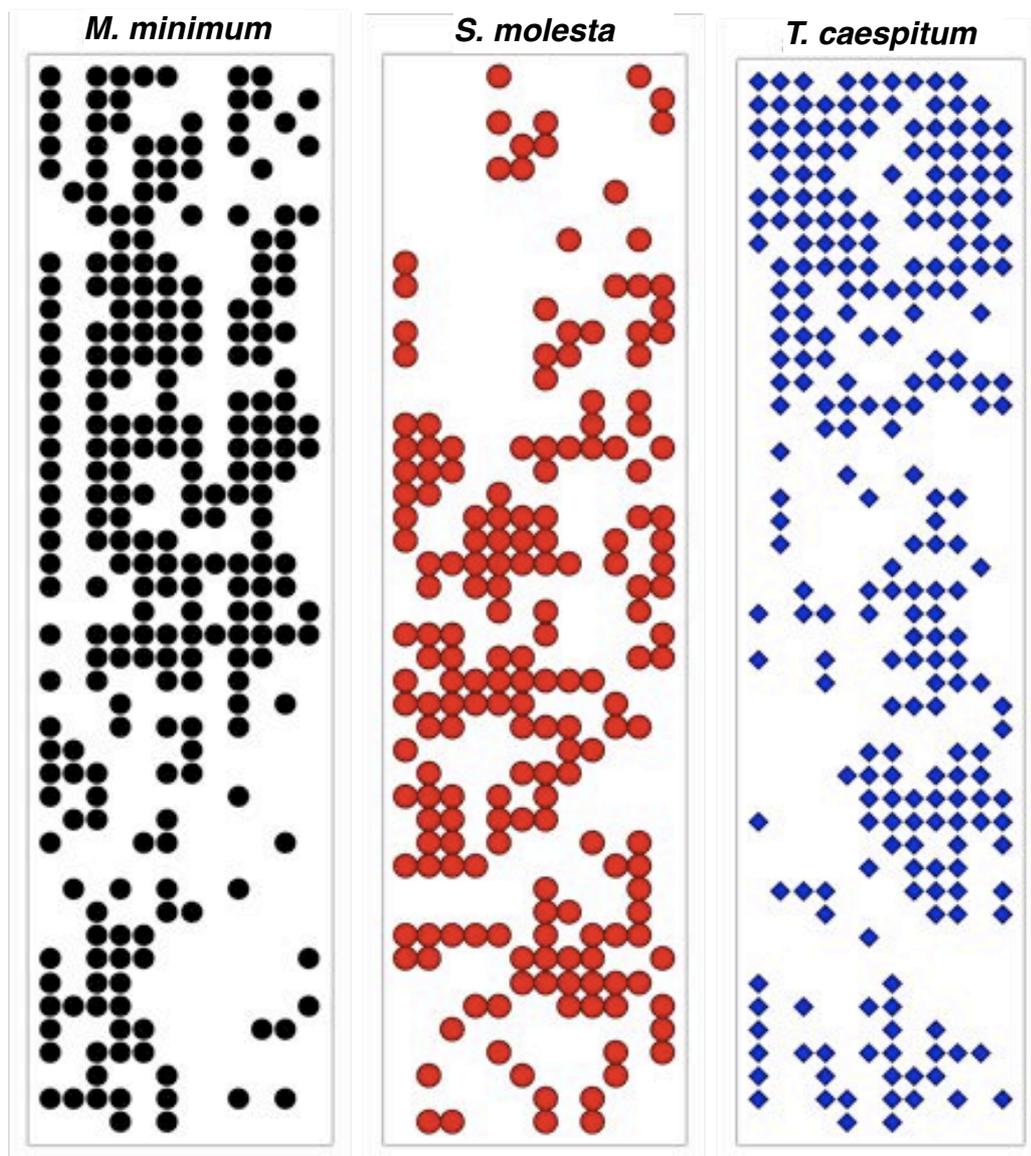
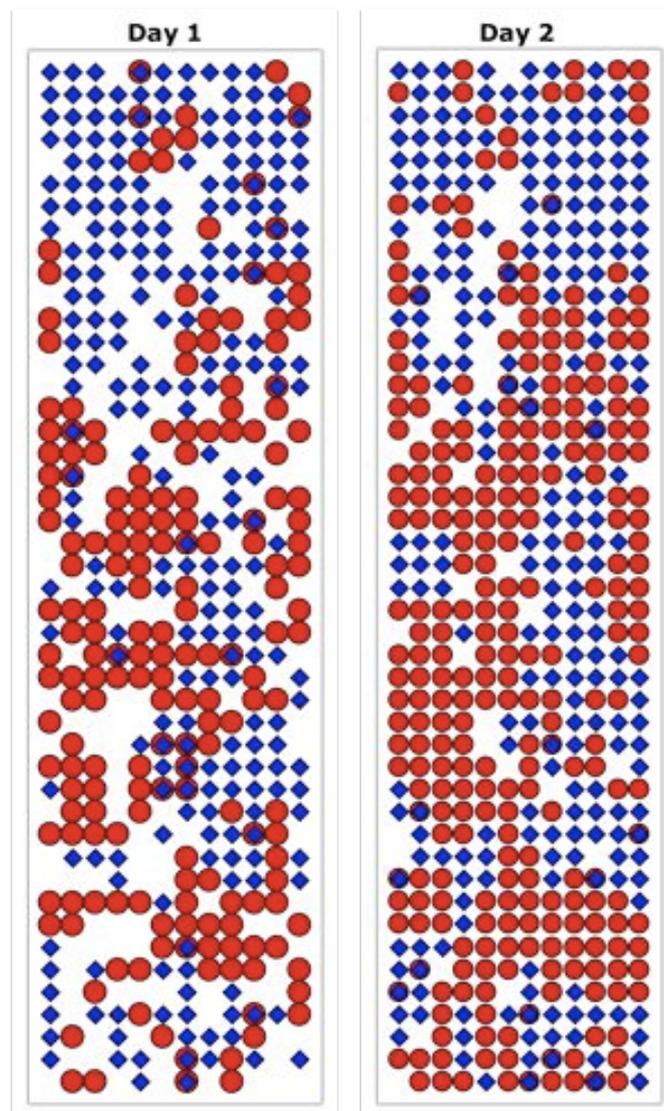
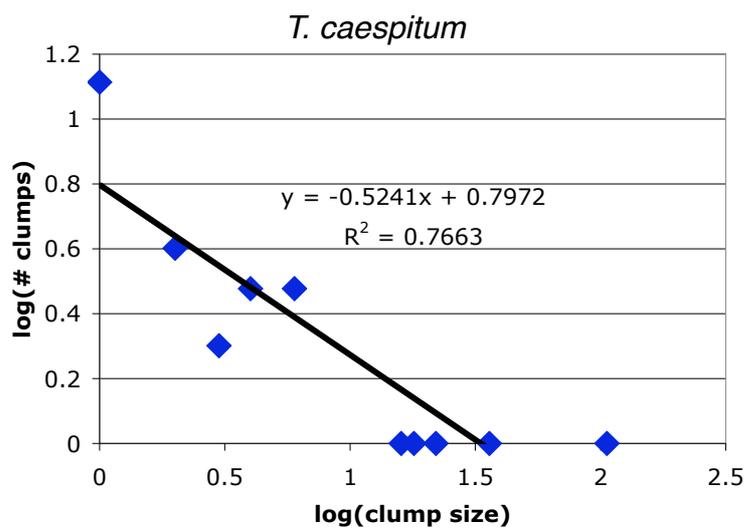
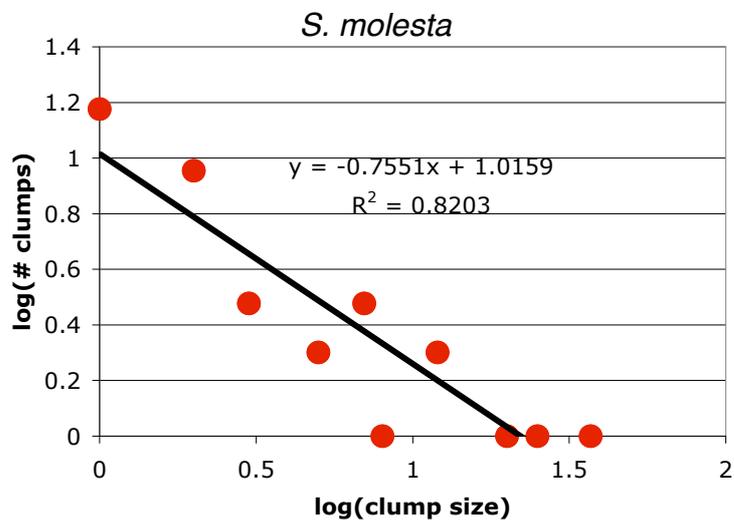
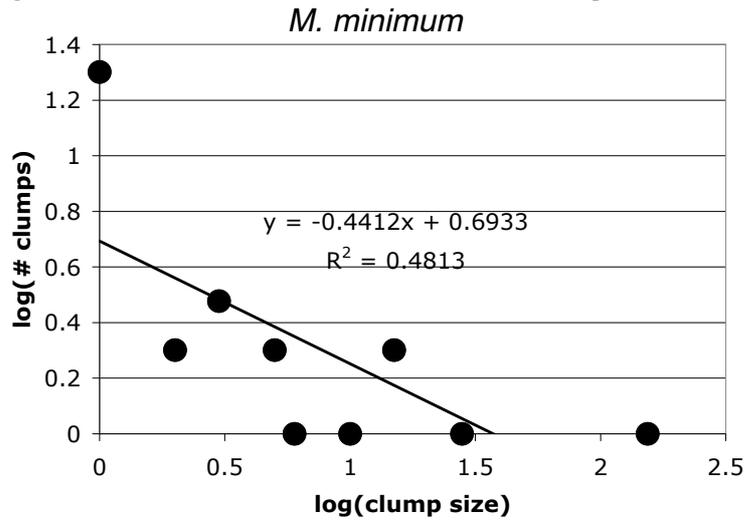


Figure 3. Exclusive distribution of two ant species on both days. Red circles represent *S. molesta*. Blue diamonds represent *T. caespitum*.



The cluster size distributions of these three species on log-log axes are quite different from each other: for *S. molesta*, the distribution almost fits a straight line (a power law distribution) with an R^2 of 0.82, while for the other two there is deviation from a linear regression (Figure 4). There were many one-bait clusters of *M. minimum* and one very big cluster of *T. caespitum*, resulting in clump-size distributions that were poorly fit by a power function ($R^2 = 0.4813$ and 0.7633 , respectively).

Figure 4. Cluster size distributions of the dominant ant species.



DISCUSSION

The clump size distribution of *S. molesta* was well described by a power function, which suggests that the spatial distribution of this species in this plot arises through a process of local expansion with spatial constraint. The clump size distribution of *M. minimum* and *T. caespitum*, in contrast, did not clearly follow either a power law or an exponential distribution. *T. caespitum* produced a weak power log due to the excessive size of some of the clumps. However, this may have been an artifact of the two meter distance between baits; what looked like a single, large clump using a distance of 2 meters between baits might have been resolved into two or more clumps had we used a sample grid with a finer resolution. Therefore, it is possible that *T. caespitum* is also spreading via local expansion with spatial constraint, but that our sampling methodology obscured the pattern. *M. minimum* also did not produce a power law clump size distribution. *M. minimum* lacked a power law because it had many single clumps. This may be due to a scramble competition foraging mode, which involves reaching baits first and then retreating when other, more dominant, competitors arrive. The excess single clumps (compared to the expected power law distribution) may result from *M. minimum* initially dominating the entire plot and subsequently being excluded, with the small clumps being transitory remnants of a broader distribution.

Of the three species, *S. molesta* and *T. caespitum* appeared to compete for territory and thus mutually exclude each other. An overlay of their distribution patterns revealed that their spatial distribution is non-random and negatively correlated. Areas were either dominated by *S. molesta* or dominated by *T. caespitum*. *M. minimum* appeared to randomly coexist with both species.

While we attribute the distribution pattern between *S. molesta* and *T. caespitum* to self-organization and not edaphic or climatic conditions because the field was homogenized by the scraping of topsoil and removal of plant growth in 1988, it is possible that in the twenty years that have passed, wind distributed seeds and other randomly established plants have created microclimates and made the field more heterogeneous. For example, in the middle of the field there was an individual *Eleaegnus umbellate* (autumn olive). The shade from the autumn olive changes the temperature of the soil beneath it. The nutrient and water requirements for the autumn olive are different from the requirements of other plants in the field. In order to rule out edaphic conditions as a factor in the distribution patterns, the study would need to include measurements of soil temperature, moisture, and density at each bait site.

Another important consideration is that there are other processes that have been shown to generate a power law distribution (Pascual et al. 2002). Therefore, although the clump size distributions obtained in this study are suggestive of local expansion with spatial constraint, it is possible that other mechanisms may be responsible for the observed patterns, and further investigation would be required to rule out these other processes. Furthermore, the limited spatial extent of our system prevented us from obtaining a large range of clump sizes, so the horizontal range of the clump size data is less than one would ideally use when fitting a power function. However, even with these caveats, this analysis can provide a useful foundation for developing further hypotheses about the underlying interactions and dynamics in this system.

Because native ants are keystone species in their respective habitats as seed dispersers, biocontrols, and soil aerators, it is crucial to understand the characteristics and strategies of

invasive ants. The invasion by *T. caespitum* (*T. caespitum* is an introduced species from Europe) provides the opportunity to diagnose the mechanisms of competitive asymmetries. Is it possible that *T. caespitum* is more successful at sequestering territory and food resources than the native ants, and, if so, why? Consider the following: *T. caespitum* can use the sun to navigate and does not need to depend on pheromones (Holldobler and Wilson 1990). Is it possible that the native ants, specifically *S. molesta*, cannot detect the pheromones of *T. caespitum* because *T. caespitum* does not always leave a pheromone trail? *S. molesta* is cleptobiotic. *S. molesta* invades the nests of other ants and takes food sources including larvae. Perhaps *S. molesta* cannot follow *T. caespitum* to its nest because *T. caespitum* is “invisible” because it uses light, and not pheromones, to navigate. Also supporting the “invisibility hypothesis” is that fact that *T. caespitum* is non-native while *S. molesta* is native. The two have not coevolved, thus *S. molesta* and *T. caespitum* may not have matched pheromone producing and pheromone detecting abilities. Is “invisibility” responsible for the competitive asymmetry between *T. caespitum* and the native ants?

This study contributes important information on the interactions between the two native species *S. molesta* and *M. minimum* and the invasive species *T. caespitum*. Continued monitoring at this study site may provide a deeper understanding of the competition dynamic between *S. molesta* and *T. caespitum*, the outcome of biological invasions, and the mechanisms of successful invasion. The use of a power functions to describe spatial distributions may be an important tool to help understand the range expansion of non-native ants and the displacement of native ants.

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HABITAT SELECTION AND SPACIAL WEB DISTRIBUTION PATTERN OF FILMY DOME SPIDER (ARACHNIDA: ARANEAE: LINYPHIIDAE)

JINGCHUN LI

ABSTRACT

Three spider population located in E. S George Reserve were investigated in this study. Spider species was confirmed to be filmy dome spider (*Neriene radiate*). The habitat selection of those spiders was studied. The desired stem structure of the scouring rush (*Equisetum hymelae*) seemed to be the primary factor that influenced the spiders' selection. Within each population, the spatial distribution of webs were mapped and analyzed. Their distribution seemed to follow both power law and exponential function under small web scale and fit power law function better under large web scales. Since the different web scales were manipulated instead of real data, further prediction of the population dynamic is limited. Several factors that might affect the web scale and aggregation in natural population were discussed.

INTRODUCTION

Spiders are the most dominant invertebrate predators in various environments. They can act as biological control agents in many ecosystems, especially in agroecosystems. Effective incorporation of web-building spiders in pest management strategies requires knowledge of factors such as prey distribution, spider-spider interactions and spatial distribution patterns of spiders at both large and small scales (Birkhofer et al., 2007). An understanding of the features that influence spider distributions is important for predicting future population dynamics and maximizing their potential for biological control.

The dominant web-building species in North American belong to four families: Linyphiidae, Theridiidae, Tetragnathidae, and Araneidae (Culin and Yeorgan 1983a, b). The wide spread species filmy dome spider (*Neriene radiate*) belongs to the family Linyphiidae. It spins a fine, dome-shaped web in the understory vegetation. This species has a typical annual life cycle (Wise, 1984). In the E. S. George Reserve, three filmy dome spider populations were found in the experimental ponds area. Since the environmental variation is relatively small but the spider distribution shows high heterogeneity, these ponds make a good study system to evaluate the factors that may affect habitat selection of filmy dome spiders.

In terms of large scale habitat selection, due to the limited disperse ability of web weaver spiders, it is considered that structural complexity is a primary factor in determining initial web site selection (McNett & Rypstra 2000). The association between spider abundance and environmental parameters including vegetation structural was studied in this research. It is expected that vegetations which provide favored structural complexity would attract more spiders. At small scale, the spider webs formed clusters within each population. In most ecological examples, clusters are formed through various biological interactions manifest in a spatial context (Vandermeer & Perfecto, 2006). Spacing patterns among individuals in groups reflect compromises between conflicting pressures: attraction to conspecifics in a successful

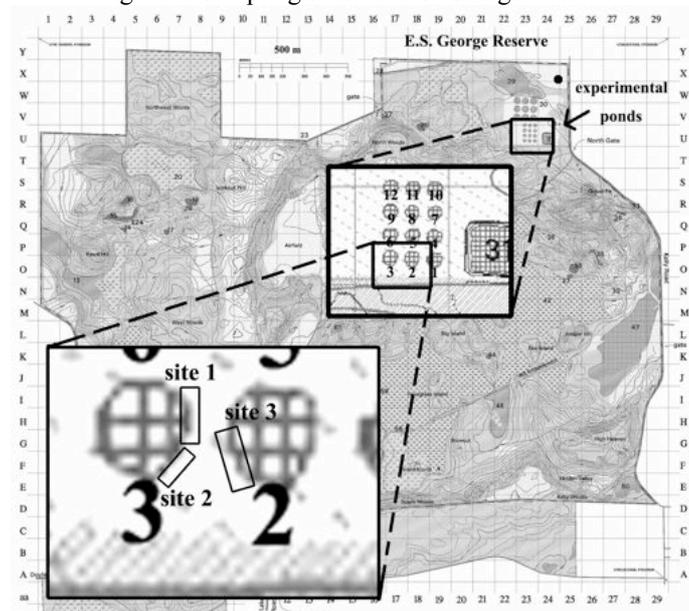
habitat, increased competition or intraspecific aggression due to proximity and risk of predation (Rayor & Uetz 2000). The cluster patterns of those spider webs were also investigated. For web weaver spiders, since it is unlikely to know the quality of prey before a web is built, competition for food source might not affect their distributions. The study sites did not show obvious heterogeneity, thus it is also unlikely that those spiders selected certain microhabitat to avoid predation from birds. The potential causes for cluster distributions could be competition for web constructing space, competition for mating opportunities, avoiding cannibalism, etc.

METHODS

Study Site

The E. S. George Reserve (ESGR) is a 525-hectare fenced preserve located in Livingston County, Michigan, about 25 km northwest of Ann Arbor (approximately 42° 28' N, -84° 00' W). There are 12 small, man-made experimental ponds located in the north east corner of ESGR. All the ponds were constructed to be 15 meters in diameter and 1 meter deep and can be individually drained and filled. In order to make the ponds the topsoil was removed and thus the vegetation around the pond is the result of primary succession. Predominate vegetation cover in most of the ponds is hybrid cattail (*Typha x Glauca*). Three major populations of filmy dome spider were found (based on numbers and density of spider webs) along pond 2 and 3, according to which three sampling sites were set (figure 1.).

Figure 1. Sampling sites in E. S. George Reserve



Field survey

Data for environmental factors were collected on September 21, 2008, from 8:00am to 10:00am, by a group of students carrying project on amphibian parasites (Patterson et al., personal communication). 11 ponds (pond 6 was eliminated because it is over-run by *Phragmites*) were surveyed and measurements were taken including: water temperature, pond depth, dissolved oxygen content, conductivity and vegetative species richness and abundance.

Spider web distribution was investigated on October 12, 2008, from 8:00am to 9:30am, while spider webs are still visible with morning dews on them. In each site, every individual web was located and marked with a flag. One transect was set in each sampling site and the x-, y- coordinates of every web were recorded. The percentage covers of scouring rush (*Equisetum hymelae*) from pond 1 to pond 6 were estimated and the number of spider webs along those six ponds was counted respectively.

Spiders (N=7) were randomly captured from occupied webs in the study sites and specimens were stored in 75% ethyl alcohol in a vial for further identification.

Taxonomy

All samples collected were examined under dissecting microscope in the laboratory in the Museum of Zoology, University of Michigan. Photos were taken by Canon PowerShot SD1100IS 8MP digital camera. Sex and maturity of the spiders were determined. The spiders were identified to species level according to keys and personally communication with Professor Howard Don Cameron (University of Michigan, Museum of Zoology).

Data analysis

The environmental factors data were imported in SPSS 16 statistical package. Descriptive statistics were used to determine the uniformity of the ponds. All the other data were analyzed by using Microsoft Excel 2003. Simple linear regression was employed to characterize the relationships between the percentage cover of scouring rush and spider abundance.

The positions of spider webs in each study site were mapped according to their x and y coordinates. Each web was represented by a hallow circle on the map. Since the distributions of spider webs found in all sites are notably clumped, the relationship between cluster sizes and the frequencies of each size were investigated. On the map, intersect circles were considered to belong to the same cluster. Cluster size was determined by the number of webs within the cluster. Data from all three sites were combined for this analyze.

The frequencies of each cluster size (represented by the number of clusters at the same size) were calculated (including size 1). Cluster size was plotted against size frequency. A power-law function and an exponential trend line were added to the plot respectively. A series of size scales were applied on the hallow circles. For each scale, similar 'size vs. frequency figure' was plotted, power law and exponential trend lines were added. The fitness of power low trend line and exponential trend line (represented by R^2) under different scales were compared.

RESULTS

Seven spider species were collected from the field including two males and five females, body size ranging from 2mm to 5mm. All of the spiders are juveniles whose external genitalia hadn't been fully developed. However, based on their web

characters, body coloration and other morphological traits, the specimens were confirmed to be the same species: *Neriene radiata* (Arachnida: Araneae: Linyphidae), commonly called filmy dome spider. The sheet webs observed in the field have diameters from 5cm to 15cm. Each web was occupied by an individual spider.

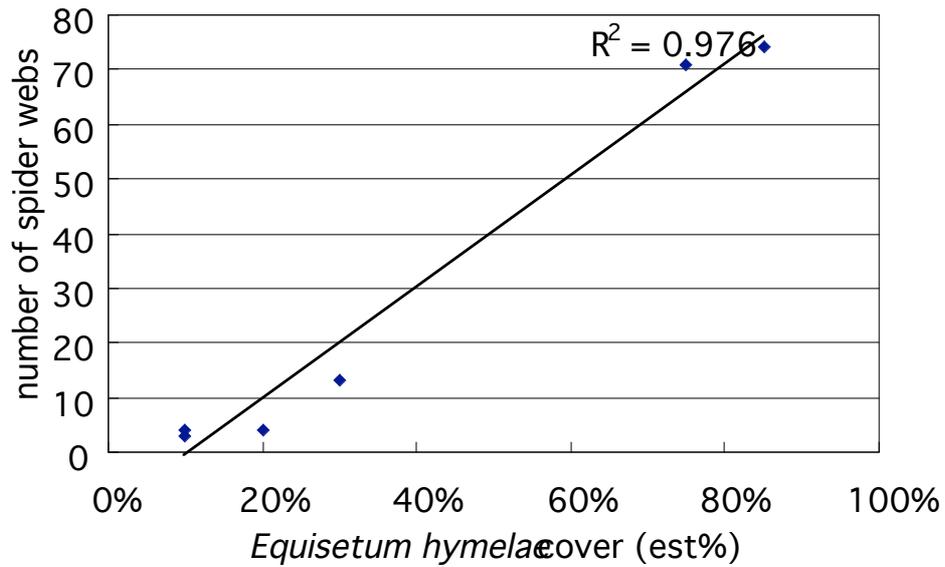
According to the field survey, water temperature showed little variation among the eleven ponds. However, certain variations were detected in terms of plant diversity, estimated percentage cover and dominant plant species (table 1). Pond 2, 3 and 8 have relatively fewer species compared to other ponds. The percentage vegetation cover for pond 3 is distinctly lower than all other ponds. Also, pond 3 was dominated mainly by scouring rush instead of hybrid cattail.

Table 1. Environmental parameters of the 11 experimental ponds

Pond ID	Water Temp.(C)	Cover (est.%)	Total Plant Species	Dominant Plant Species
1	16	50	10	<i>Typha x glauca</i>
2	16.1	30	6	<i>Typha x glauca</i>
3	15.7	5	8	<i>Equisetum hymelae</i>
4	15.6	55	13	<i>Typha x glauca</i>
5	15.7	70	10	<i>Typha x glauca</i>
7	15.8	80	13	<i>Typha x glauca</i>
8	17.1	50	8	<i>Typha x glauca</i>
9	17.1	30	13	<i>Typha x glauca</i>
10	16.1	65	9	<i>Typha x glauca</i>
11	17.2	55	10	<i>Typha x glauca</i>
12	17.1	60	9	<i>Typha x glauca</i>
Mean	16.32	50.00	9.66	
SD	0.66	21.21	2.30	
variance	0.44	450.00	5.29	

For pond 1 to 6, the relationship between percentage cover of scouring rush and spider abundance (represented by the number of spider web) was investigated (Fig.1). A strong positive relationship was discovered ($R^2=0.976$). Pond 2 and 3, where the three major spider populations were found, also had the highest percentage cover of scouring rush (85% and 75% respectively). While the other ponds had low percentage cover and only several discrete webs were detected. Two distinct size of scouring rush were found along each ponds, probably belonged to different age stages. One kind was thin with stem diameters below 2mm. The other is fairly strong with stem diameters greater than 8mm. All spider webs were constructed on the former, not a single spider web was found on the bigger rush.

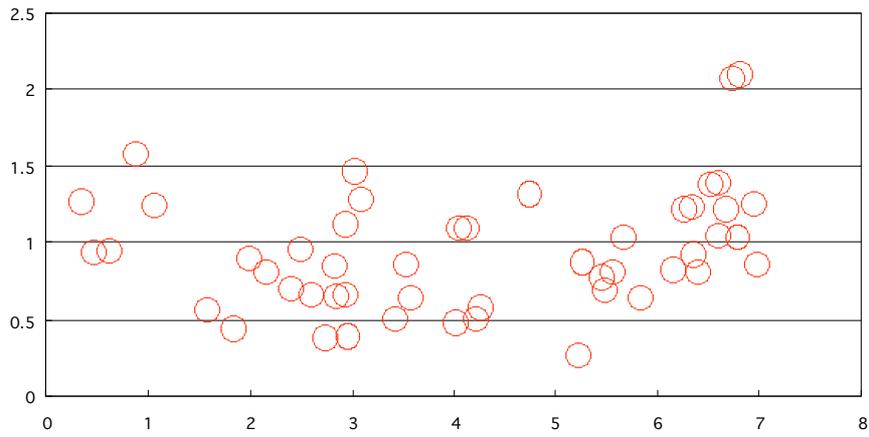
Figure 2. Relationship between percentage cover of scouring rush and spider abundance



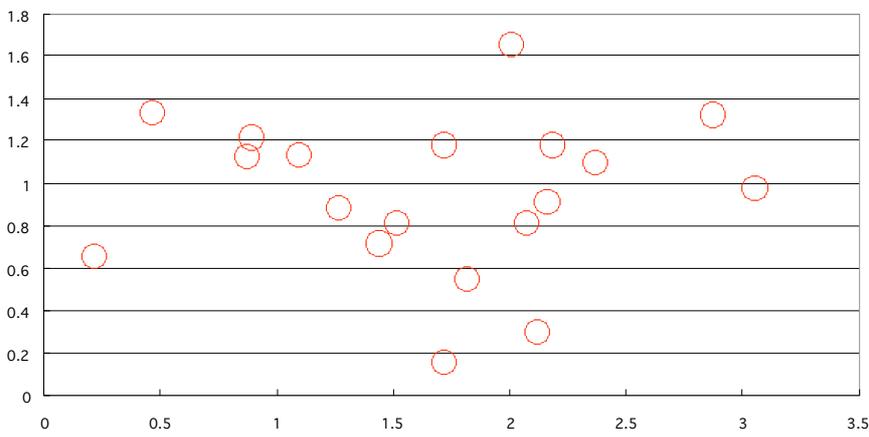
A total number of 121 spider webs were censused in the three study sites (50, 19 and 52 respectively). The relative position of each web within site was plotted (Fig. 2). In all sites, webs were not randomly distributed. Clusters were formed within each population (variance-to-mean ratio for the three sites are 1.7, 2.0 and 1.6 respectively). Cluster sizes ranged from 2 to 4 under scale 10.

Figure 2. Spider web distribution map of the three sites (scale size: 20 pounds)

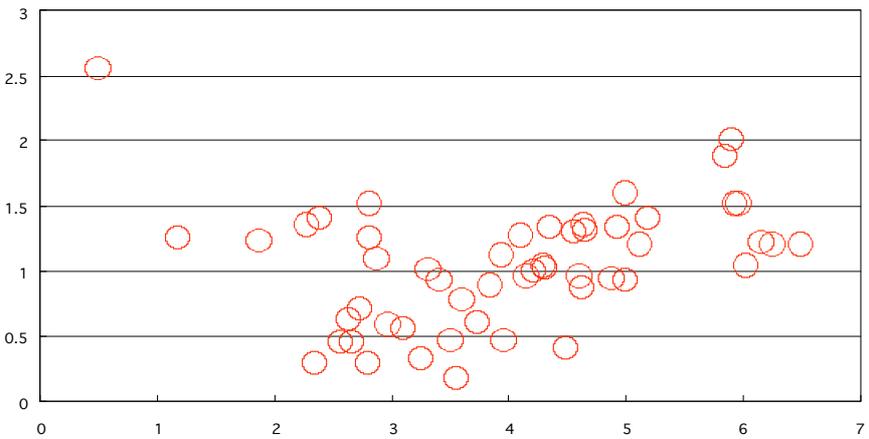
Site 1



Site 2



Site 3



In order to investigate the spatial distribution pattern of the webs, cluster size was plotted against size frequency, a trend line was added follow power-law function (Fig.3). The high value of R^2 indicated a good fitness. To confirm the result, the

natural log of cluster size against the natural log of frequency was also plotted, a linear trend line was added, which showed the same fitness (fig.4).

Figure 3. Spatial distribution pattern with power law trend line (scale: 20 pounds)

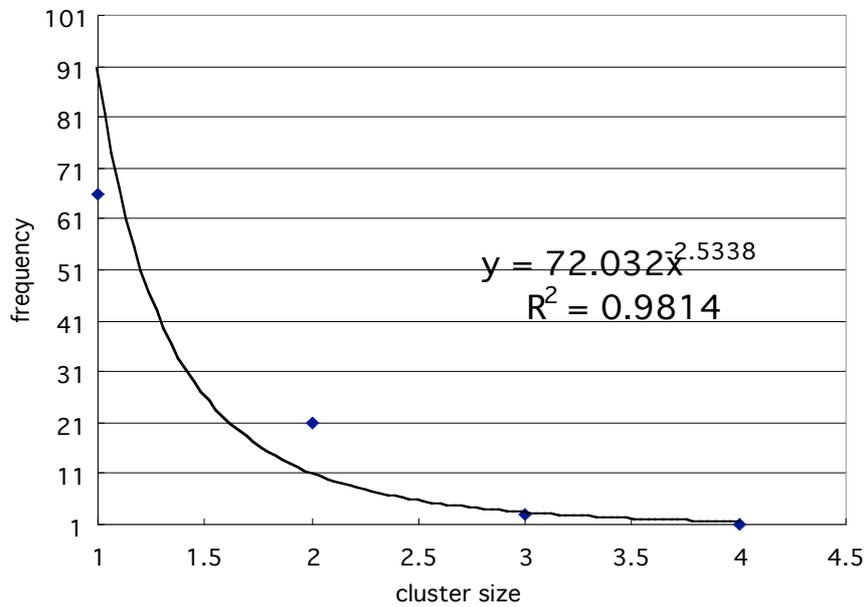
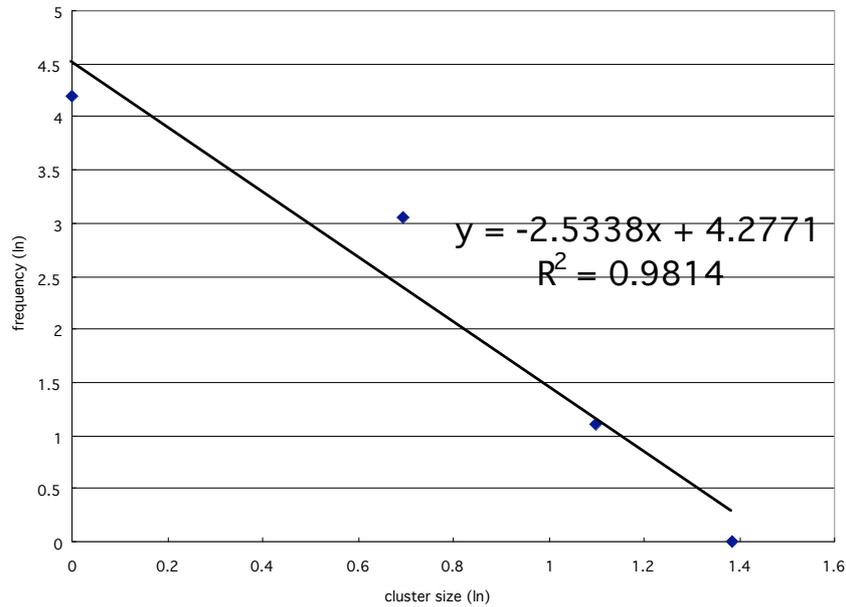


Figure 4. Log-log plot of cluster size and frequency (scale: 20 pounds)



However, when adding an exponential trend line to the same figure (Fig. 5), similar high fitness was found ($R^2=0.99$). A semilog graph was also plotted (Fig.6), the linear trend line also showed high fitness.

Figure 5. Spatial distribution pattern with exponential trend line (scale: 20 pounds)

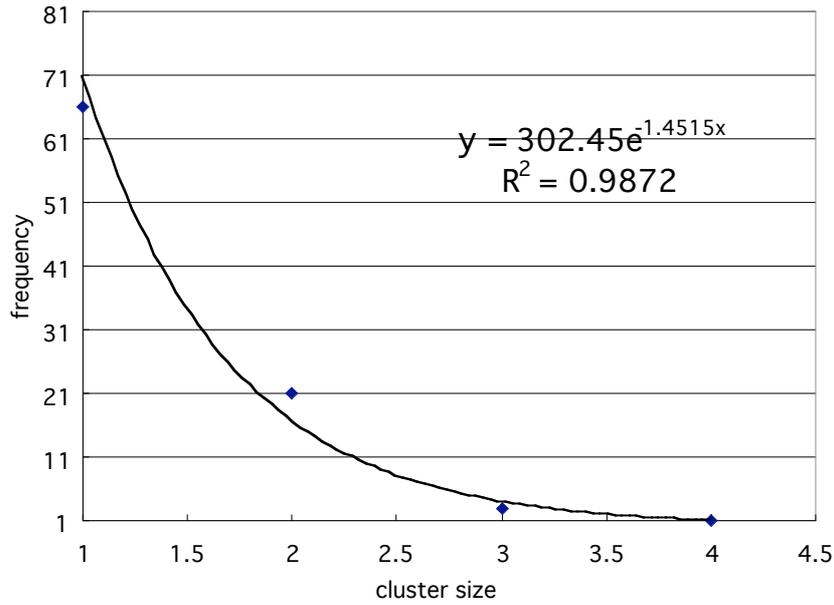
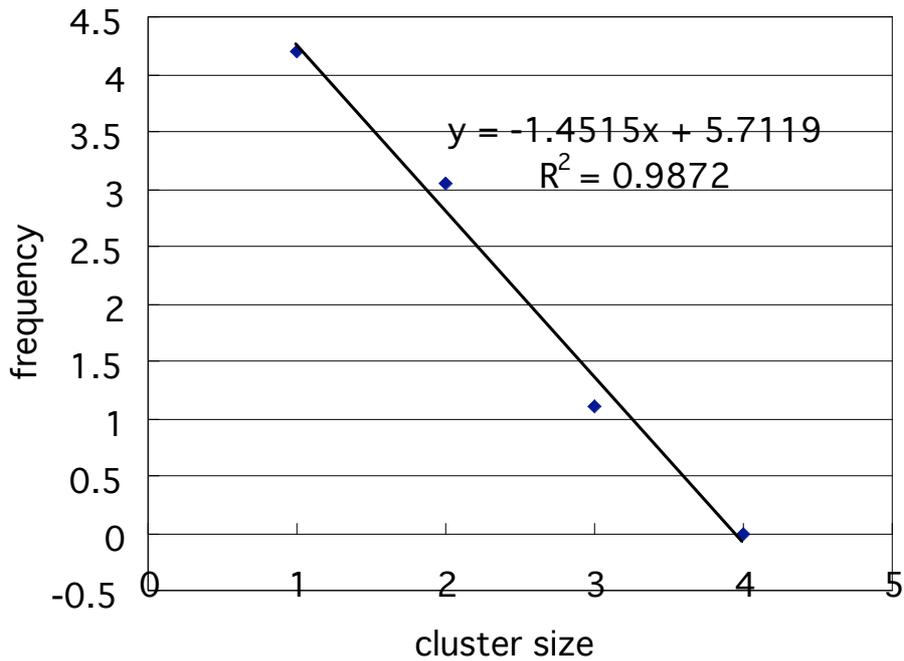


Figure 6. semilog plot of cluster size and frequency (scale: 20 pounds)

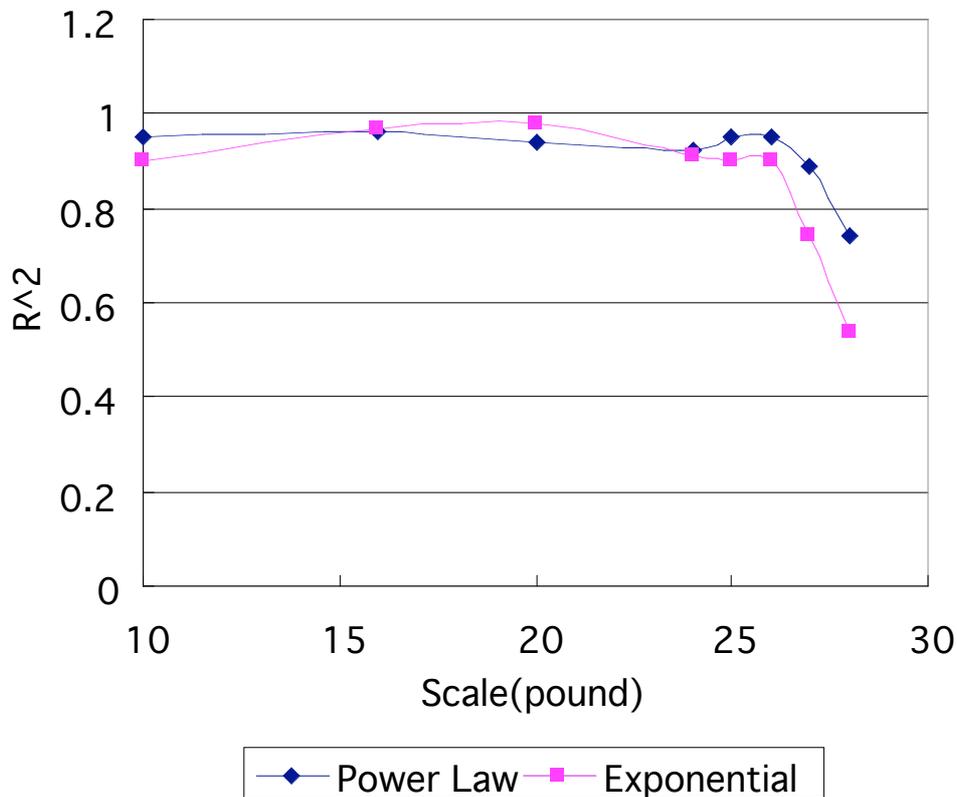


In order to further investigate the web distribution pattern, a series of manipulated web scales were applied in the map. Web sizes were ranged from 10 pounds to 28 pounds (table 2). With the increasing of web size, more webs become intersectant, thus the largest cluster size grow from 4 (scale 10) to 11 (scale 28), cluster size of 5-9 were also formed with intermediate scales (data not shown). When the scales were small, both power law and exponential trend lines showed relatively good and similar fitness (scale 10-26). However, as the scale continue to increase (scale 27 and 28),

both fitness begun to decline, and the fitness for exponential function turned down faster than that of power law function (table 2, fig. 7).

Scale	R ² (Power law)	R ² (Exponential)
10	0.95	0.99
16	0.96	0.97
20	0.98	0.98
24	0.92	0.91
25	0.95	0.90
26	0.95	0.90
27	0.89	0.74
28	0.74	0.54

Figure 7. fitness of power law and exponential trend line



DISCUSSION

The filmy dome spider is a common species in North America. Female spiders lay eggs in spring and hatchlings emerge thereafter. The spiders stay over winter as juveniles and become sexually mature the next spring. Thus all specimens collected appear to be juveniles at this time of year. According to web size and body length, it is possible that most spiders in the three populations were newly hatched this spring.

The filmy dome spiders construct permanent webs once a web site is established. Silk is added to the original web from time to time (Herberstein, 1998). Thus after the habitat was selected, the spatial distribution pattern of webs tends to be less dynamic. Several major factors might influence habitat selection of spiders. For instance, prey availability, predation and environmental factors etc. For web weaver spiders such as filmy dome spider, webs are costly to build. Since it is unlikely to know the quality of prey before a web is built, spiders' ability to sample different location as they search for optimal foraging site is limited. Thus, in terms of habitat selection, food source might not be a critical factor.

The abiotic factors among the experimental ponds were fairly uniform. However, the number of spider webs seems to be closely associated to the abundance of scouring rush. This native perennial plant is unbranched, consists of a single central stem with multiple overlapping joints. Their density is very high along pond 2 and 3. Each of the spider webs was constructed among several stems, and the heights of each web are similar. Since the spiders seemed only prefer thin rush stems with diameter below 2mm, it is possible that even the vegetation type is not a critical factor for their habitat selection. It is the high density of unbranched stem structure which is particular important for web construction of filmy dome spiders.

Within each population, the distribution of scouring rush is pretty uniform, but the spider webs are notably clustered. Their distribution seemed to follow both power law and exponential function under small web scale and fit power law function better under large web scales. By small web scale, we assume that there are few interactions among spider individuals. Thus the growth of spider population can be considered as density independent, which can follow the exponential function. It is hard to distinguish between power law and exponential under such condition because the largest cluster size is so small so the data points are limited. As the web scale become larger, the interaction becomes intense and can form certain kind of spatial constrain, which can be characterized by a power function since such pattern is usually interpreted as a signal of self-organization resulting from spatial extension (Vandermeer & Perfecto, 2006).

Several explanations may apply to the spatial cluster pattern of the webs. The spiders observed in this study were all in the same life stage, which may lead to the possibility that those spiders were offspring of similar populations from last year. Due to the poor dispersal ability of the juvenal spiders, siblings hatched from same egg sac may start to construct webs while they were still not dispersed from each other, thus form clusters of different sizes. On the other hand, web aggregation could also be a result of conspecific cuing, as documented by Hodge and Storfer-Isser (1997): individuals searching for web sites favored patches with webs over web-free areas, leading to clusters of spiders. In the conspecific cuing model, individuals were using the presence of other individuals as an indicator of habitat quality. The presence of experienced conspecifics often indicates high quality habitats. Also, since the web location of spiders often reflects favorable microhabitat, the clustered distribution could simply result from underlying environmental heterogeneity in small scale, which was not detected in this study.

However, the web scales are manipulated in the map, which may not necessarily reflect real conditions, because the interactions among spider individuals within

population have not been qualified. Thus no further predictions of the spider population dynamic can be made. In order to define the interaction scale more accurately, several factors have to be considered and quantified. Among which the most important is the degree of intraspecific competition. The spiders might simply compete for more space to build web, food availability, mating opportunity, or even place with less predator etc. Only by understanding more about the interactions within spider population, can we predict their spatial distribution in more accuracy.

ACKNOWLEDGEMENTS

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SPATIAL DISTRIBUTION OF *VITIS SPP.* IN A TEMPERATE FOREST CANOPY

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ABSTRACT

Understanding spatial patterns of populations is a fundamental goal of ecology. In populations exhibiting spatially constrained growth, frequency distributions of species cluster size tends to result in a power function. This study investigates whether *Vitis spp* growth in the canopy of a temperate forest is spatially constrained. The resulting clump size frequency distribution found from sampling *Vitis spp* presence across a four-hectare forest plot indicates these lianas are spatially constrained. Additionally, these lianas are significantly more likely to be found near a large forest gap, possibly a result of seed dispersal by birds. Lianas play an important role in the structure and function of forests, therefore determining the mechanisms driving their growth patterns is an important part of understanding forest dynamics.

INTRODUCTION

The development and maintenance of spatial patterns are considered a fundamental problem in ecology (Levin 1989). Spatial heterogeneity exhibited by populations has important consequences for population dynamics (Levin 1989). The development of these patterns may result from exogenous (habitat heterogeneity) or endogenous (intrinsic biological factors) factors (Vandermeer et al. 2008). Where endogenous factors are driving pattern formation, the resulting distribution of organism cluster size frequently follows a power function (Vandermeer and Perfecto 2006). The existence of a power function in cluster size frequency may provide evidence that endogenous biological factors cause the distribution of a population to be spatially constrained (Vandermeer, pers. comm. 2008).

In the case of woody vines (lianas), the endogenous biological factors leading to spatially constrained growth may be the interaction of individual vine shoots. When an individual vine first begins to expand into a forest canopy (for example, in a young forest) one would expect that vine to exhibit unconstrained (exponential) growth. However, after reaching the canopy, vines tend to form a carpet of leafy vegetation over time (Castor-Esau et al. 2004). As the density of shoots of the individual vine begins to increase in the canopy, the shading caused by leaves of overhead shoots may lead to growth constraints in lower shoots. Shading of vine leaves in the species *Vitis vinifera* caused by high shoot density resulted in leaf senescence and bud necrosis (Wolf and Warren 1995; Bertamini and Nedunchezian 2001), both of which may adversely affect vine growth of the whole individual.

In this study I investigate whether lianas of the genus *Vitis* are spatially constrained in their growth in the canopy of a temperate forest. If *Vitis* growth is spatially constrained in the forest canopy, I expect to find a power function in the frequency distribution of *Vitis* cluster size. However, if *Vitis* canopy growth is unconstrained, the cluster size frequency distribution should

follow an exponential function. Additionally, I seek to determine whether forest gaps influence the spatial distribution of *Vitis* canopy growth.

METHODS

The location of this study was Big Woods forest, an 18-hectare plot in the northeast section of the E.S. George Reserve (Pickney, MI). All trees over 10cm circumference at 1.3m height in Big Woods are tagged and referenced to a 500m x 400m grid map. To maximize my sampling size in the limited time available for the study, setting up sampling transects was avoided. Instead, I used the tagged trees to georeference my sampling along the X-axis of the forest plot.

Tree tag numbers were recorded and point samples of *Vitis* presence were taken 5m from each tree. After recording data for the sample point, the next tree tag was marked a further 5m from the previous sample point. Thus *Vitis* presence was sampled at intervals of 10m.

Sampling was done by visually confirming the presence or absence of *Vitis* in a 1.5m radius of the canopy. Canopy was defined as the branches of the tallest tree(s) directly above my location. Binoculars were used to identify *Vitis* presence where canopy height exceeded 15m. The following data were recorded at each point: *Vitis* presence, *Vitis* absence, or canopy gap. Canopy gap was recorded when there were no branches or trees in the 1.5m-radius canopy sampling zone.

All recorded points were georeferenced to the Big Woods grid map and transferred into shapefile format. ArcMap 9.2 (ESRI, 2006) was used to analyze the spatial distribution of the *Vitis* points. All presence points were buffered by circular polygons according to a range of clustering parameters (5m-20m) – the radial distance at which multiple presence points begin to overlap. For each clustering parameter overlapping buffers were aggregated into single polygons, and the number of points within all resulting polygons were calculated.

To explore the spatial pattern of the *Vitis* dataset, the frequency distributions of cluster size were plotted on both a log-log graph and log-linear graph for each clustering parameter. Regressions were performed for each resulting distribution.

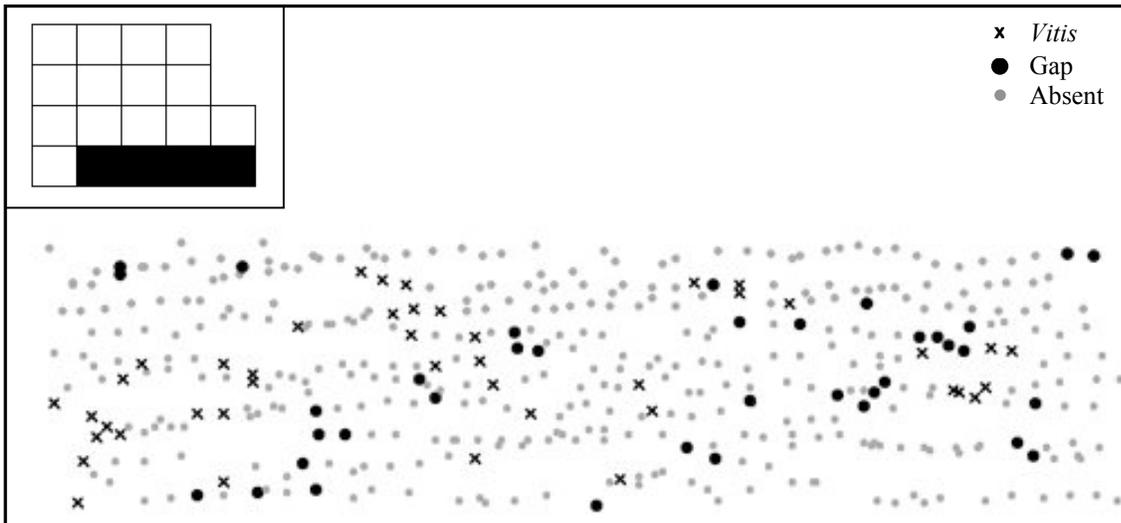
To measure distance of liana presence points to other data features a nearest neighbor analysis was performed. First, the Big Woods dataset was transformed into discrete polygons using a clustering parameter of 2m. This had the effect of revealing large forest gaps in the dataset. The analysis was performed within the *Vitis* point dataset, and between the *Vitis* point dataset and the Big Woods polygon dataset (*Vitis* point-Edge). Within the *Vitis* dataset, nearest neighbor distance between all presence points (*Vitis-Vitis*) and between presence points and gap points (*Vitis-Gap*) was calculated. Between datasets, the nearest neighbor distance between all *Vitis* presence points and forest polygon edges (*Vitis-Edge*) was calculated.

RESULTS

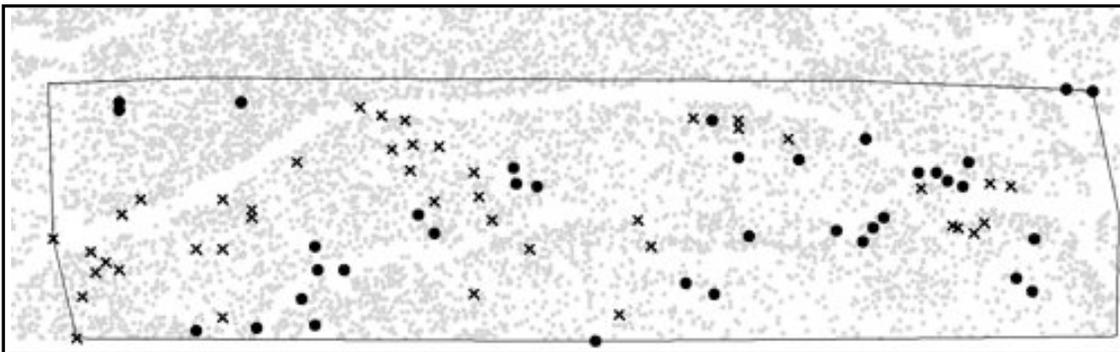
Data was collected for 430 individual canopy points across 3.9 hectares of Big Woods forest (Figure 1a). *Vitis* was found to be present in 10.2% (n=44) of the points, while gaps were found in 8.6% (n=37). This resulted in a *Vitis* canopy presence of 11.2 points per ha.

Figure 1: a) Location of all canopy points in the survey area with inset showing the surveyed quadrants (shaded) of Big Woods, b) locations of *Vitis* presence and gap points bounded by the minimum convex polygon layered on the Big Woods point dataset, c) locations of *Vitis* presence and gap points bounded by the minimum convex polygon layered on Big Woods dataset discrete polygons (shaded).

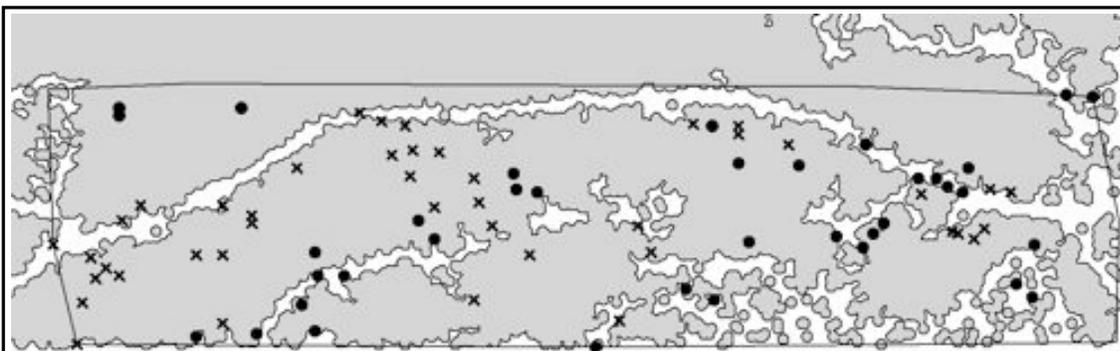
a.



b.

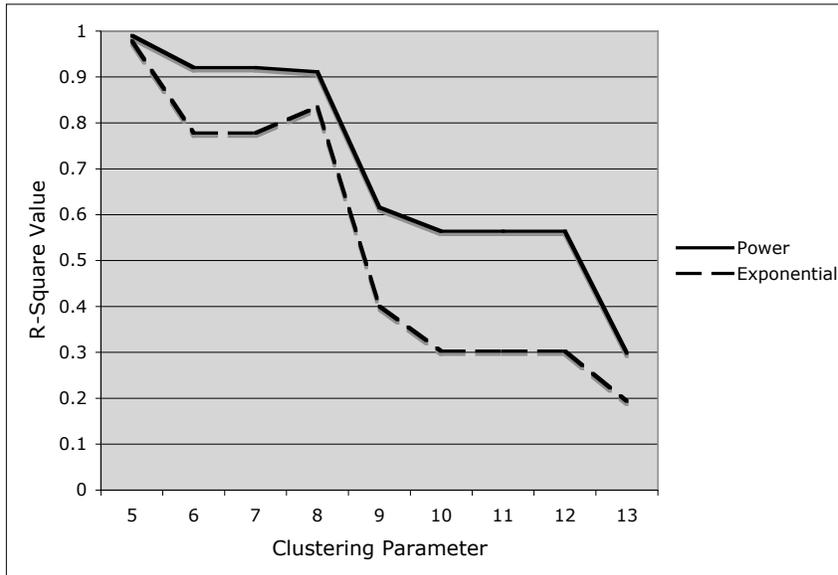


c.



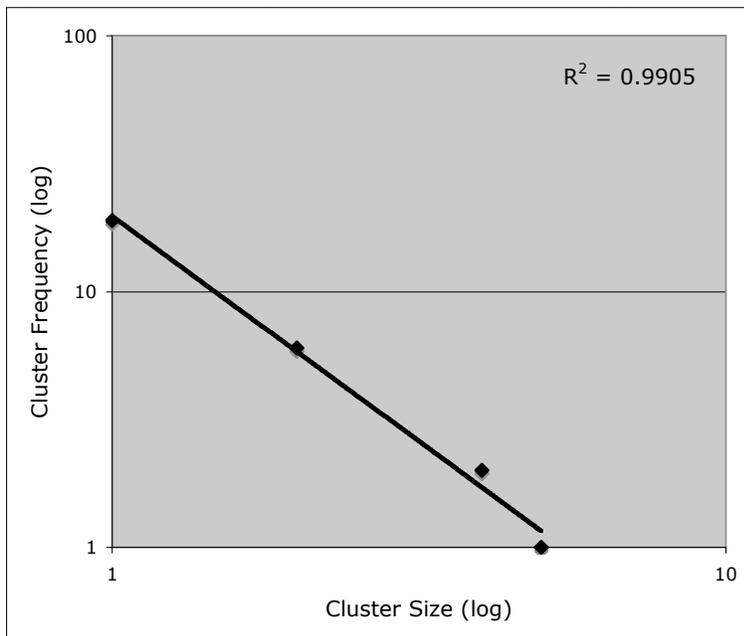
Of the sixteen clustering parameters used, only the first nine (5-13m) resulted in multiple *Vitis* clusters of the same size. Each of these clustering parameters' r-square values for power and exponential regressions are plotted in Figure 2. There appears to be a sharp decline in the explained variation in cluster size above a clustering parameter of 8m. Overall, the power regression outperforms the exponential regression in its ability to predict variation in cluster size.

Figure 2: R-square value by clustering parameter for power and exponential regressions



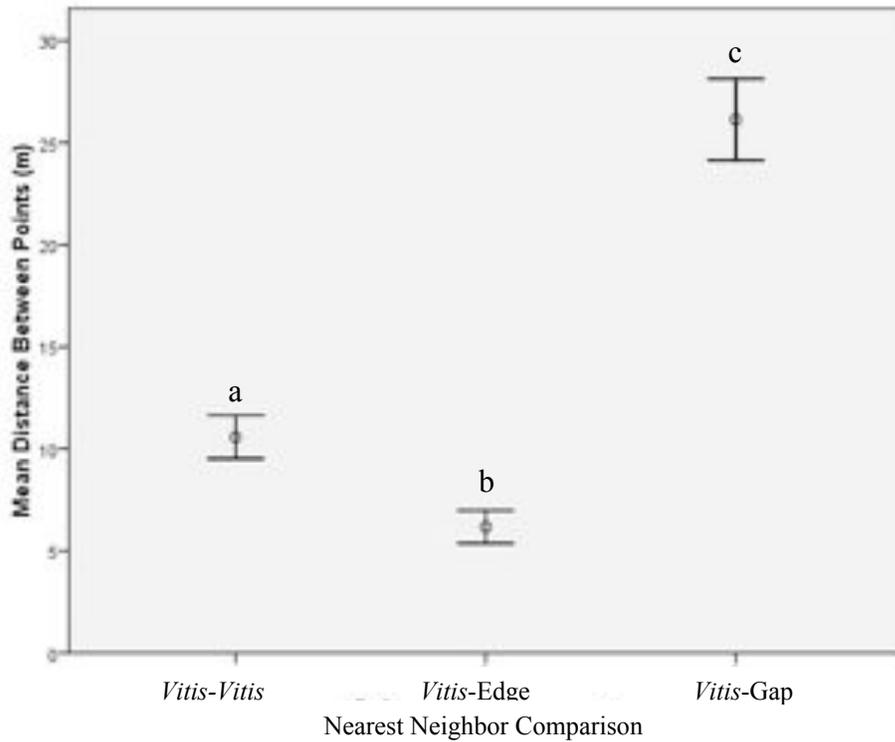
The frequency distribution of *Vitis* clusters for the clustering parameter with the highest r-square value (5m) is presented in Figure 3. Based on the regression line and approximate linearity of points, the data appear to follow a power function.

Figure 3: *Vitis* cluster frequency and cluster size (clustering parameter = 5m)



Big Woods data before and after the discrete polygon transformation by clustering are shown in Figure 1b and 1c, respectively. The nearest neighbor analysis resulted in a mean distance among *Vitis* points of 10.5m, and 26.1m among *Vitis* points and gap points, while distance between *Vitis* points and forest gap edges was found to be 6.2m (Figure 4). *Vitis* is more likely to be found near a forest edge than near another *Vitis* point or a gap point as measured by a one-way ANOVA, $F(2,127)=56.834$, $p=0.000$. A Games-Howell post-hoc test found a significant difference ($p<0.005$) between each of the factors.

Figure 4: Mean distance between points for each nearest neighbor comparison. Different letters indicate a significant difference ($p<0.005$).



DISCUSSION

The frequency distribution of *Vitis* cluster size is indicative of a power function. This provides support for spatially constrained growth of *Vitis* in the forest canopy. Shoots of individual *Vitis* vines in this system may have reached a density at which higher shoots shade the leaves of lower shoots acting to reduce the growth rate of the entire plant. This mechanism may explain the patchiness of *Vitis* found in the survey area of Big Woods (Figure 1b). The scale at which this spatial constraint occurs may be 8 meters as evidenced by the regression's adherence to the power law at or below this clustering parameter (Figure 2).

However, the sample size collected for this study may not be large enough to draw any firm conclusions. In order for a frequency distribution to exhibit a power function, there should be at least three orders of magnitude expressed across the data (Vandermeer, pers. comm., 2008).

Yet, this initial result does provide enough support for further investigation with a sufficient sample size.

An alternate explanation for the patchiness of *Vitis* in this forest plot may result from the presence of large gaps. There is one maintained access road that runs through the study area (Esker road) and an abandoned road that runs approximately parallel to the access road. These two disturbances provided most of the large forest gaps in the study area (most of the gaps recorded by the survey were the result of treefalls or small spaces in-between canopy branches). *Vitis* was significantly more likely to be found near one of these large forest gaps than near another *Vitis* vine or a small gap (Figure 4). Birds spend significantly more time foraging for seeds and depositing them along temperate forest edges than in the forest interior (Malmborg and Willson 1988). *Vitis* fruits are dispersed by birds (Stiles 1980) and the resulting patchy distribution of *Vitis* may therefore be a result of dispersal along these disturbances.

Other exogenous factors important to consider are the topography and aspect of the forest plot. Much of the *Vitis* was found on the south facing slope of the Esker road (Figure 1b), and the topography of this area is very steep. These factors may contribute to the pattern of *Vitis* seen in the study plot because any autochorous dispersal would likely be contained to this side of the Esker road.

In order to clarify the mechanism that leads to the patchy distribution of *Vitis* canopy growth, future studies should expand the range and size of the sampling. If there is in fact a power function in the frequency distribution of cluster size, a larger sample size should help meet the requirement that it be present across three orders of magnitude. Conducting the study across a larger range of forest should allow for sampling in areas where there are no large gaps. If the cluster size distribution still follows a power function, that would provide evidence against the hypothesized bird dispersal mechanism. Future studies may also consider refining the sampling technique by setting up proper transects to ensure equal spacing of sample points. Analysis of the topography and aspect of the forest plot should be a part of any follow-up study.

Determining the mechanisms behind the spatial distribution of organisms is an important goal of ecology. In the case of lianas, investigating whether endogenous or exogenous mechanisms drive their pattern formation is important for understanding forest dynamics. Lianas are important components of forest structure and function (Schmitzer and Bongers 2002). Trees infested with lianas have higher mortality rates (Phillips et al. 2002), exhibit decreased growth and biomass (Laurance et al. 2001), and reduced fecundity (Kainer et al. 2006). If lianas are not spatially constrained by an endogenous biological factor, there is potential for exponential growth within forest systems lacking an exogenous constraint mechanism; with clear consequences for the dynamics of those forests. Knowledge of the growth patterns of lianas in forest ecosystems is therefore important for understanding forest dynamics.

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SPATIAL DISTRIBUTION, AGGRESSIVENESS, AND BUDDING OF THATCH NESTS OF *FORMICA OBSCURIPES*

SENAY YITBAREK

ABSTRACT

This study examines the spatial distribution of colonies and behavioral interactions of *Formica obscuripes* along the edges of a swamp. Large-scale spatial patterns have been reported to occur in many biological systems. Although much work in theoretical ecology has alluded to the emergence of spatial patterns, relatively few experimental studies have been able to demonstrate this principle in nature. We were interested to understand the spatial distributions of ant colonies and their associated behavioral characteristics. We mapped mound nest of *F. obscuripes* located along the edges of a swamp and used distances between neighboring colonies as a proxy for determining the spatial distribution. Furthermore, we examined aggressive behavior between colonies to account for the budding process, whereby mated queens might be closely related satellite colonies of the same species. Our study shows a clustered spatial distribution of ant colonies that exhibit polygonous behavior. We found evidence for the budding process to occur on a small spatial scale. Future studies should assess the effects of shading on the spatial distribution of colonies and also apply molecular methods to understand the genetic relatedness among ants.

INTRODUCTION

In recent decades, a large body of literature has emerged in theoretical ecology that shows that ecosystems undergo spatial self-organization. As was first demonstrated through Alan Turing's (1952) work on the chemical basis of morphogenesis, large-scale spatial patterns occur in many systems and they emerge from initial conditions through local interactions (Rietkerk 2008). Similarly, many biological systems exhibit spatial self-organization ranging from coat patterns in leopards to vegetation patterns in arid ecosystems, and to the spatial distribution of organisms in both natural and managed ecosystems (Rietkers 2008, Vandermeer 2008).

Spatial patterns emerge out of dynamical interactions (Perfecto 2008). Despite rapid advances in our understanding of pattern formation in ecosystems, relatively few empirical studies have been able to demonstrate spatial pattern formation due to the inherent patchiness of ecosystems (Perfecto 2008). One increasing area of research has been to understand the underlying spatial-temporal dynamics used by social insects to construct their colonies (Theraulaz 2005). This study attempts to understand spatial

pattern formation of ant colonies by *F. obscuripes*, and their associated behavioral interactions.

F. obscuripes are prairie ants and they construct their nests above ground made out of thatch (composition of plant material) that is used to regulate temperature and humidity levels. *F. obscuripes* are known to be aggressive towards intruders on their nests and are considered omnivorous foragers. They tend aphids in return for honeydew while also acquiring additional resources from floral nectarines and plant materials. *F. obscuripes* colonies are characterized as polygynous, whereby queens lay multiple eggs in a single nest. Although no colony formation has thus far been recorded, *F. obscuripes* deploy flights and polygyny to form new mound nests. Typically, the mated queens and workers leave their parental nests to form new nest in a process known as budding. As a result dense satellite colonies can be formed near the parent colony, but mated queens can also invade nests that are already occupied thereby functioning as a temporary social parasite (?).

With this natural background in mind, we examined the occurrence of colony formation of *F. obscuripes* mound nest around the Big Swamp edges at the E.S. George Reserve. In particular, we were interested in examining the spatial distribution of mound nests around the Big Swamp and to understand the behavioral interactions between neighboring colonies and the appearance of a “budding effect”

METHODS

Study Site

This study was conducted at the E.S. George Reserve in Michigan. Mound nest sites were found along the edges of the Big Swamp and nearby a dirt road on the reserve. Commonly occurring plant species on the site were shrubs, forbs, and grasses. Vegetation was largely absent on the mound nest itself. However, the edges of the mound nest displayed encroaching patches of vegetation. The temperature remained relatively high (> 25 C), which provided conducive conditions for ant activity.

Field Experiment

A grid map was used to determine the locations of five mound nests around the edges of the Big Swamp. Only four active mound nests were selected and distances between neighboring colonies were measured. Subsequently, four random points were selected and 1000 iterations were performed using the MATLAB program to determine the spatial distribution of mound nests. Individual workers of *F. obscuripes* were collected from each site to test for aggressive behavior. Individual workers from each site were introduced and observed for a period of 30 minutes. Introduced workers were identified as either “accepting” (coded 0) or “biting/killing” (coded 1) neighboring workers.

RESULTS

Individual workers of *F. obscuripes* were identified at all four mound nests. The neighboring colonies displayed a clumped spatial distribution with an observed average distance of 144 meters between colonies (figure 2). We found a significant relationship for the clumped distribution among neighboring colonies ($P=0.0124$), which shows that 1.2% of the random drawings were clumped or more than initially observed.

Aggressive behavior analysis suggests polygyny among the first three colonies (figure 3). After introduction of individual workers between the first three colonies, ants displayed no aggressive behaviors. However, when introducing individual workers from the fourth mound nests, we observed aggressive behavior towards individual workers from the first mound nest. These results demonstrate that the “budding effect” could possibly occur among the first three mound nests.

Figure 1.

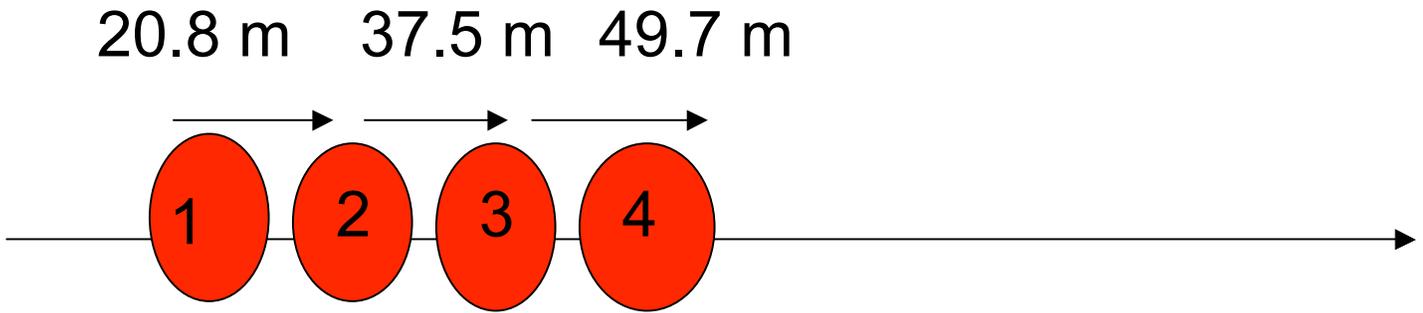


Figure 2. Spatial representations of colonies. 1000 random drawings were performed showing that colonies are further apart as compared to the initially observed colonies. As a result the initially observed colonies are more clustered than our random expectations.

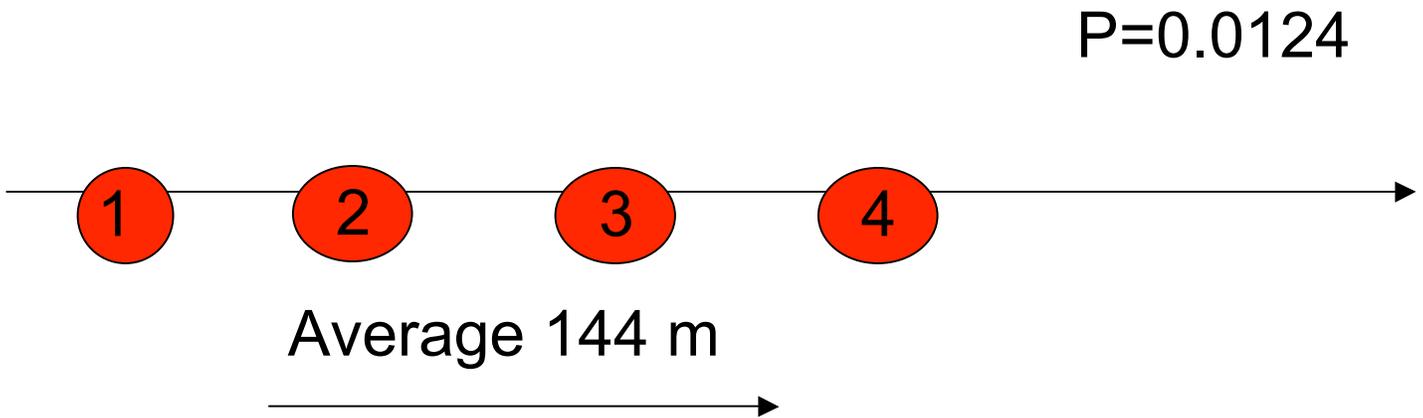
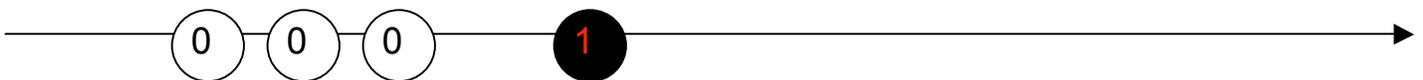


Fig 3. Aggressive behavioral analysis. Colonies numbered as "0" represent polygony whereas the colony numbered as "1" indicate an aggressive colony.



Discussion

The mound nests of *F. obscuripes* exhibited a clustered spatial distribution around the edges of the Big Swamp. The iterated neighboring distances between colonies were statistically significant as compared to the actual distances measured among colonies. We observed intra-specific aggressive behavior for the fourth mound nest as compared to the first three mound nests. The *F. obscuripes* workers of the first three mound nests appear to be polygynous due to weak inter-specific aggressiveness. The formation of satellite colonies near the parent colony demonstrates that a budding process could be occurring on relatively small spatial scale.

The relative distances between the neighboring colonies were far smaller than we encountered under complete randomness. However, it's important to realize that these mound nests occurred at a small spatial scale, relatively few in number, and isolated in a highly disturbed area. The occurrence and absence of mound nest around the edges of the Big Swamp are most likely related to seasonal spatial-temporal variation (Kenne & Dejean 1999). For example, during the rainy season mound-nests can increase rapidly which provide optimal conditions for brood development in the warmest mound nests due to thermoregulatory mechanisms. However, in the dry seasons nests tend to disappear unless they are sheltered from the sun by trees (Kenne & Dejean 1999). Thus, future studies should focus on seasonal spatial-temporal variations. For example, the differential impact of shading effect on mound nests may influence colony sizes and the spatial distributions.

Polygyny was strongest among the first three mound nests, whereas the fourth mound nest showed the greatest aggressive behavior. Therefore, relatedness for the fourth mound nest decreased due to the rejection by the mound nest workers of the mated queens or the establishment of an entire new colony by different species of ants. Future directions could incorporate PCR-technique to assess the genetic relatedness among species of ants. In addition, the mechanism for insemination of the females remains unclear as well as the extent to which secondary polygynous workers impact the budding process.

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NEST SITE ABUNDANCE AND SPECIES COMPOSITION OF NUT-DWELLING ANTS IN THE E.S. GEORGE RESERVE, MI, USA.

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ABSTRACT

Ants are one of the most diverse orders of macro-invertebrates, functioning as generalist predators and scavengers, and providing important ecosystem services such as seed dispersal, soil aeration and biocontrol. Most ants are not considered highly partitioned based on habitat specializations, and are therefore in competition for spatial resources. We looked at nest-site limitation among cavity nesting ant species in a temperate forest in southeastern Michigan, USA. We collected and opened large tree seeds in 1m² quadrats along three 100m transects and compared the percent of available nest sites that were occupied to the number of available nest sites in each quadrat. Although we found no evidence of nest-site limitation, we did find a possible preference among ants for certain cavity sizes.

INTRODUCTION

Ants are one of the most diverse orders of macro-invertebrates, with over 20,000 estimated species which compose up to 50% of animal biomass in some ecosystems (Philpott & Foster 2005). Ants function as generalist predators and scavengers, and provide important ecosystem services such as seed dispersal, soil aeration and biocontrol. The function of ants is especially important because of their incredible abundance and diversity in most sub-alpine environments worldwide. Some ants are considered keystone species structuring the biotic environment surrounding their nest sites (Vandermeer & Perfecto 2006). Ants in tropical regions have been found to influence key agricultural pests and limit pest outbreaks by stabilizing the community interactions (Perfecto & Vandermeer 2006, Liere & Perfecto 2008). Though their presence in the temperate forests is less apparent, ants still compose a remarkable portion of animal biomass and carry-out functions critical to forest dynamics.

The range of ants nesting behavior further reflects their diverse nature. Nest sites range between species and include everything from hollow twigs to bioengineered mounds. Despite the range of nesting behaviors, the 20,000 plus species of ants do not niche partition relative to their diversity, and most ants are not considered highly partitioned based on habitat specializations (Armbrecht *et al.* 2004). Thus, different species of ants are in competition for spatial-temporal nest resources. Some ant species such as army ants have adapted to existence in the absence of nests. Most however, engage in strong competition for spatial resources. Due to the intensity of competition, in most communities, ants are assumed to be nest-site limited (Armbrecht *et al.* 2004). Under these conditions, the superior competitors are assumed to out compete other ants (Philpott & Foster 2005, Armbrecht *et al.* 2004) thus limiting species diversity.

We set out to determine whether this competition-exclusion dynamic was present in a restored temperate forest reserve in southeastern Michigan. To address this question, we studied cavity nesting ants occupying large tree seeds. We hypothesized that if nut-nesting ants were nest site limited, a higher percentage of nuts would be occupied if fewer nests were available, and that

in the presence of competition, ants would more likely demonstrate some level of species specific habitat preferences.

METHODS

Our study was conducted in the University of Michigan E.S. George Reserve on September 21, 2008. We laid three 100m transects, all of which were located in oak/hickory dominated canopies. Two were located in Big Woods and the third was located near the Old Field. We collected all unopened nuts inside 1m² quadrat every 20m along each transect. Nuts from each quadrat were kept separate in paper bags and were labeled with the transect and quadrat from which they were collected. Nuts were cracked open and data was recorded on the type of nut, the size of the nut at its largest length, the quality of the nut (green, rotten, or in between), if the nut was hollow, and if the nut contained ants. Ants found inside the nut were preserved in ethanol for identification. All ants collected were identified by S. Philpott.

Data was analyzed using Microsoft Excel. Nut species preference was evaluated using a two sample t-test. Nut size preference was assessed using a One-way ANOVA.

RESULTS

Seven species of ants were found inside 298 hickory nuts and 136 acorns: *Lasius alenius*, three different *Leptothorax Sp.*, *Myrmica punctaventrtris*, *Ponera pensylvanica*, and *Tapinoma sessile*. *Leptothorax Sp.* were found in 62% of the inhabited nuts, *M. punctaventrtris* and *P. pensylvanica* were found in 20.7% and 10.3% of the nuts, respectively, and *L. alenius* and *T. sessile* were found in 3.4% of the nuts (fig. 1).

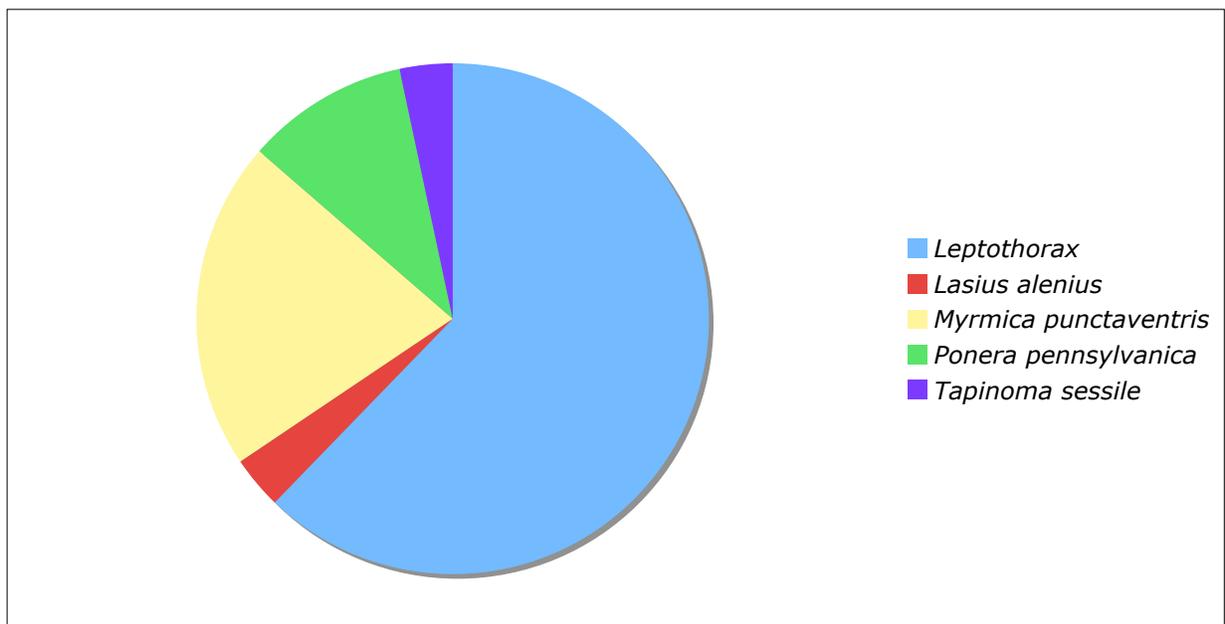


Fig. 1. The percentage of inhabited nuts that were filled by each species of ant

L. alenius, *P. pensylvanica*, and *T. sessile* were found only in hickory nuts, while 83.3% of *Leptothorax* and *M. punctaventrtris* were found in hickory nuts. The remaining 16.7% of both

species were found in acorns. However, due to the unequal sample size of hickory nuts and acorns, no preference for either nut was observed in general ($p=0.78$, fig. 2), or by ant species.

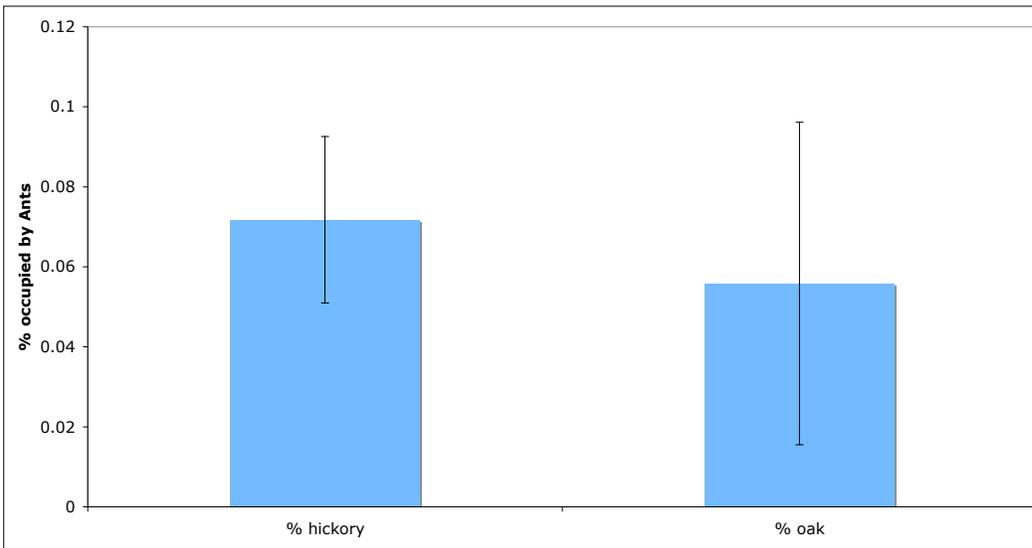


Fig. 2. There was no overall preference of ants for tree species ($p=0.78$).

The nuts that we collected differed in size, ranging from 2mm to 38mm in diameter at the greatest length. None of the nuts 31-40mm in size were occupied, while 20.9% of 21-30mm nuts, 6.68% of 11-20mm nuts, and 0.42% of 1-10mm nuts were occupied. There was a trend toward size preference among ants collectively (ANOVA, $p=0.095$, figure 3).

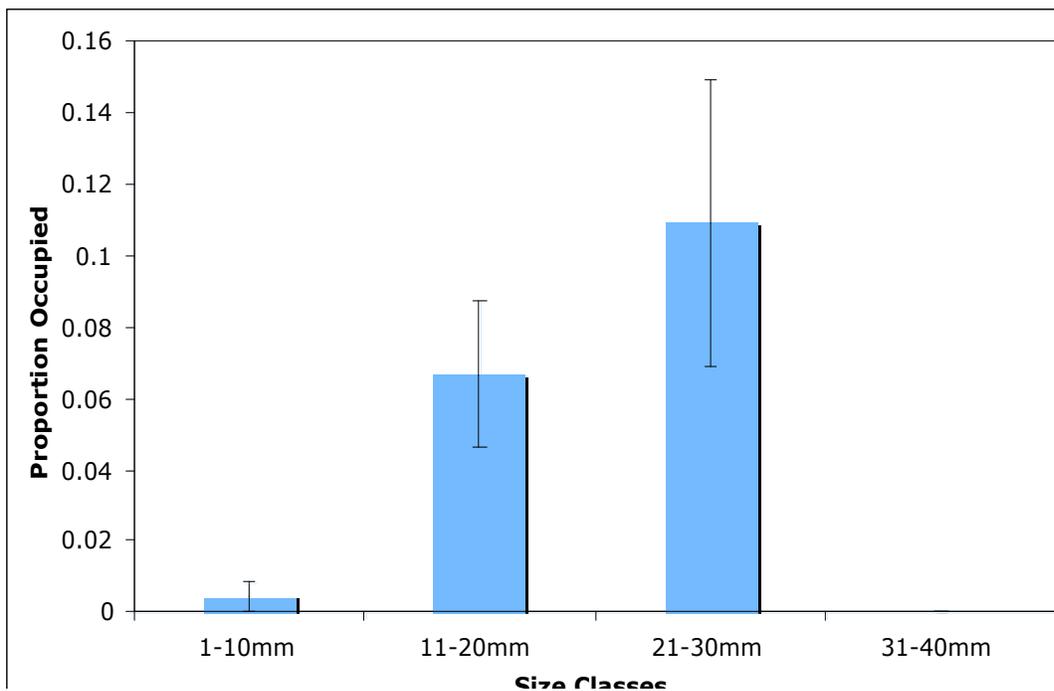


Fig. 3. There was a trend toward size preference among ants (ANOVA, $p=0.095$) with 0.42% of 1-10mm nuts occupied, 6.68% of 11-20mm nuts occupied, 20.9% of 21-30mm nuts occupied and 0% of 31-40mm nuts occupied.

In each quadrat, the number of available nuts ranged from one to 60. Percent occupied ranged from 0-28% of hollow nuts. No correlation was found between the most used nest size (11-30mm) availability and the percentage occupied (fig. 3).

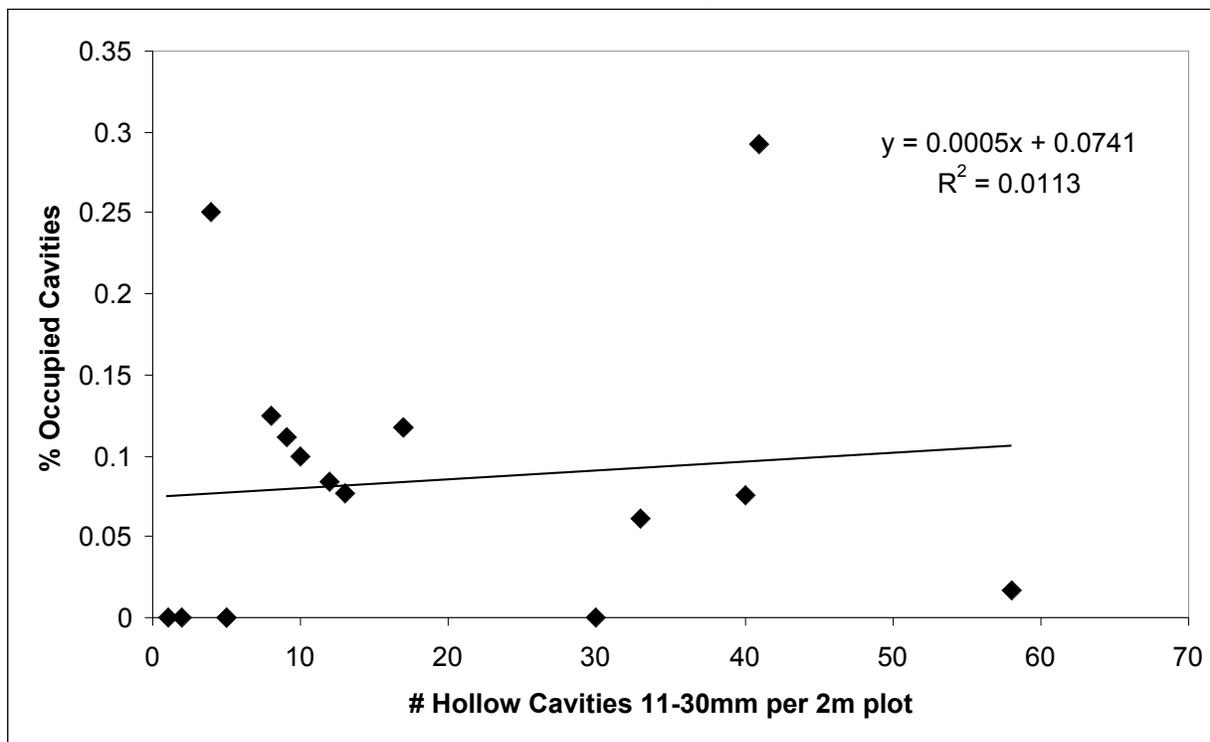


Fig. 3. The percentage of nuts occupied by ants compared with the total number of available nuts in each 1m² quadrat.

When broken down into species, *L. alenius* appeared to prefer nut sizes of 11-20mm, *P. pennsylvanica* preferred nut sizes of 21-30mm, and *M. punctiventris* and *Leptothorax* appeared split between preferring 21-30mm and 11-20mm nut sizes (fig. 5).

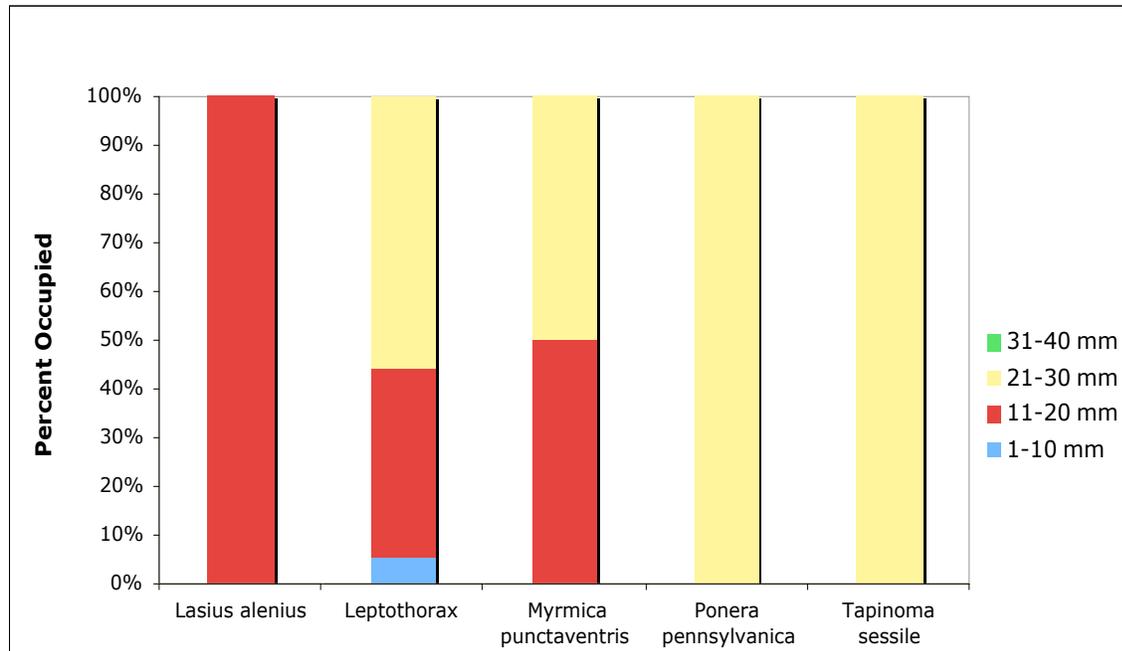


Fig. 5. The percentage of each species occupying nuts of four different size classes.

DISCUSSION

Basic ecological theory requires a limited resource in order to observe competition. In the case of nut-nesting ants on the E.S. George Reserve, this limiting resource stipulation is not met, at least in terms of habitat availability.

Ants are commonly considered nest-site limited when the majority of habitable sites (>50%) are occupied (Philpott & Foster 2005). In our study, the occupation observed at a given site never reached more than 30%, and most often hovered around 0-10% nuts occupied. Due to the low percentage of occupied nuts, the density of nest occupations would not be expected to vary with the number of hollow nuts, as has been suggested in nest site limited ant communities (Philpott & Foster 2005, Bryne 1994).

Possibly, it is the over-abundance of nest sites that has allowed seven similar sized species of nut-nesting ants to co-exist on the ESGR. Whether or not this co-existence is stable is undetermined. It is important to note that this year is considered a masting year, and therefore a superabundance of acorns are available. Given the abundance of acorns, it is not surprising that the ant occupation rates are low. In a non-masting year, there would likely be greater nest site limitation. In addition, because acorns are not only variable by year, but also a transient resource, relative nest site limitation may be more strongly visible in the early and late season of any year when fewer acorns are on the ground. Long term dynamics may also have an important affect on ant community dynamics. Given the continuing shift from oak/hickory to red maple (*Acer Rubrum*) forests across the eastern United States (Abrams 1992, 1998), it is expected that nest sites will become increasingly scarce and competition increasingly fierce. This change in forest dynamics could result in reduced nut-nesting ant diversity. In a site limited system, it is possible habitat generalists such as *Leptothorax Sp.* and *Myrmica punctiventris*, which were both found across a range of nut sizes and in both tree species, will have an advantage over more specialized species. Further experimentation on nest site limitation and habitat preference is necessary to address how the shift in canopy composition will affect the diversity of cavity nest ants.

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WHO COMES FIRST?
A CONTINUATION OF “ANTS IN SPACE”: FORAGING STRATEGIES AND TEMPORAL
DYNAMICS OF THREE ANT SPECIES ON THE E.S. GEORGE RESERVE

ANDY MACDONALD, DOUG JACKSON, LEILING TAO, RACHEL HESSLER, EMILY
SLUZAS, WILLIAM WEBB, AND JOHN VANDERMEER

ABSTRACT

Observations of the time of arrival and foraging behavior of three ant species (*Tetramorium caespitum*, *Solenopsis molesta*, and *Monomorium minimum*) were made in order to determine the foraging strategies and temporal dynamics of the three species of ant. The goal was to determine interactions between the three species, one of which is an introduced species from Europe (*T. caespitum*), and their respective foraging strategies. The experiment was meant to test a hypothesis generated from a previous study at the site: that *M. minimum* is a “scramble competitor” and would therefore arrive at the tuna baits that were set first, and that *S. molesta* and *T. caespitum* would gradually competitively exclude *M. minimum* as superior “confrontational competitors.” These hypotheses were found to be false as *M. minimum*, in every case, did not arrive first and was found to be an effective “confrontational competitor” with the ability to competitively exclude the other two species. Rather, *T. caespitum* was observed to have the characteristics of a “scramble competitor” and may be replacing *S. molesta* at the site. These findings have implications for ecosystem function at the site (as an invasive ant species may be replacing a native species), as well as for the understanding of the mechanisms of biological invasion in general.

INTRODUCTION

A recent study of the spatial distribution of foraging ants in a field at the E.S. George Reserve showed that the clump size distribution of the ant *Monomorium minimum* deviates from a power law, with small clump sizes being overrepresented (Jackson et al. 2008). In this system, a power law distribution of clump sizes was thought to be indicative of a self-organization process characterized by local expansion with spatial constraint. The deviation from a power law at small clump sizes was interpreted as evidence that *M. minimum* may be employing a scramble competition foraging strategy. Based on observations made as well as the fit to a power law of the spatial distribution of ants, it was also concluded that *Tetramorium caespitum* and *Solenopsis molesta* are likely contest competitors, overpowering *M. minimum* as they arrive at available food resources.

Scramble competitors employ a strategy that depends on having superior resource discovery and dispersal abilities compared to the species they are in competition with; superiority in these characteristics compensates for the scramble competitor’s inferiority in direct competition, and allows it to coexist with species that are otherwise competitively dominant (Vandermeer et. al. *in prep*). According to this hypothesis, the temporal dynamics of the three dominant ants in the field would be as follows. *M. minimum*, the scramble competitor, is able to find tuna baits more quickly than the ants that are superior competitors. Therefore, *M. minimum* initially dominates a large majority of the baits. However, the competitively dominant species, *Tetramorium caespitum* and *Solenopsis molesta*, eventually discover the baits and exclude *M.*

minimum. During this transitional stage when *M. minimum* is being excluded from baits, the spatial distribution of *M. minimum* is characterized by many small, isolated clumps of *M. minimum* that are in the process of being eliminated by *T. caespitum* and *S. molesta*, and hence the clump distribution has more small, isolated clumps than would otherwise be expected.

A qualitative analysis of the spatial distributions of *M. minimum*, *S. molesta*, and *T. caespitum* also appeared to support the hypothesis that *M. minimum* is a scramble competitor and *T. caespitum* and *S. molesta* are competitively dominant. *M. minimum* was distributed broadly throughout the study plot on the first day, but was much less common when the site was surveyed the following day, suggesting that it had been driven from the baits by the other ants. *T. caespitum* and *S. molesta* were distributed in mutually exclusive clumps that became even more sharply defined by the second day, showing a clear competitive interaction.

Although the clump size distribution of *M. minimum* was suggestive of scramble competition, there are clearly other hypotheses that could explain the observed pattern. Therefore, to directly test the hypothesis that *M. minimum* is a scramble competitor, we investigated the temporal dynamics of ant recruitment to tuna baits. Our expectation, based on the hypothesis that *M. minimum* acts as a scramble competitor, was that *M. minimum* would quickly find and recruit to tuna baits, but would then be driven from the baits by the more competitive species, *T. caespitum* and *S. molesta*.

MATERIALS AND METHODS

Study Site

This study was undertaken at the E.S. George Reserve in Livingston County, Michigan. The site of observation was located in a field west of the George Reserve experimental ponds, the topsoil from which had been removed in 1988. Consequently, this site has a relatively homogenous vegetation pattern consisting of grasses and shrubs, as well as relatively homogenous soil type and topography. Temperature and cloud cover fluctuated throughout the day, presenting a potentially significant yet uncontrollable variable to the study.

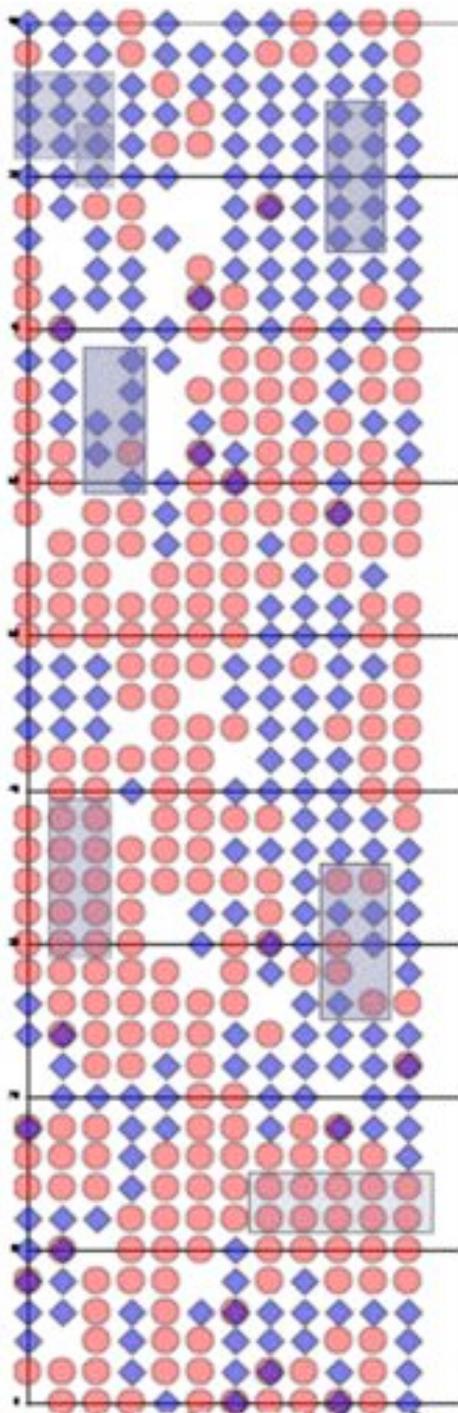
Study Organisms

Three primary species of ant were found to be present at the site, *Tetramorium caespitum* (an introduced species from Europe), *Monomorium minimum*, and *Solenopsis molesta* (Jackson et. al. 2008). The behavior and foraging strategies of these three species were the primary focus of this study.

Field Experiment

Observation plots were set up within the study site based on areas determined to be dominated by a particular species of ant (Jackson et. al. 2008). Six total plots, each consisting of 10 tuna baits placed two meters apart from each other, were set up. Two of the plots were in areas where *Tetramorium* was found to be dominant, two where *Solenopsis* was found to be dominant, and two where there was no clear indication of dominance (shaded areas of Figure 1). The baits were observed every five minutes to determine instance of first arrival. They were monitored every five to ten minutes thereafter to observe the foraging strategies of the three ant species. Data were collected from 10:30-12:30 pm and a final observation was made at 3:30 in the afternoon to see how competition over the baits played out.

Figure 1. *S. molesta* dominance represented by red circles, *T. caespitum* dominance represented by blue diamonds



RESULTS

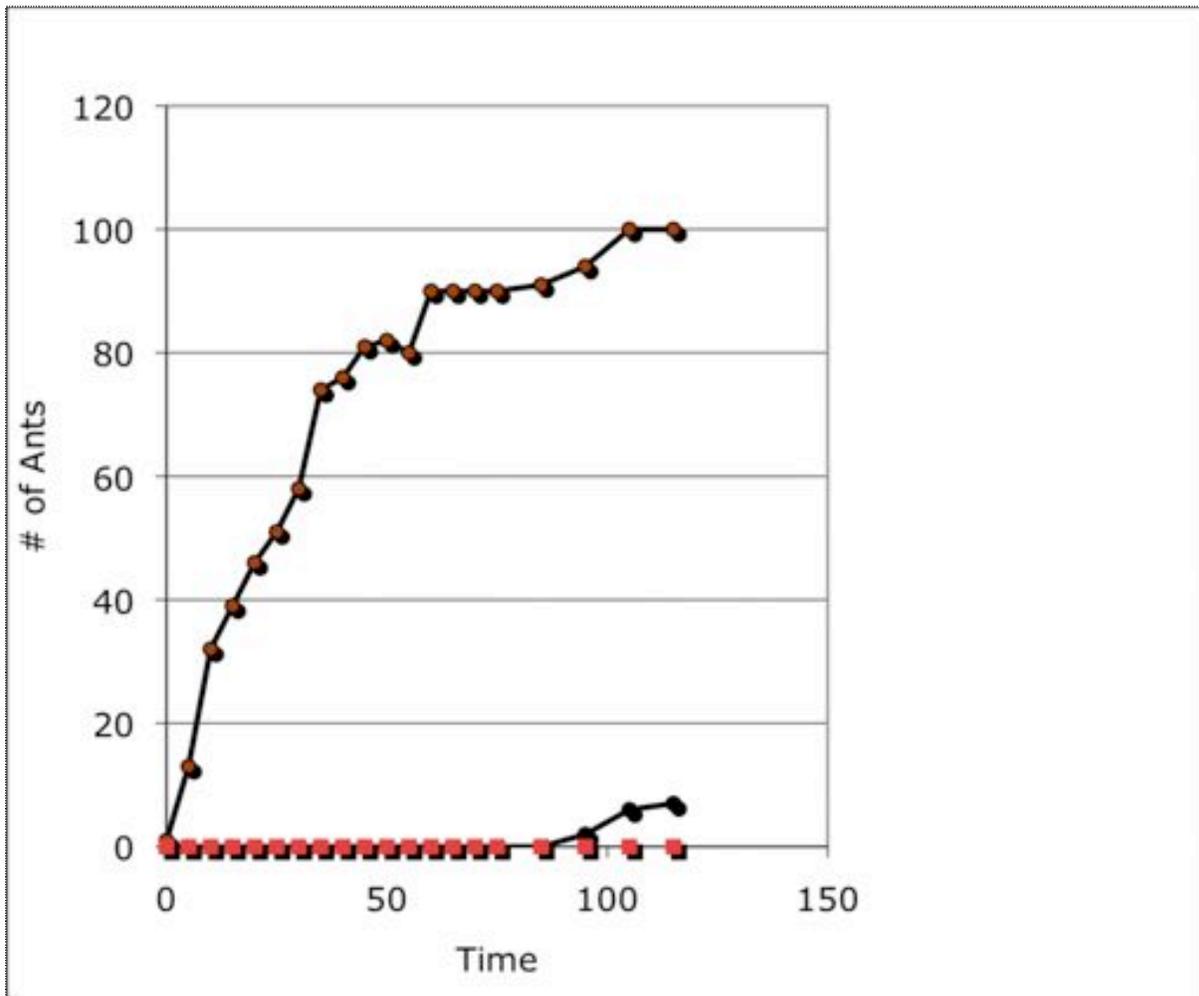
Our expectation, based on previous findings at the study site, was that we would observe *M. minimum* arriving at the baits first as a scramble competitor in this system and that *S. molesta*

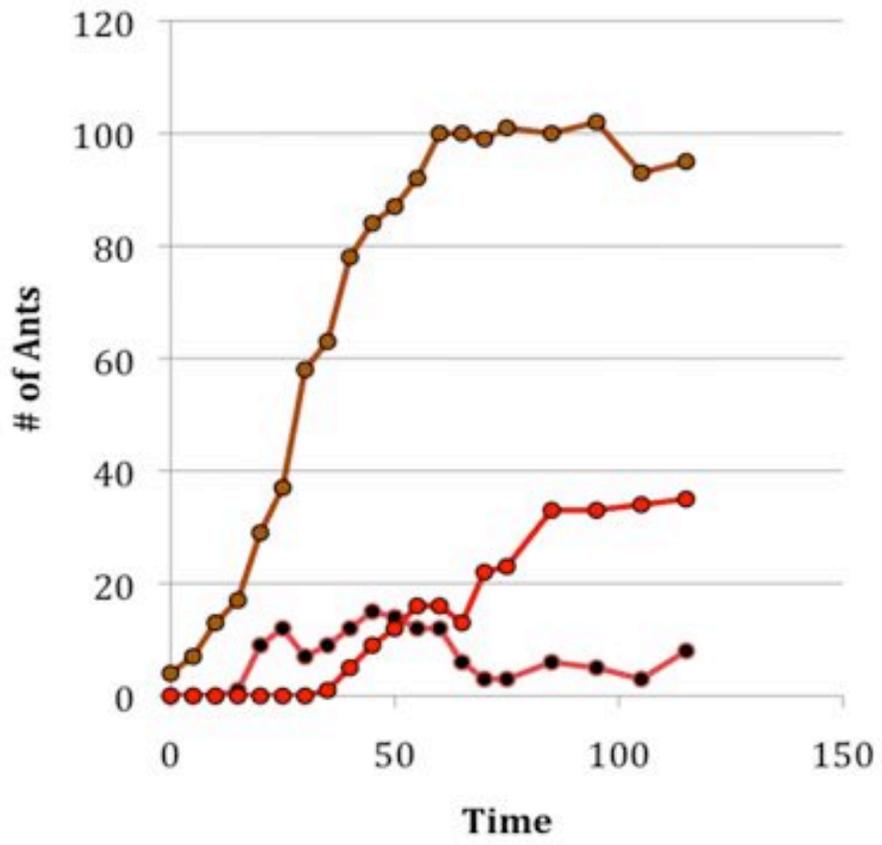
and *T. caespitum* would eventually competitively exclude *M. minimum*. In fact, we observed nearly the opposite of this scenario:

Each of the below graphs (Figure 2) represents the amalgamation of all ten tuna baits over the course of the initial two hour period of observation in each of the six study plots. Time (X) vs. number of ants (Y) is plotted for each of the three primary ant species.

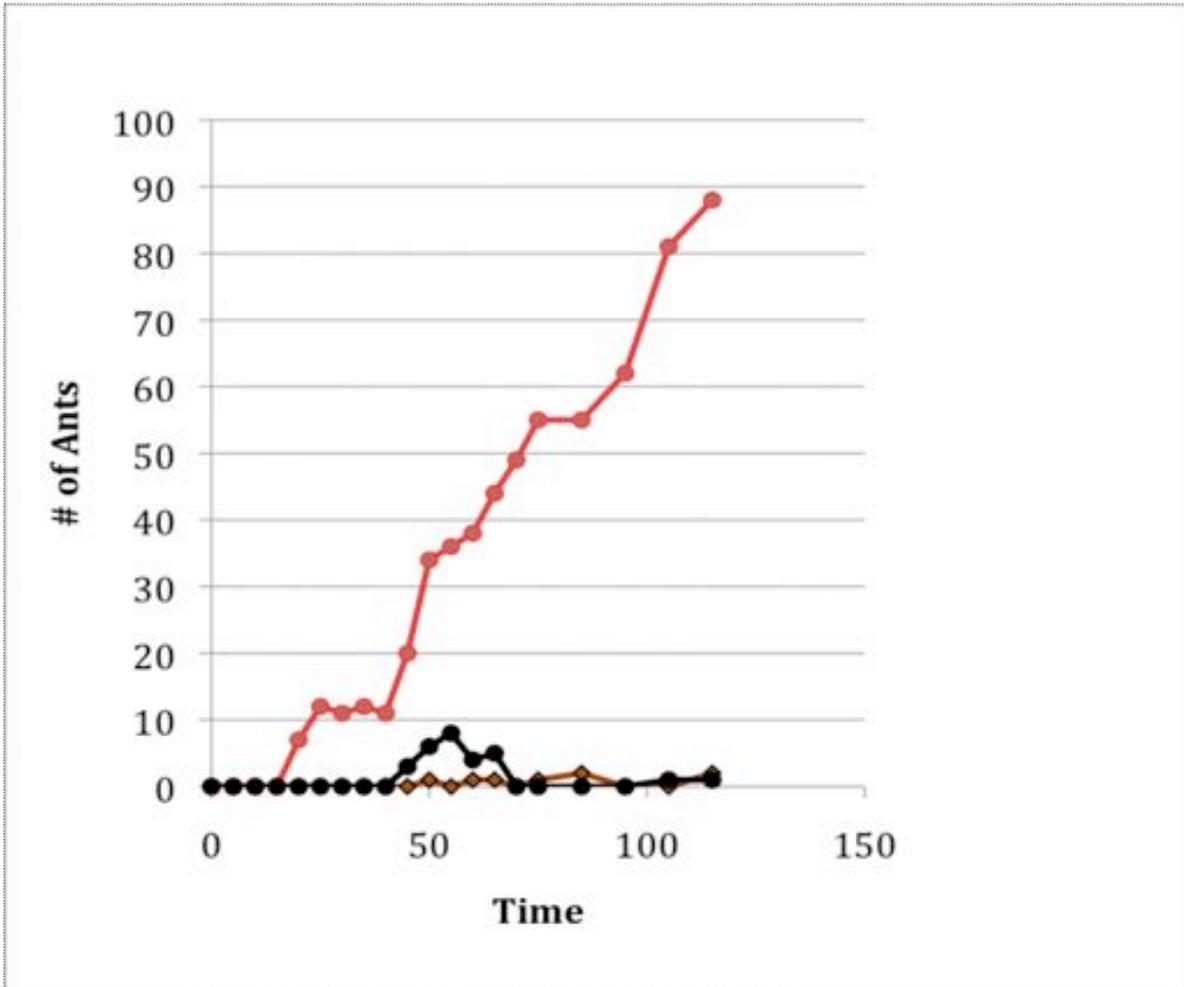
Figure 2. Brown dots represent *T. caespitum* (first two graphs (a) indicate *T. caespitum* dominance), red dots represent *S. molesta* (second set of graphs (b) represent *S. molesta* dominance), and black dots represent *M. minimum* (third set of graphs (c) represent plots where there was no clear cut dominant species)

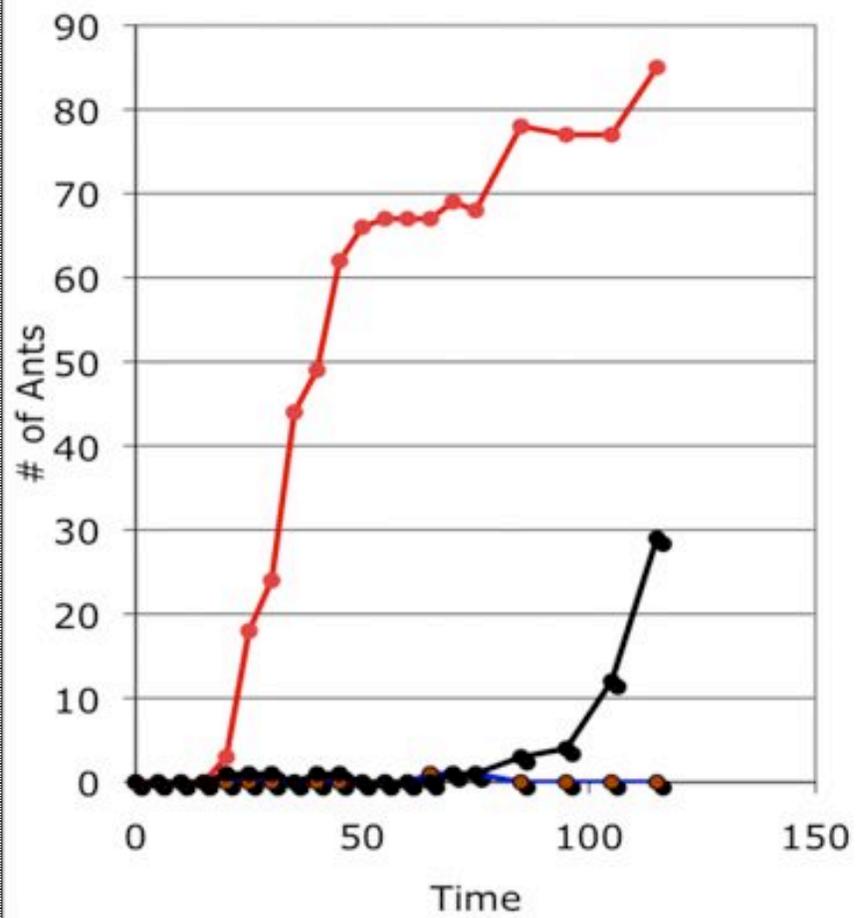
a)



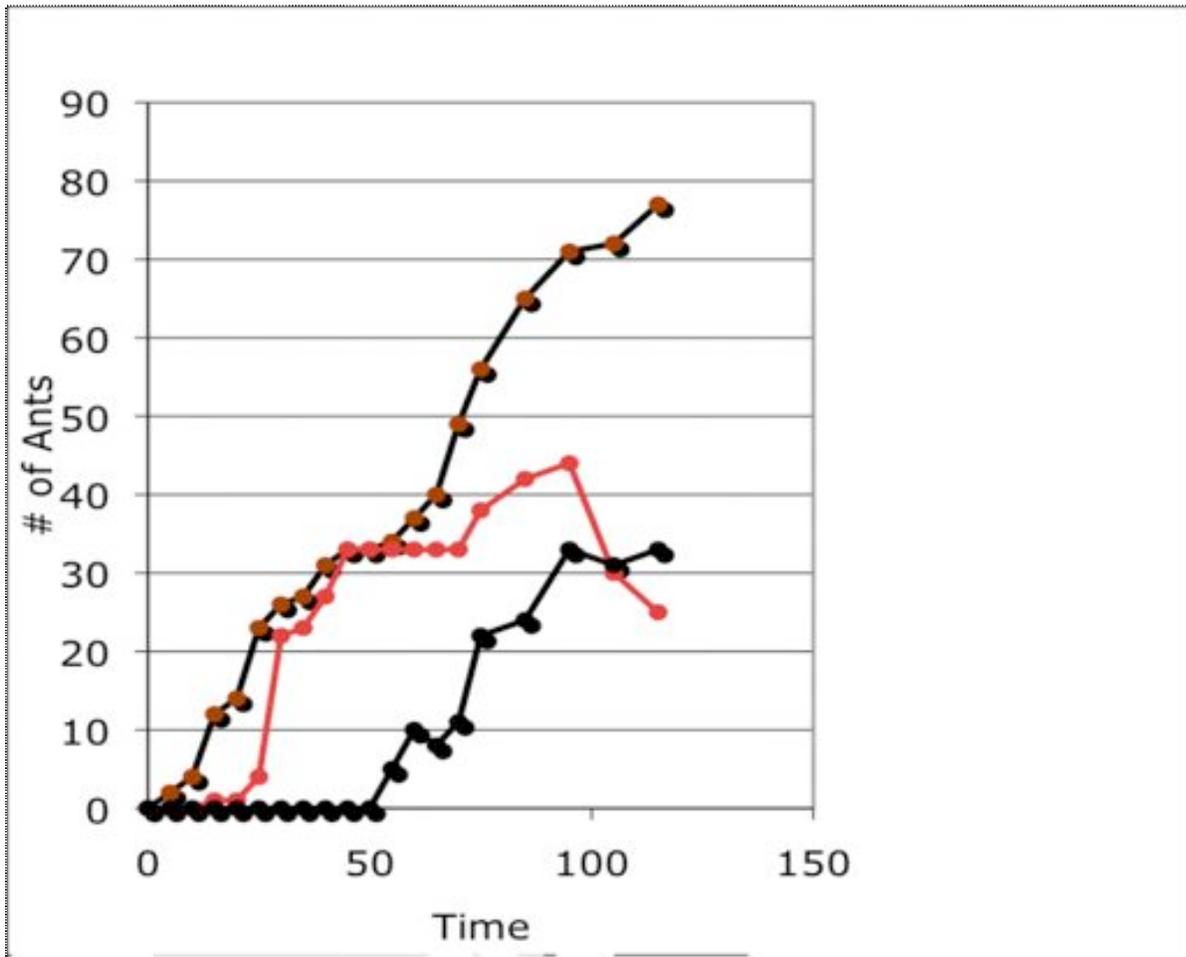


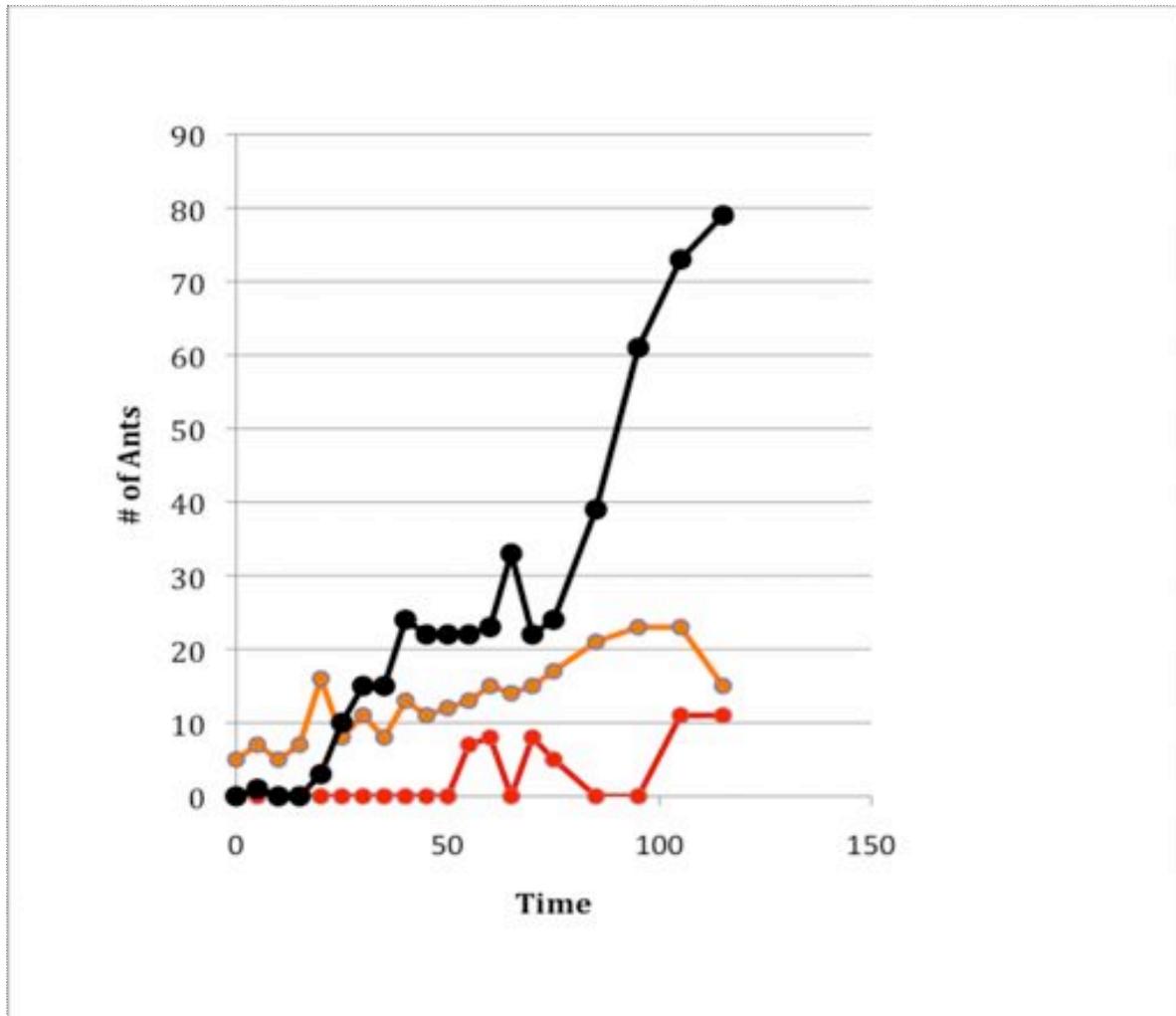
b)





c)

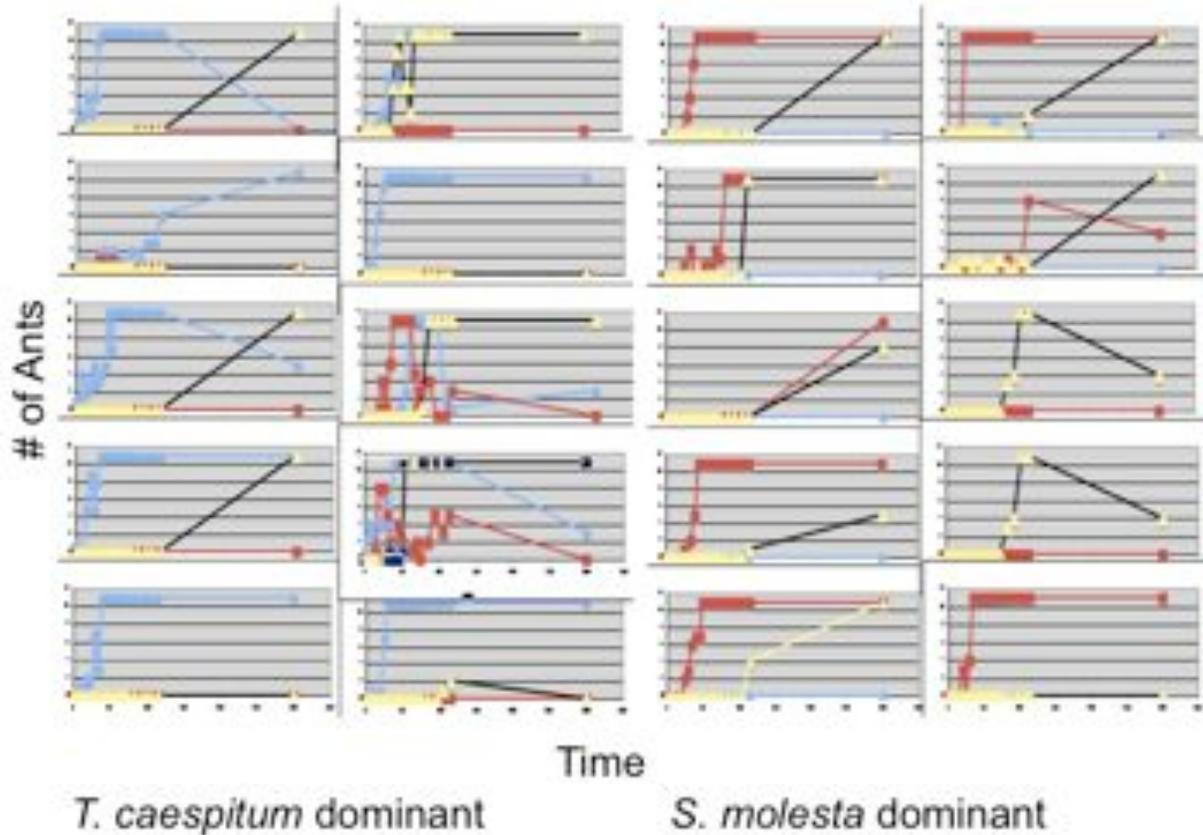


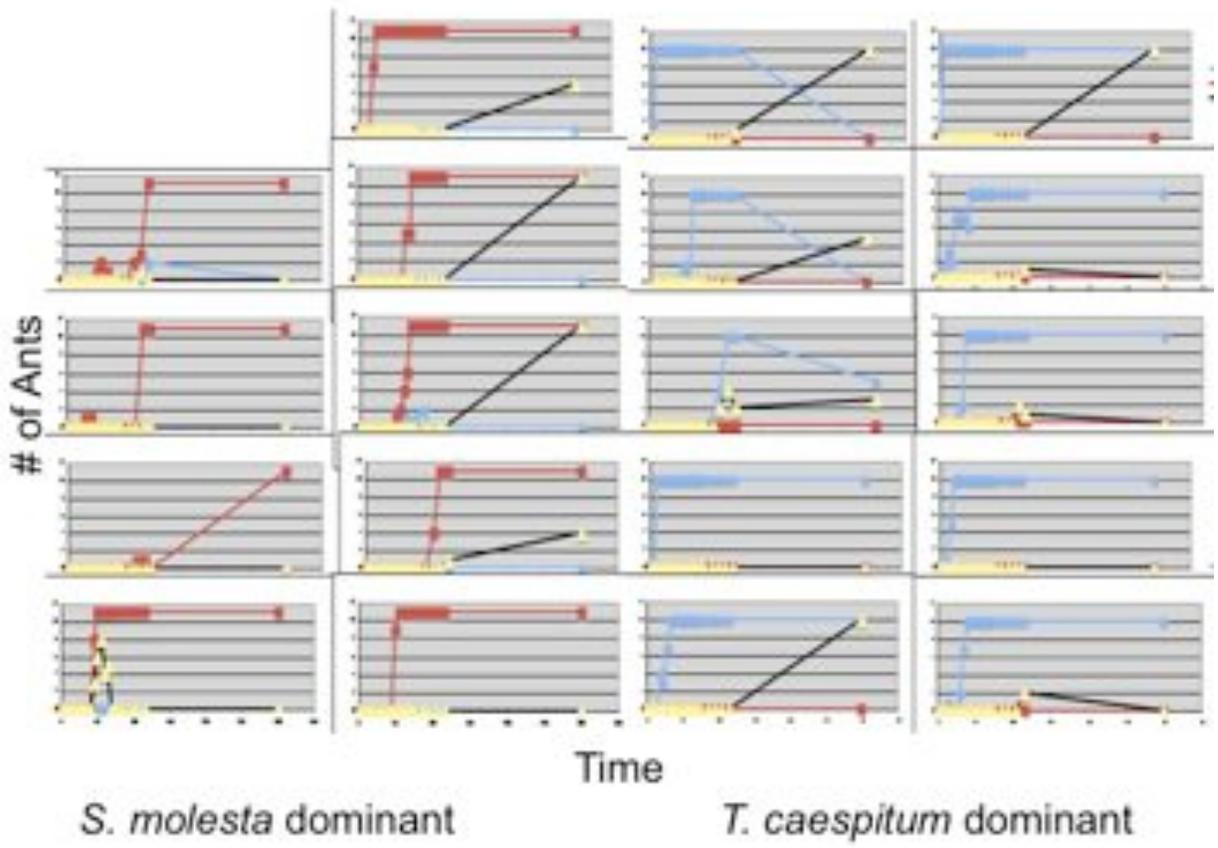


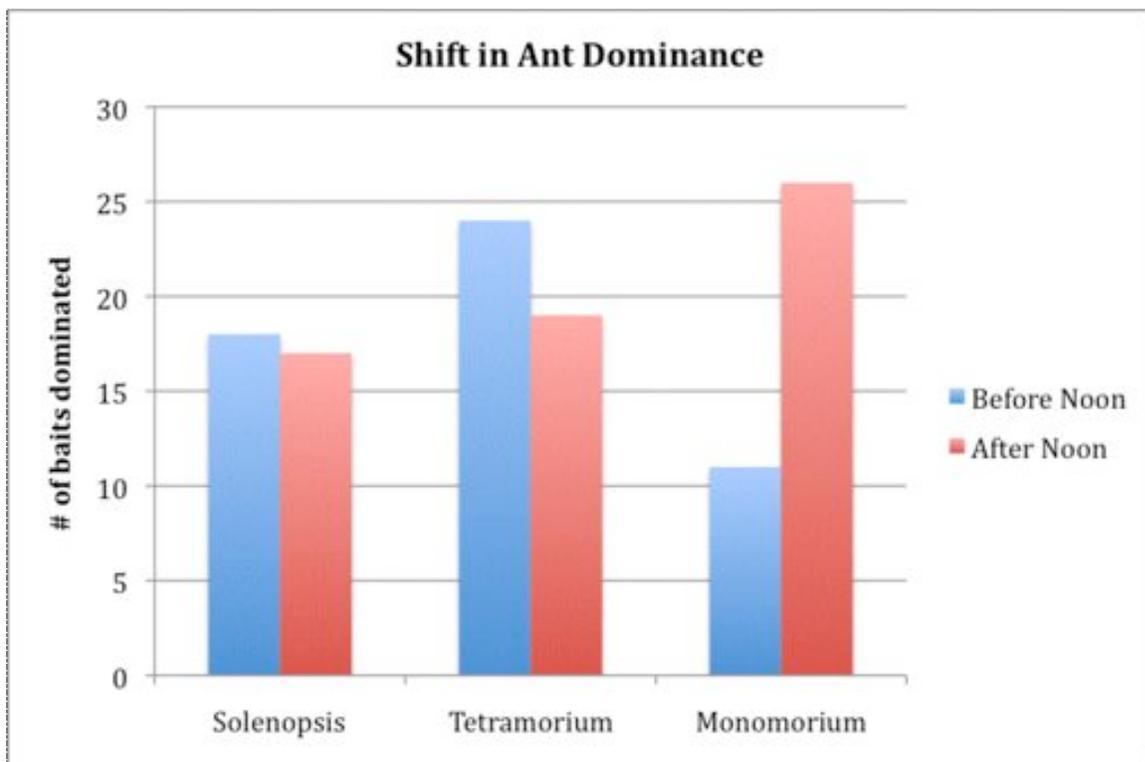
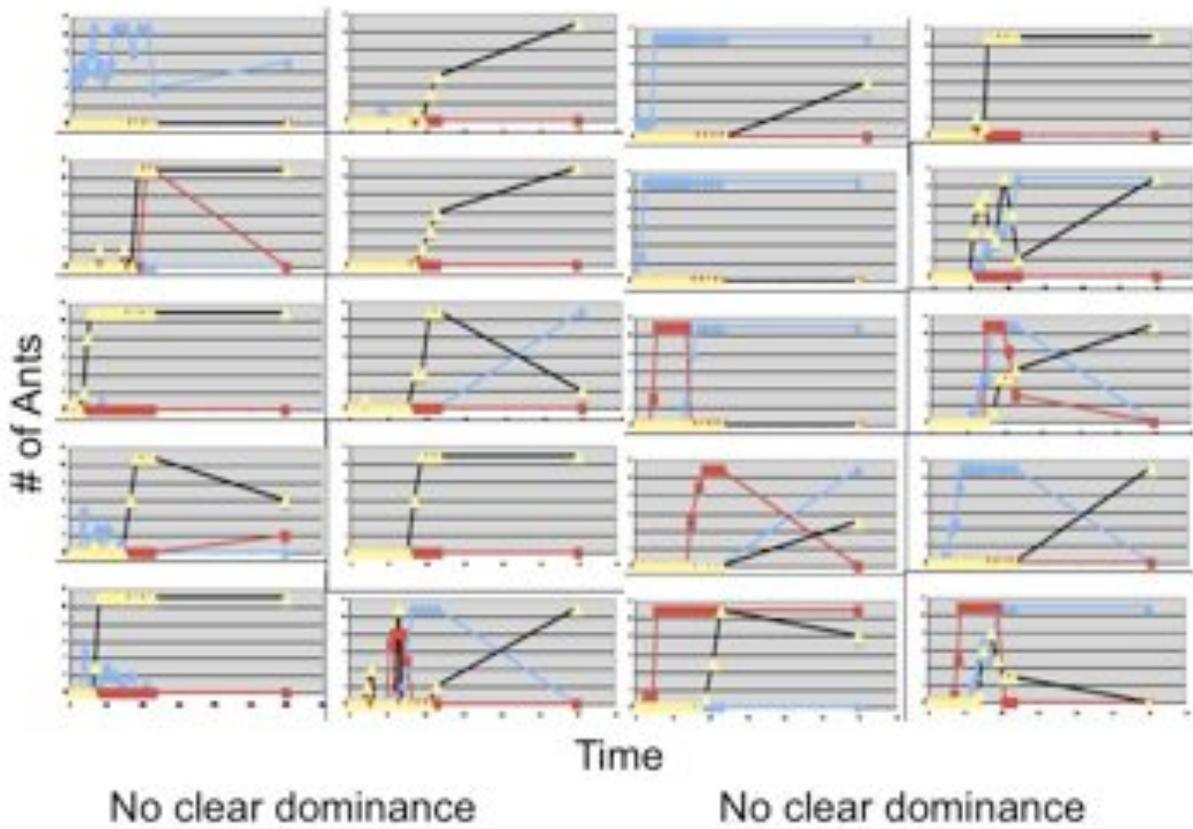
It is clear that *M. minimum* did not arrive first in any of the study plots and in many instances did not arrive until well after *S. molesta* and/or *T. caespitum* arrived. It was also found, based on the final observations made, that *M. minimum* replaced both *T. caespitum* and *S. molesta* as the dominant ant species present at a number of the baits (represented below in *Figure 3*).

Each of the graphs below (*figure 3*) represents the data collected at a single bait over the course of the observation period with the addition of the final observation made at 3:30 pm. It is clear that in a number of cases, *M. minimum* outcompetes both *S. molesta* and *T. caespitum* to gain control over the baits (represented by the black lines in the figure below).

Figure 3. In the below graphs, blue lines represent *T. caespitum*, red lines represent *S. molesta*, and black lines (with yellow triangles) represent *M. minimum*. Ant abundance of the three dominant species was recorded over the course of three hours and is represented below. It is clear in a number of cases that *M. minimum* outcompetes *S. molesta* and *T. caespitum* in order to take over at the bait. Sites labeled with *S. molesta* dominance or *T. caespitum* dominance based on Jackson et. al. (2008). Bar graph depicts shift in ant species dominance from the morning to the afternoon (all of the tuna baits are included) – there is a decline in *S. molesta* and *T. caespitum* dominance and a sharp increase in *M. minimum* dominance from the morning to the afternoon.







DISCUSSION

Our hypotheses, that *Monomorium minimum* would arrive first at the baits and that both *Solenopsis molesta* and *Tetramorium caespitum* would gradually competitively exclude *Monomorium minimum*, were not supported by our observations in the field. In fact, what we observed was nearly the opposite of what was expected: *M. minimum* did not arrive first at any of the baits, but rather arrived much later and, in many instances, was found to be in open competition with, or competitively excluding, both *S. molesta* and *T. caespitum*.

Reasonable explanations for these seemingly counterintuitive findings could be based on factors unaccounted for in sampling and observation (such as temperature, habitat type, or other environmental factors), or potential errors in the initial findings that lead to this study. One potentially significant oversight was the dismissal of temperature as a contributing factor. Early in the period of observation it was foggy and cold while later in the afternoon (when we saw *M. minimum* begin to forage) it was sunny and considerably warmer. It could be that foraging strategies are temperature dependent and our two-hour observation may not have been indicative of the actual relationship between the three primary ant species at the site. Habitat type, which was assumed to be homogenous across the study site, may have contributed to the findings as well. Mapping the vegetation type and density may be helpful in perceiving a general pattern between habitat type and particular ant species' foraging activities, which could potentially account for observations made at the site.

On the other hand, the initial identification of *M. minimum* as a scramble competitor from the previous study may not have been an accurate interpretation of the data collected. Based on our data and observations, the behavior of *M. minimum* was much more indicative of a dominant "confrontational" competitor and that of *T. caespitum* fit the role of scramble competitor well. A revised interpretation would perhaps look like the following: *T. caespitum*, an introduced species, is gradually replacing *S. molesta*, the species observed to be the weakest of the three competitors, as a scramble competitor in this system while *M. minimum* is filling the role of the dominant "confrontational" competitor. This interpretation, of course, is based on the assumption that system equilibrium will be reached when two species of ant fulfill the mutually exclusive roles of "scramble competitor" and "confrontational competitor" (Vandermeer et. al.).

However, it is possible that the study site, which is in the temperate zone, does not mimic those studied in the tropics and could potentially be defined by very different spatial and temporal dynamics and interactions between ant species. An alternate interpretation of the findings therefore may look like the following: diurnal and seasonal variations (of temperature for example) may be allowing for the co-existence of more than two ant species in this system in contrast with the tropics, which experiences far less temporal variation. This temporal separation of dominance could be allowing for the success of a number of much more widely varying foraging strategies in this system. To test this interpretation it would be necessary to analyze the effects of temperature (and perhaps other environmental factors) on ant activity over a much longer period of time in order to assess any differences at different temperatures. It would also be interesting to run these same experiments and make the same observations at different times of the year as well to assess the role of seasonal variation.

Returning briefly to the issue of replacement of a native ant species by an invasive: due to the great importance of ants as keystone species in their respective habitats, as seed dispersers, biological pest controls in agroecosystems, soil aerators, and even pollinators, it is crucial to

understand the unique functions and characteristics of invasive ants. If in fact *T. caespitum* is replacing *S. molesta* in this system, which we hypothesize may be the case, it is important to understand how this will affect ecosystem function and biotic interactions. This evolving relationship between *T. caespitum* and the native ants provides an interesting new dynamic for study and elicits new hypotheses, which could explain, in part, the observations made in this study. It has been found that *T. caespitum* is capable of using the sun to navigate and does not need to rely on pheromones (Holldobler and Wilson 1990). It could be possible that the native ants in this system (particularly *S. molesta*, a “cleptobiotic” ant meaning it will invade the nests of other ants in order to steal food) are incapable of detecting the pheromones of *T. caespitum* because it does not always leave a detectable pheromone trail. The ability to use light to navigate, effectively making *T. caespitum* “invisible” to the native ants, is a huge evolutionary advantage and could be significantly aiding in the replacement of *S. molesta*, a native ant, by *T. caespitum*, an invasive. Further supporting this hypothesis is the fact that *T. caespitum* has not co-evolved with the native ants and therefore may not have matched pheromone producing and detecting abilities with those of the native ants (Jackson et. al. 2008).

Whatever the case may be, the importance of this study is clear. Our findings suggest the potential for greater diversity and differentiation of function of ant species in ecosystems within the temperate zone (and potentially other organisms not studied as of yet). New light has also been shed on the dynamics between *T. caespitum*, an invasive ant, and the native ants to this system. Continued monitoring and study of this site may reveal the mechanisms for invasion and the outcome of such a biological invasion and replacement of a native ant species. The effects of *T. caespitum* on ecological stability provided by native ant species could be identified and the potential for biological mitigation could be explored.

ACKNOWLEDGEMENTS

We would like to acknowledge Dave Allen, Huijie Gan, Ivette Perfecto, Colibri Sanfiozeno-Barnhard, and Senay Yitbarek for laying the foundation for this study with their work on “Clump size distribution of ants as a signal of self-organization with spatially constrained local expansion” at the site of study utilized for our own field experiment.

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TEMPERATURE AS A POSSIBLE MECHANISM FOR CO-EXISTENCE BETWEEN TWO ANT SPECIES

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ABSTRACT

Competition affects many important aspects of ecosystems, and being able to predict these competitive interactions and their influence on communities is very important to understanding the distribution, composition and abundance of species. To gain a better understanding of interspecific competition and the mechanisms that allow coexistence between competing species, we observed two ant populations, *Prenolepis imparis* and *Myrmica americana*. *P. imparis* is known for its ability to forage at near freezing temperatures, and we wanted to see if the difference in temperature preferences between the two ant species is a possible mechanism for coexistence. In order to do this, we baited 60 sites and observed the presence or absence of either species as the temperature rose throughout the morning.

INTRODUCTION

Ecologists spend a great deal of time and energy trying to understand and predict the effects of competition on communities. Competition affects many important aspects of ecosystems, including the composition, abundance, and distribution of species in local communities (Alinvi, 2007). Understanding competitive interactions is particularly important today, as interspecific relationships that have taken millions of years to develop are being thrown off balance by mass extinctions, habitat destruction, changes in migration patterns, and invasive species.

The basic tenet of the competitive exclusion theory is that two species competing for the same resource will be unable to coexist—the better competitor will out-compete the other. However, several factors have been found to allow for coexistence between competing species including temperature, resource size, resource type, and parasitoids (Alinvi, 2008). The ability for competing species to coexist is critical for the maintenance of biodiversity in communities.

Ants are an excellent model for interspecific competition (Perfecto, 1994) because of their ability to monopolize space and resources in a manner very similar to plants (Cerde, 1997; Alinvi, 2008). In addition, they are crucial members of an ecosystem, aerating soil, dispersing seeds, and aiding in the nutrient cycle, so being able to predict the effects of competition on ant populations may be important for the preservation of ecosystems. It has often been found that foraging behaviors differ between sympatric ant species based on temperature (Cerde, 1998; Cerde, 1997), and this may be one factor contributing to the diversity we see in ant species.

In this study, we look at the competitive interactions between *Prenolepis imparis* and *Myrmicana americana*. *P. imparis* is known as a cold-weather species, foraging at temperatures just above freezing (Talbot, 1943), and it is often inactive in the summer's warmest months (Tschinkel, 1986, Talbot, 1943). *M. americana*, on the other hand, are typically active at warmer temperatures (Talbot, 1946). In our study, we sought to understand to what degree the changes in temperature from early morning until early afternoon affect competition between *P. imparis* and *M. americana*.

To determine this, we set out tuna fish baits in the early morning and monitored ant foraging at these sites, comparing arrival times for *P. imparis* and *M. americana*. We believed that *P. imparis* would arrive first at the bait sites during the cooler part of the day, but would be gradually excluded from the sites as the temperature increased and *M. americana* began foraging.

METHODS

Our experiment was located on Hourglass Island at the E.S. George Reserve near Pinckney, MI on September 28, 2008. This island is located in a swamp and is dominated largely by oaks in the red oak sector. We set up our grid on the north side of the island.

We set up six rows of flags, two meters apart, each with ten flags placed every two meters. Canned tuna was placed at each of the 60 flags, and one person observed each row. At 9:10 we made our first observations. Systematically, we observed each flag in our row to determine ant activity and noted presence or absence of *P. imparis* and *M. americana*. We went through each row every 20-25 minutes until 10:55, and one last observation was made at 1:40 pm. At each time interval, we noted the temperature.

RESULTS

We observed two dominant ant species (*P. imparis* and *M. americana*) occupying 60 tuna baits during the five-hour survey at our study site. The relative proportion of *P. Imparis* to *M. americana* increased with temperature, with the highest temperatures recorded at 18 and 19.5 Celcius (fig 1). When evaluating the site occupancy of both ant species, two distinct patterns emerged. *M. americana* was found to forage dominantly in the morning and afternoon at most of the sites. *P. imparis*, however, remained largely absent during the coolest periods of the day (fig 2). The foraging activity level for *P. imparis* and *M. Americana* both followed a similar trend, with activity increasing quickly from the start of the experiment, peaking about 100 minutes into the experiment, and then declining slowly until the end of the trial.

Fig 1. Proportion of baits occupied by *P. Imparis* to baits occupied by *M. Americana* with temperature.

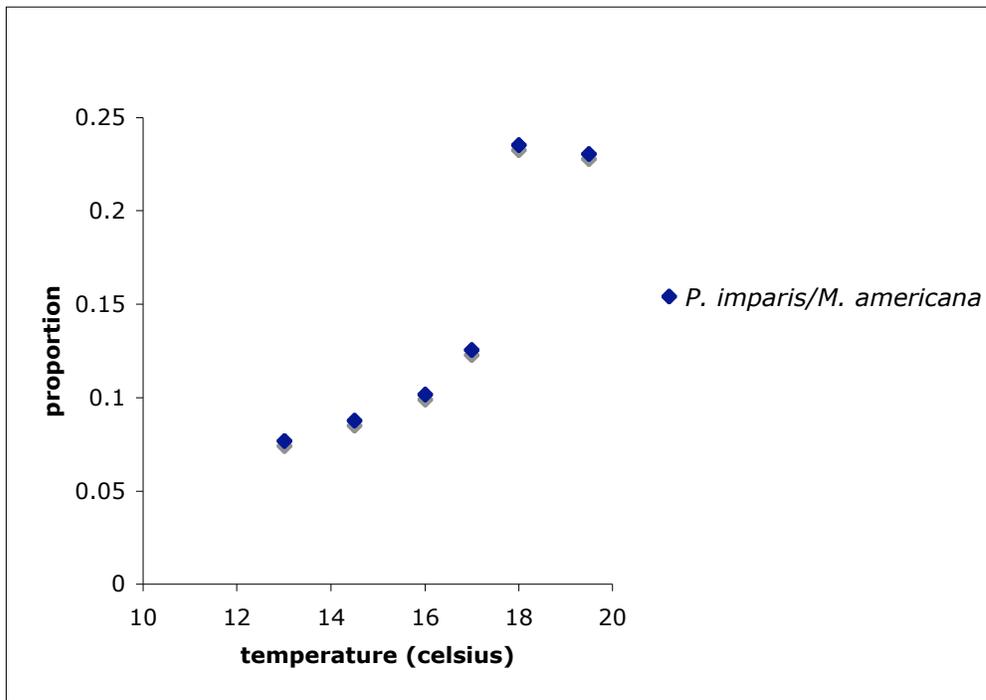
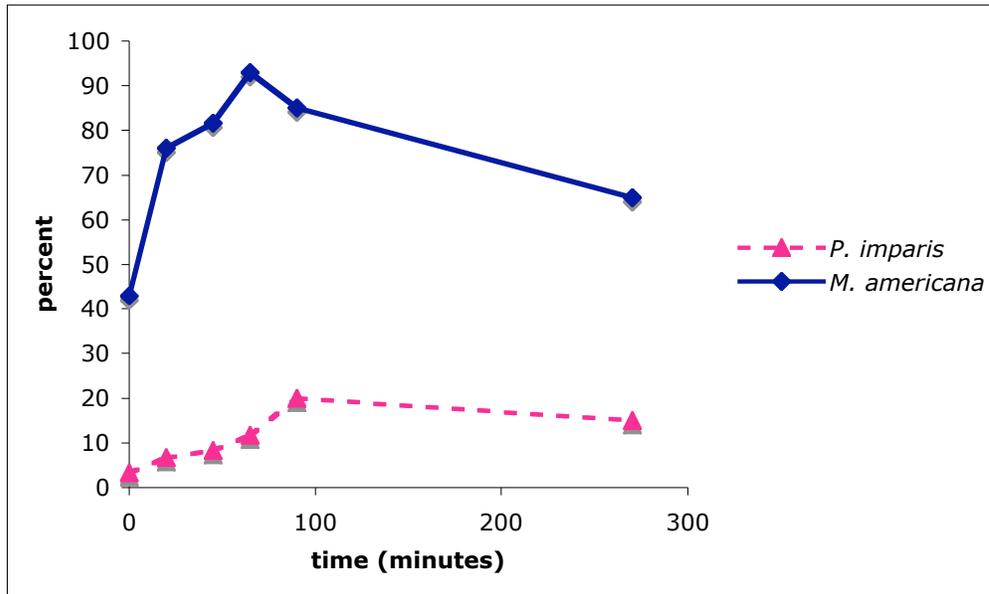


Fig 2. Percentage of bait sites occupied by *M. Americana* and *P. Imparis* with time.



DISCUSSION

Our results appear to disprove our hypothesis that *P. imparis* are more active at cooler temperatures than *M. americana*. When we checked our sites initially, only two sites out of 25 with ants had *P. imparis*, and those sites were shared with *M. americana*. The presence of *P. imparis* increased as the temperature rose, and in fact, the proportion of *P. imparis* to *M. americana* was highest at our two highest temperatures: 18°C and 19.5°. This goes against our hypothesis, in addition to the popular belief that *P. imparis* are more active in cooler weather. However, upon further investigation, it seems that there may be another explanation: a study done in 1943, showed that *P. imparis* are most active between 7°C and 10°C (45-50°F) (Talbot, 1943). Our coolest temperature was already above this range, at 13°C. Our warmest temperature was 19.5°C—well above the preferred foraging temperature of the *P. imparis*, and in fact, around the temperature when *P. imparis* activity drops off considerably. In a similar study, *M. americana americana* activity was shown to peak between 15°C and 27°C (Talbot, 1946). By our third time point, the temperature was within this range. It would have been necessary to begin the study earlier in the morning or possibly even on a cooler day in order to see the trend one would expect, given the data from these studies.

Since we know that our trials were run at temperatures higher than those preferred by the *P. imparis*, it is necessary to look at other factors in order to explain our results. The most likely explanation for the increase in proportion of *P. imparis* to *M. americana* we saw as the temperature rose may have more to do with time and the location of the tuna fish bait than temperature. It is possible that the nests of *P. imparis* were further away from our experimental plot than those of *M. americana*, so *P. imparis* would arrive

later to the tuna fish bait sites. Another explanation is that the nests of *M. americana* are widespread throughout the experimental plot, whereas the nests of *P. imparis* are confined to one area of the plot. This possibility is supported by the fact that the first of the *P. imparis* were found at sites in the northwest corner of the experimental plot, and they appeared to spread from there. We saw no *P. imparis* in the southeast corner. This suggests that *P. imparis* may have a nest closer to the northwest corner.

M. americana and *P. imparis* followed nearly the same trend in terms of the percentage of sites occupied as time progressed from the first time period to the last. This trend may be explained simply by the typical foraging behavior of ants: when an individual ant discovers a food supply, it will then recruit other ants from its nest to the site. Therefore, one would expect to see an increase in ant presence as time goes on, and the slight drop at the last time point might be explained by satiation.

Given the information we now have about temperature and activity level of *M. americana* and *P. imparis*, a repeat of this study could prove to be an excellent example of temperature as a mechanism for co-existence between competing species. Without this difference in foraging behavior, it is possible that one of the two ant species would be able to out-compete the other, extirpating the population of the weaker competitor. A study completed on a cooler day would probably show the results that we had expected with *P. imparis* arriving first and dominating the bait sites while the weather was cooler and *M. americana* arriving later, as the temperature rose closer to their preferred foraging temperature and further away from the preferred foraging temperature of the *P. imparis*. This foraging pattern would allow coexistence between the two species, which would in turn, help in maintaining biodiversity in the community.

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EFFECTS OF TEMPERATURE AND TIME ON ANT FORAGING

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ABSTRACT

Previous research at George Reserve on the spatial distribution, temporal dynamics, and foraging strategies of three coexisting ant species, *Monomorium minimum*, *Tetramorium caespitum*, and *Solenopsis molesta* revealed broad patterns of foraging territories and glimpses of potential temperature preferences. However, previous research did not record the temperature specific to each bait site, did not consider the effect of the timing of bait placement on foraging, and used varied data collection methods throughout the trials. This study measured temperature at each site, the effect of the timing of bait placement on foraging, recorded data consistently from 8 a.m. to 4 p.m., and recorded the presence of ant species at 48 bait sites separated into 4 groups. Each grouping was placed within the known territories of four different ant species *M. minimum*, *T. caespitum*, *S. molesta*, and *Prenolepis imparis*. Results revealed that the timing of bait placement did not have an effect on the final outcome of the dominant species or ant abundance present at each bait site. However, two of the ant species, *M. minimum* and *T. caespitum*, showed a significant increase in activity within a specific temperature range, while *S. molesta* and *P. imparis* did not. Because *T. caespitum* is an invasive species, the mechanisms it employs to outcompete and displace native species are important to habitat conservation, as native ants are keystone species participating in seed dispersal, soil aeration, and a host of other vital ecosystem interactions.

INTRODUCTION

Two recent studies of the ant community present in the field adjacent to the E. S. George Reserve experimental ponds have yielded data suggestive of the spatial distribution, temporal dynamics, and foraging strategies of the three primary species of ant present (*Monomorium minimum*, *Tetramorium caespitum*, and *Solenopsis molesta*).

The initial study was undertaken in order to determine the spatial distribution of foraging ants at the study site and to infer from that observed distribution the interactions and dynamics between foraging ant species shaping that distribution in this particular system. In this system, a power law distribution of clump sizes was thought to be indicative of a self-organization process characterized by local expansion with spatial constraint. The deviation from a power law at small clump sizes was interpreted as evidence that *M. minimum* may be employing a scramble competition foraging strategy (Jackson 2008). Scramble competitors are characterized by superior resource discovery, dispersal, and recruitment abilities. This strategy results in temporal separation of dominance. This dynamic theoretically allows for the coexistence of two

species of ant utilizing the same resources and the same habitat (Vandermeer, et. al.). Jackson et al. (2008) also concluded that the spatial distribution of both *S. molesta* and *T. caespitum* was indicative of a capable “confrontational” competitor, therefore allowing *S. molesta* and *T. caespitum* to competitively exclude the scramble competitor, *M. minimum*.

A follow up study (MacDonald et al. 2008) conducted on this system expanded on these initial findings to determine “who comes first” or, in other words, what are the temporal dynamics governing species interactions and what are the foraging strategies employed by the three species of ant that maintain these dynamics and system equilibrium? In this study, contrary to the assumptions made in the initial study, it was found that *M. minimum* is an effective confrontational competitor, as it was observed to be competitively excluding both *S. molesta* and *T. caespitum*. *T. caespitum* was observed to be outcompeting *S. molesta* head to head and *S. molesta* was generally observed to be the weakest of the three competitors. It was concluded, based on these observations, that *T. caespitum*, an introduced species, may be gradually replacing *S. molesta* in this system, and that *M. minimum* may be filling the role of a confrontational competitor and *T. caespitum* that of a scramble competitor. An alternate interpretation of these observations could be that the study site, which is in the temperate zone, does not mimic those studied in the tropics and could potentially be defined by very different spatial and temporal dynamics and interactions between ant species. An alternate interpretation of the findings therefore may look like the following: diurnal and seasonal variations (of temperature, for example) may be allowing for the co-existence of more than two ant species in this system, in contrast with the tropics, which experiences far less temporal variation. This temporal separation of dominance could be allowing for the success of a number of much more widely varying foraging strategies in this system. To test this interpretation, it would be necessary to analyze the effects of temperature (and perhaps other environmental factors) on ant activity over a much longer period of time in order to assess any differences at different temperatures (MacDonald et al. 2008).

It was this potential for temperature-dependent foraging strategies (particularly given the reliance of ants on pheromones for foraging, the effectiveness of which depends on temperature) that led to the current study. Based on these previous studies, we hypothesized that the foraging strategies of the three ant species, particularly *M. minimum*, are dependent on temperature. This temporal separation of foraging would allow for coexistence of all three species and would explain the incongruity of past observations. An alternate hypothesis that would explain the tendency of *M. minimum* to dominate baits late in the day is that the amount of time since a bait is placed has a strong influence on the competitive hierarchy, with *M. minimum* able to dominate baits a given amount of time after the baits are placed.

To test these hypotheses, we staggered the placement of baits by two hours to separate the effects of time and temperature to assess the effects of each variable on ant foraging (which species arrives first and which is able to competitively exclude others given variation in time and temperature). If temperature, or something else correlated to time of day, is the key determinant of foraging activity, we would expect that workers of a given species would appear at all baits at approximately the same time, regardless of how much time had passed since the baits were placed, i.e., there would generally be synchrony across baits. In contrast, if time since a bait is placed is the dominant factor, we would expect that foragers of a given species would appear at

baits a certain amount of time after they were placed, meaning that there would be asynchrony across baits in the appearance of a given species. As an additional test of the effects of temperature on ant foraging, we also investigated the timing of recruitment of a fourth ant species, *Prenolepis imparis*, which had been observed to be active at lower temperatures than the three dominant ant species.

METHODS

Study site

This study was performed at the E.S. George Reserve in Livingston County, Michigan, in the same site used in Jackson et al. (2008) and MacDonald et al. (2008). The site was located in a field where primary succession has been progressing unhindered following the removal of topsoil in 1988. This site is a relative homogenous environment with sparse vegetation, grasses, and shrubs.

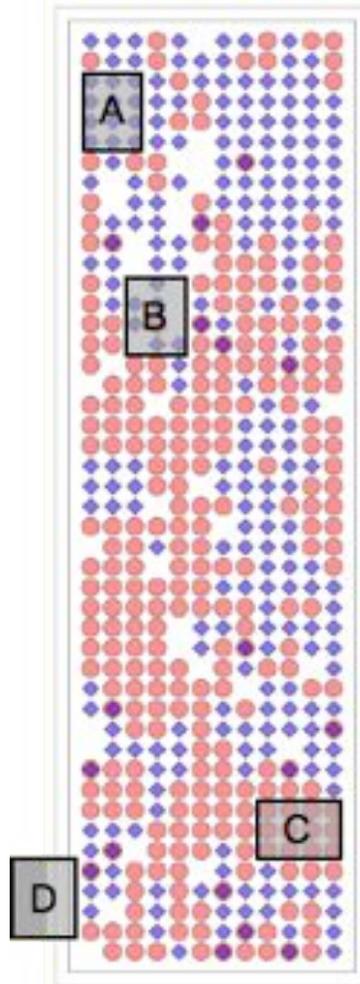
Field experiment

We selected three 12-bait regions from within the 96 m by 22 m plot used in Jackson et al. (2008) and MacDonald et al. (2008). One region was shown to be dominated by *T. caespitum* in Jackson et al. (2008), one was dominated by *S. molesta*, and one was a region that was contested by *T. caespitum* and *S. molesta*. We created an additional 12-bait region just outside the main plot in an area where another ant species, *Prenolepis imparis*, had been previously observed (Figure 1).

In each of these four regions, we placed 3 tuna baits at 8:00 a.m. on September 28, 2008. Three more tuna baits were added every 2 hours, so that by 2:00 p.m. all 12 baits had been placed at each site. We recorded temperature at each sample time in all sites except the *P. imparis*-dominated site using thermometers placed on the ground in full sun to estimate the relative changes in temperature that ants foraging on the ground would experience.

Following the initial appearance of a foraging ant at one of the 48 tuna baits, at 9:55 a.m., we checked the baits every 5 minutes, noting the abundance of each of the four target species (*T. caespitum*, *M. minimum*, *S. molesta*, and *P. imparis*). If there were < 10 ants, we counted all of them, otherwise we simply recorded that there were 11 or more. After 12:00, we increased the sampling period to 10 minutes because there were no longer significant changes between the 5 minute samples.

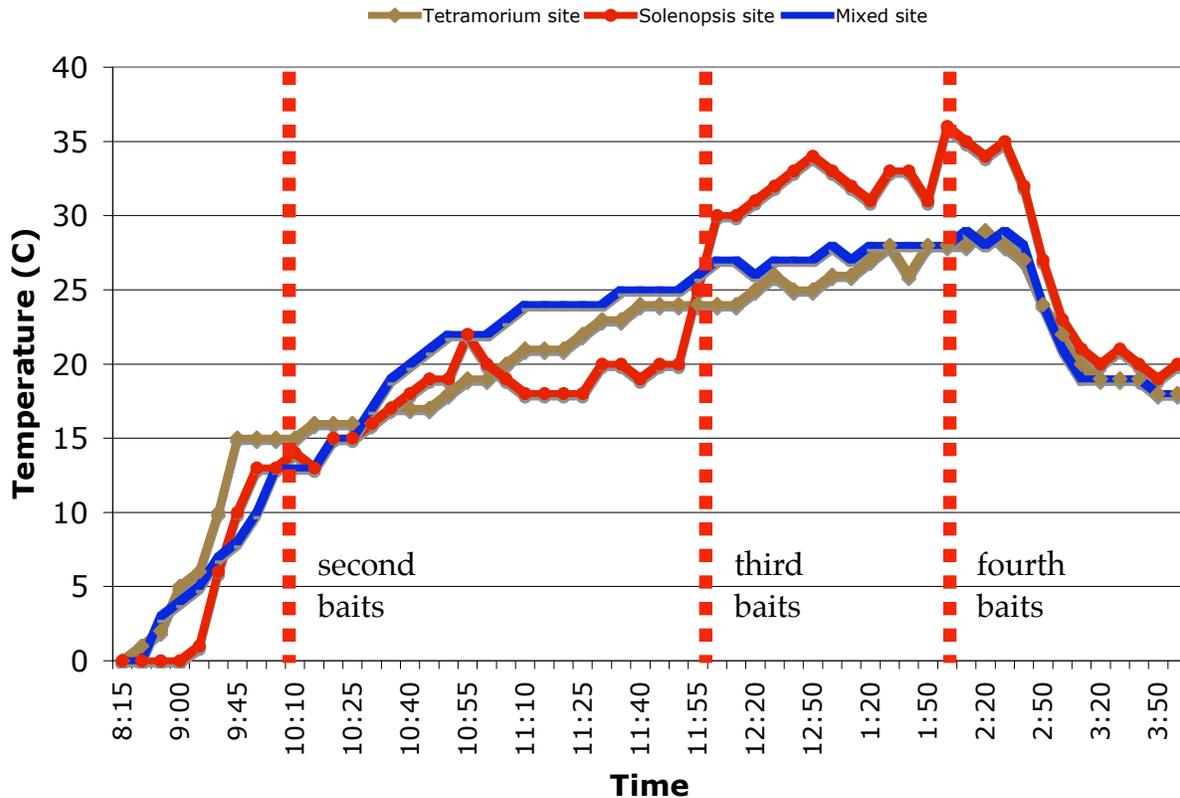
Figure 1. Location of study regions with respect to the 96 X 22 m used by Jackson et al. (2008) and MacDonald et al. (2008). Circles represent baits where the presence of foraging *S. molesta* was recorded in Jackson et al. (2008); diamonds represent presence of *T. caespitum*. Region A was a *T. caespitum*-dominated region, C was an *S. molesta*-dominated region, and B was a contested region. Area D was an additional region outside of the 96 m X 22 m study plot where foraging *P. imparis* had previously been observed.



RESULTS

The temperature rose throughout the day at all three sites where we measured temperature until it peaked at approximately 2:50 due to the sun being obscured by clouds. The temperature reading at the *S. molesta* site was lower than the other sites between approximately 11:00 and 12:00 because the thermometer was shaded by a fence; at 12:00, the thermometer was placed in full sun so it would more closely match the other sites (Figure 2).

Figure 2. Temperature versus time for the *T. caespitum*-dominated site, the *S. molesta*-dominated site, and the contested (mixed) site. Note that these do not correspond to air temperatures, as these temperatures were taken using thermometers in full sun.



Ant abundances for each site, for baits placed at different times, are shown in Figures 3-6. The dashed lines indicate when the baits were first placed at each group of sites; no observations were taken at sites prior to the placement of baits.

In the *P. imparis*-dominated site, only the first set of baits showed significant, sustained activity (Figure 3). The first ant recorded at any site occurred at the *P. imparis*-dominated site — a *P. imparis* worker that appeared at approximately 9:55 a.m. This site was subsequently invaded by *M. minimum* at approximately the same time as *M. minimum* invaded the other sites at which it occurred. *S. molesta* also appeared at this and other sites at approximately the same time; *T. caespitum* appeared at roughly the same time in the *T. caespitum* sites and the previously contested sites. In general, there was approximate synchrony of all species across sites, i.e., if a species occurred at a site, it arrived at approximately the same time in all of the sites, as long as the baits had already been placed in that site (Figures 3-6).

Between the four species, both *T. caespitum* (ANOVA, $df = 225$, $P = 0.000$) and *M. minimum* (ANOVA, $df = 225$, $P = 0.000$) were significantly more active within a specific temperature range. *S. molesta* and *P. imparis* did not demonstrate significant differences in activity between temperature ranges. *T. caespitum* was significantly more active in the temperature range between 20 and 30 °C (Friedman Rank, $N = 75$, $df = 2$, $P = 0.000$). *M. minimum* was also significantly more active between 20-30 °C (Friedman Rank, $N = 41$, $df = 2$, $P = 0.002$).

Figure 3. Ant abundances at the previously *P. imparis*-dominated site for the baits placed at different times. The first baits were placed at 8:00 a.m., the second at 10:00 a.m., the third at 12:00, and the fourth at 2:00 p.m. Dashed lines indicate when the baits were placed.

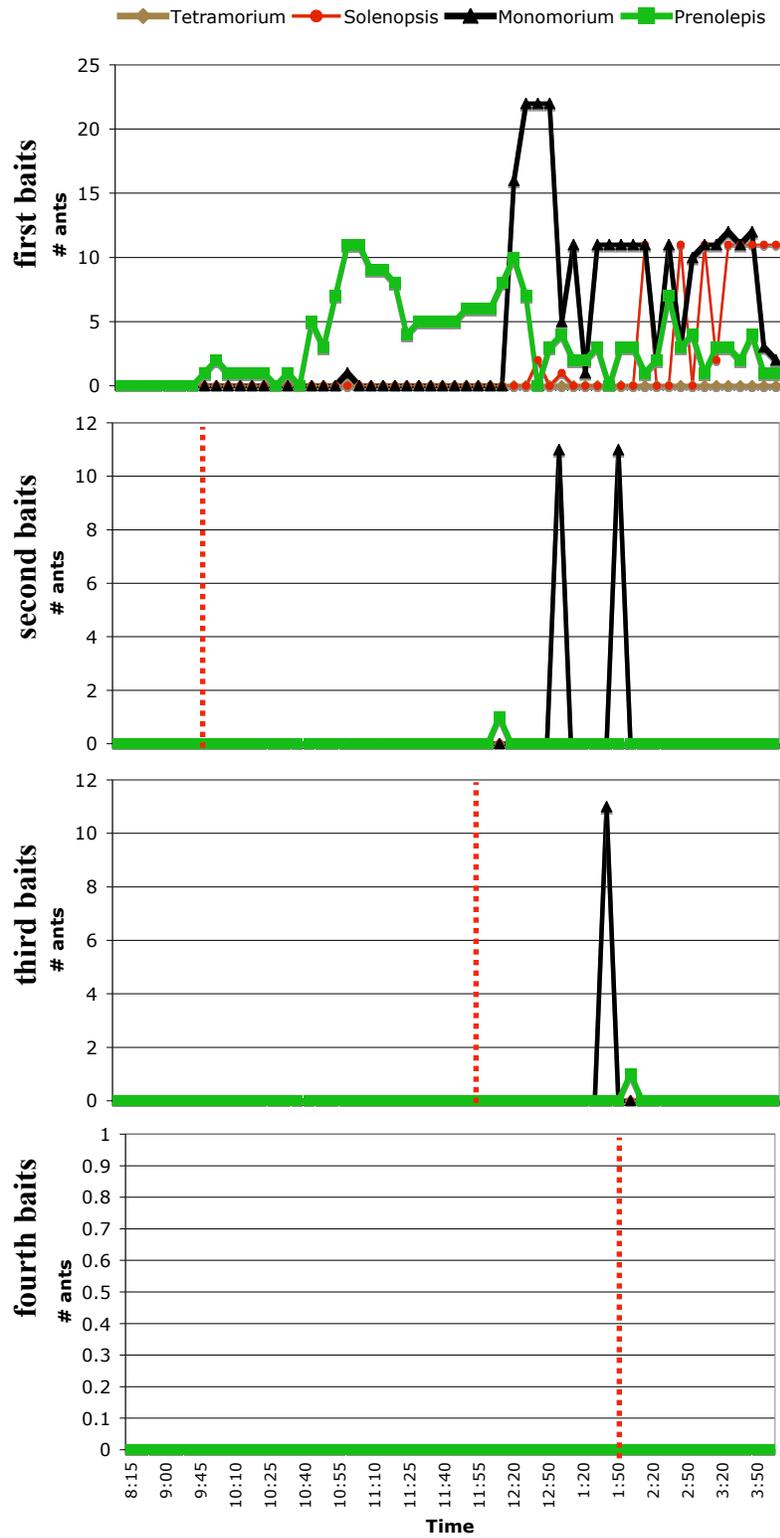


Figure 4. Ant abundances at the previously *T. caespitum*-dominated site for the baits placed at different times. The first baits were placed at 8:00 a.m., the second at 10:00 a.m., the third at 12:00, and the fourth at 2:00 p.m. Dashed lines indicate when the baits were placed.

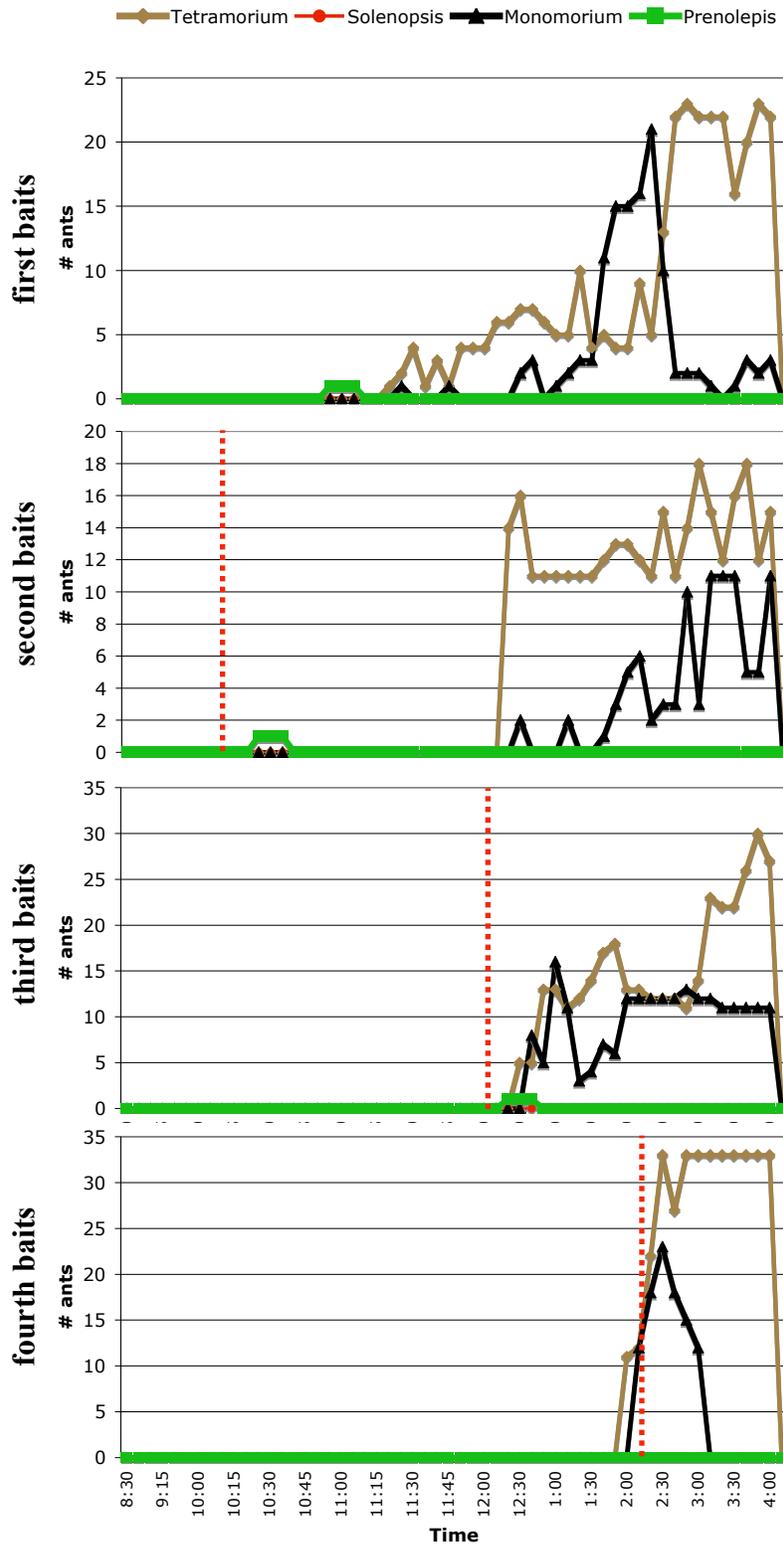


Figure 5. Ant abundances at the previously *S. molesta*-dominated site for the baits placed at different times. The first baits were placed at 8:00 a.m., the second at 10:00 a.m., the third at 12:00, and the fourth at 2:00 p.m. Dashed lines indicate when the baits were placed.

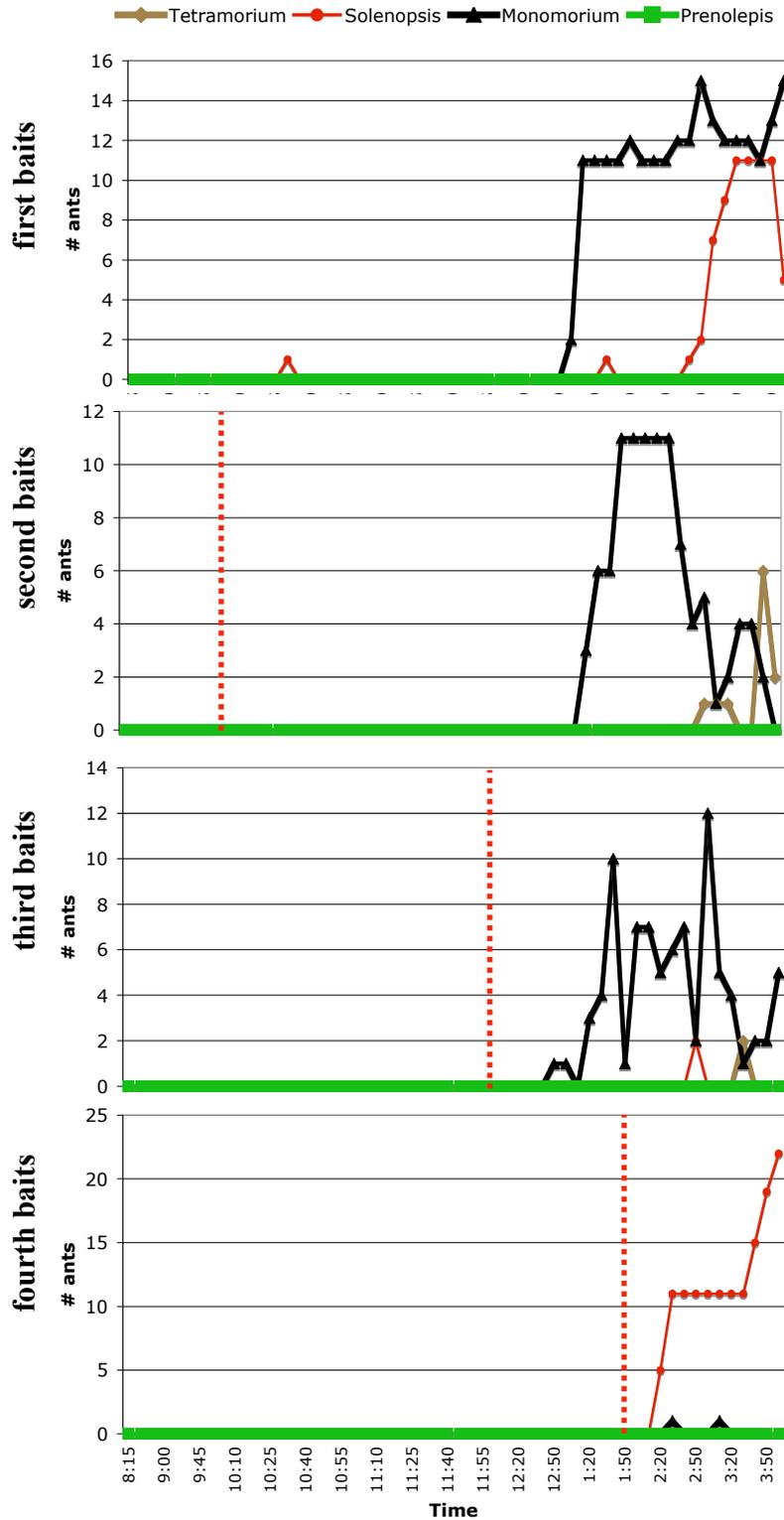
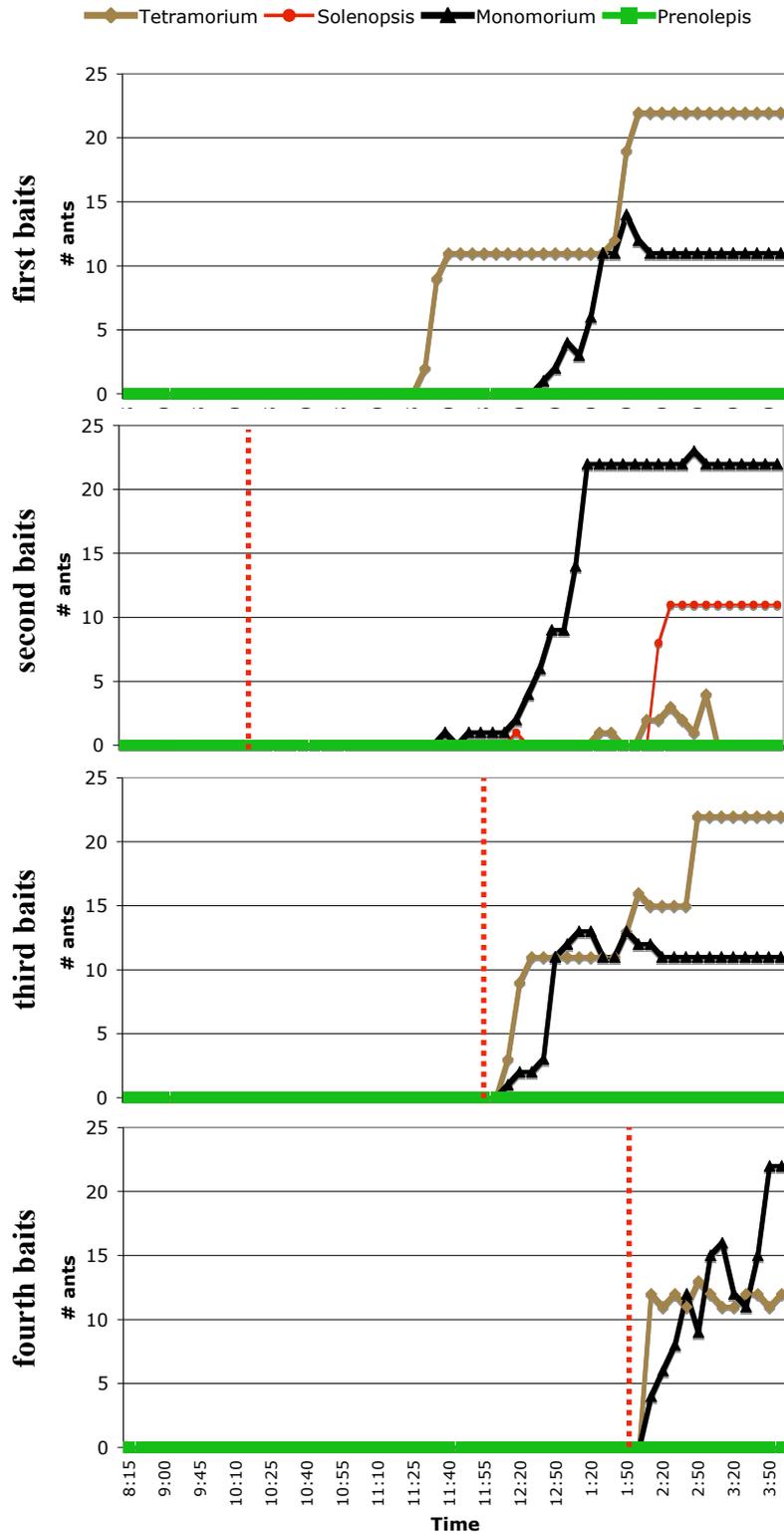


Figure 6. Ant abundances at the site previously contested by *T. caespitum* and *S. molesta* for the baits placed at different times. The first baits were placed at 8:00 a.m., the second at 10:00 a.m., the third at 12:00, and the fourth at 2:00 p.m. Dashed lines indicate when the baits were placed.



DISCUSSION

We observed that there was a general trend among all ant foragers to increase in abundance at each bait as temperatures increased throughout the day. Similarly, we found that with decreasing temperature ranges throughout the day, ant abundance at each site leveled off.

On a per individual basis, we found that *T. caespitum* and *M. minimum* showed greater foraging activity between temperatures of 20 and 30 degrees Celsius. However, *S. molesta* and *P. imparis* did not show any significant differences between temperature ranges. Thus, it may seem more likely that the underlying spatial patterns observed interact strongly with the optimum foraging ranges of *T. caespitum* and *M. minimum*.

The early appearance of *P. imparis* suggests that this species can forage at cooler temperatures than the other species, as had previously been observed by Talbot (1943). This cool-temperature foraging strategy may be a mechanism that allows *P. imparis* to coexist with the other dominant ants, which may be superior competitors.

Our results support the hypothesis that foraging is strongly affected by temperature or some other factor that is correlated with time of day. The general synchrony across sites in the arrival of the various ant species at the tuna baits strongly suggests that ants of a given species become active simultaneously across broad regions of the study plot. For example, *T. caespitum* began appearing at baits between approximately 11:20 a.m. and 12:00 noon at the baits in both the *T. caespitum*-dominated and the previously contested site (sites A and B, respectively, Figure 1, Figure 4, and Figure 6), while *M. minimum* became abundant at approximately 12:00 noon at all sites (Figures 3-6). *S. molesta* began to appear in significant numbers later in the day, at approximately 2:20 p.m. (Figures 3, 5, and 6).

Taking the combined results of this study and the studies by Jackson et al. (2008), MacDonald et al. (2008), and Chasen et al. (2008), it appears that the spatial distribution of ants in this system is the combined result of temperature, competitive interactions, and some underlying abiotic and biotic heterogeneity. *P. imparis* is able to forage at lower temperatures, and hence can exploit resources prior to the arrival of other ants. However, *P. imparis* is a relatively minor participant in this study area, so its influence on the spatial distributions of the three dominant ant species in the 96 X 22 m plot is probably negligible. The spatial distributions of *S. molesta* and *T. caespitum* are primarily determined by competitive interactions between these two species, as they competitively exclude each other (Jackson et al. 2008). However, depending on the temperature and time of day, either of these species may be excluded by *M. minimum*, which appears to forage at higher temperatures (or later in the day) based on the fact that *M. minimum* was more prevalent, and had taken baits over from *T. caespitum* and *S. molesta* by mid-afternoon in MacDonald et al. (2008). Although the results of MacDonald et al. (2008) are suggestive by themselves, the results of our study provide more substantial support for the idea that the afternoon increase in *M. minimum* was driven by temperature. While we did not observe the arrival of *M. minimum* to lag the arrival of the other ant species as was seen in MacDonald et al. (2008), the clear influence of temperature (or time of day) on the arrival of *M. minimum* demonstrates that it was not simply the time since the baits were placed that influenced the arrival of *M. minimum* observed in their study. In addition to all of these factors, Chasen et al.

(2008) showed that underlying environmental heterogeneity also influences the spatial distribution of ants in this system. Determining the relative strengths and nature of these different interactions is a clear direction for future research.

The combined results of this study and the previous work at this site (Chasen et al. 2008, Jackson et al. 2008, MacDonald et al. 2008) have revealed much about the competitive interactions and foraging behavior of the dominant ant species in this system. They have also provided a snapshot of the current distribution of ants in this location, which could provide valuable information for future studies as the invasion of the non-native species, *T. caespitum*, progresses.

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EFFECTS OF SCALE ON THE DETECTION OF SPATIAL DISTRIBUTIONS OF ANTS

DOUG JACKSON

ABSTRACT

A previous study of the spatial distribution of three ant species in a field at the E. S. George Reserve showed an exclusionary competitive interaction between *Tetramorium caespitum* and *Solenopsis molesta* and also revealed clump-size distributions that were approximately described by power laws with specific deviations. The robustness of these conclusions to reductions in the spatial scale of sampling was tested using surveys at two smaller spatial scales (0.5 m between tuna baits and 1 m between tuna baits versus a 2 m spacing used in the previous study). The qualitative results at these smaller spatial scales were unchanged from the results obtained in the larger-scale survey in terms of the exclusionary competitive interaction between *T. caespitum* and *S. molesta* and the general distributions of *T. caespitum*, *S. molesta*, and a third ant species, *Monomorium minimum*. The spatial distribution of ants was qualitatively similar at all 3 spatial scales, suggesting a fractal, or self-similar pattern; this result suggests that the approximate power-law scaling of clump-size distributions previously observed persists across, or extends to, the smaller spatial scales. The scale of experience of these ant species appears to be at or below the scale of the smallest-scale sampling (0.5 m between baits).

INTRODUCTION

The question of scale is of crucial importance in ecology. In his 1992 Robert H. MacArthur Award Lecture, Simon Levin stated that “[scale] is, I will argue, the fundamental conceptual problem in ecology, if not in all of science” (Levin 1992). The goal of science is to recognize patterns in the natural world and explain how those patterns are generated. A large proportion of the patterns in nature arise via processes that occur across multiple spatial scales. As just two of a myriad of possible examples, large-scale vegetation patterns (a patch-size distribution that follows a power law) in an arid environment can be explained by local interactions that occur at a smaller scale (Kéfi et al. 2007), and clusters of ant nests in a coffee agroecosystem are thought to be generated by local interactions between the ants and multiple associated organisms (Vandermeer et al. 2008).

Scale is important not only because it is a fundamental factor that determines how patterns emerge, but also because it is critical in terms of shaping our perceptions of these patterns. The sampling scale used in scientific investigations impacts whether or not a pattern will be detected and the nature of the patterns that are detected. According to Levin, “there is no single ‘correct’ scale on which to describe populations or ecosystems.” The appropriate scale to use when sampling depends on both the type of question being asked and the “scale of experience” of the organisms being studied. For example, habitat fragmentation at the scale of forests might be an

important component of a bird's environment, but may be unimportant from the perspective of a salamander living under a single dead log: the scale of experience of the bird and the salamander are very different, a fact that should be considered when studying these organisms.

In this study, the question of scale is investigated in relation to a previous study of the spatial distribution of foraging ants. Jackson et al. (2008) showed that the spatial distribution of foraging ants in a relatively homogeneous field showed clear competitive interactions between two of the dominant ant species in the system, *Tetramorium caespitum* (an introduced invasive from Europe) and *Solenopsis molesta*. In addition, the clump size distributions of these and the other dominant ant, *Monomorium minimum*, were used to gain inferences about the underlying processes shaping the ants' spatial distributions. However, since this study was only performed at a single spatial scale, it was unclear whether the results were robust to changes in scale. The competitive interaction between *T. caespitum* and *S. molesta*, in which they competitively excluded each other and created mutually exclusive spatial patterns, may have been an artifact of the spatial scale of sampling: what appeared as pure clumps of *T. caespitum* may have been shown to have interspersed patches of *S. molesta* had the sampling been done on a finer spatial scale. For the same reason, the observed deviation from a power law at large clump sizes for the clump size distribution of *T. caespitum* may have been a result of artificially combining multiple, smaller clumps into a single large clump (Jackson et al. 2008).

The goal of this study was to sample a portion of the region studied by Jackson et al. (2008) using finer sampling resolutions to determine the effects of scale on the results and to gain an understanding of the scale of experience of the ants in this system.

METHODS

Study site

This study was performed at the E.S. George Reserve in Livingston County, Michigan, in the same site used in Jackson et al. (2008). The site was located in a field where primary succession has progressed unhindered following the removal of topsoil in 1988. This site is a relatively homogenous environment with sparse vegetation, grasses, and shrubs.

Field experiment

Two subregions of the original 96 X 22 m plot used in Jackson et al. (2008) (Figure 1) were selected: one region that had been dominated primarily by *S. molesta* in the original large-scale sampling (Site A, Figure 2), and one that had been dominated by *T. caespitum* in the large-scale sampling (Site B, Figure 2). At each site, an initial survey was performed on October 11, 2008, (Day 1) using tuna baits that were placed in a 10 X 10 grid with 1 m spacing between baits. These surveys are represented by the larger squares in Figure 2. The following day (Day 2), a finer-scale survey was performed using a 10 X 10 grid of tuna baits with 0.5 m spacing.

On Day 1, the presence of foraging ants of the three dominant species (*M. minimum*, *T. caespitum*, and *S. molesta*) was recorded once following the placement of tuna baits. On Day 2, tuna baits were placed at 10:15 at Site A. An initial survey was performed at 11:15 a.m. and a

second survey was performed at 1:25 p.m. At Site B, baits were placed at 10:45 a.m., the initial survey was initiated at 11:45 a.m., and the second survey was performed starting at 2:00 p.m.

Figure 1. Presence of ants in the 96 X 22 m plot surveyed by Jackson et al. (2008). The plot on the left shows the location of workers of *M. minimum*. The plot on the right shows the location of the other two dominant species: diamonds represent presence of *T. caespitum* workers and circles represent the presence of *S. molesta* workers. From Jackson et al. (2008).

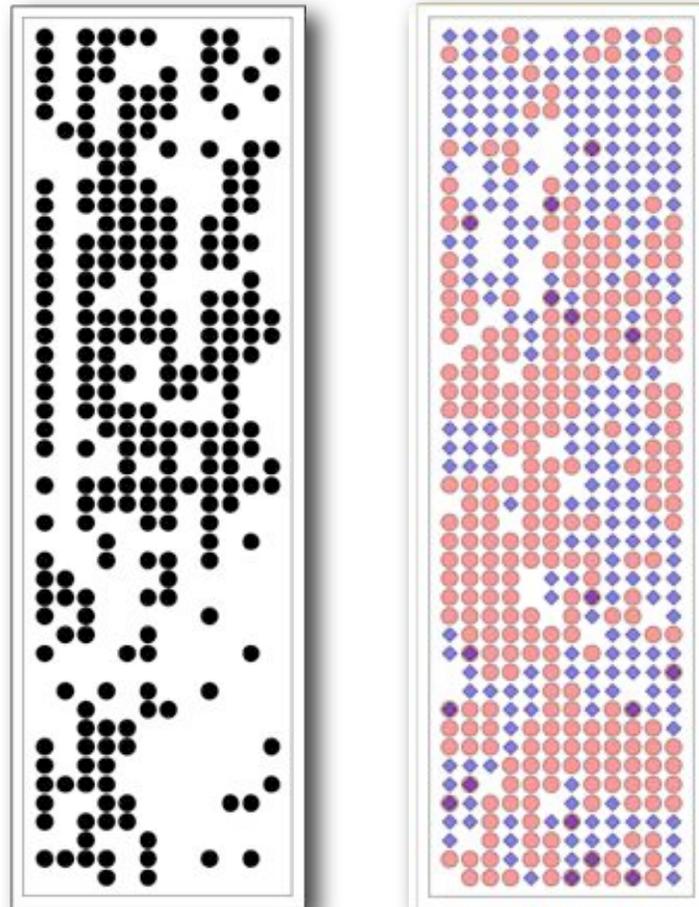
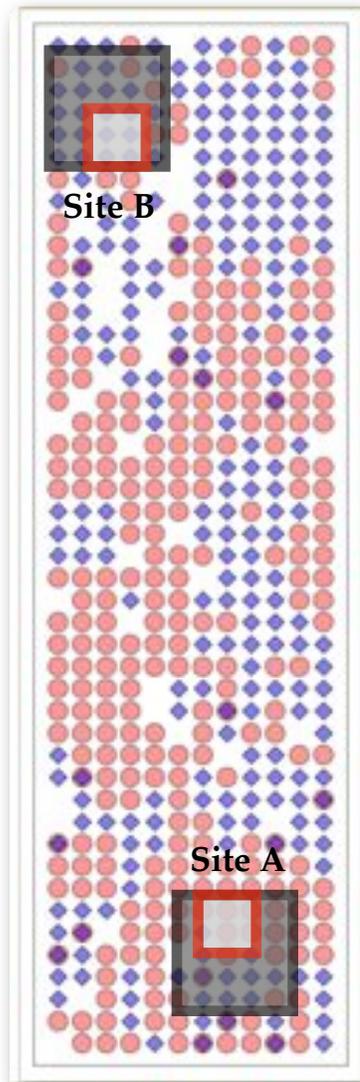


Figure 2. Location of study regions with respect to the 96 X 22 m used by Jackson et al. (2008). Large squares represent the locations of the medium-scale sampling (10 X 10 grid of samples at each site, 1 m spacing between samples); smaller squares represent the locations of the 100 baits used in the small-scale sampling (10 X 10 grid of samples at each site, 0.5 m spacing between samples).



RESULTS

The medium-scale survey at Site A performed on Day 1 was primarily dominated by *T. caespitum* and *M. minimum*, with *S. molesta* only recruiting to 3 out of 100 baits. At 50 of the baits, no ants were present. There was no overlap between *T. caespitum* and *S. molesta*. At two baits, both *T. caespitum* and *M. minimum* were present. *S. molesta* and *M. minimum* were collocated at one bait (Figure 3).

On Day 2, *S. molesta* was present at 10 out of 100 baits, *M. minimum* was present at one bait, and *T. caespitum* was present at 6 baits (Figure 4a). By the afternoon, *S. molesta*, *M. minimum*, and *T. caespitum* were present at 17, 12, and 14 baits, respectively (Figure 4b). In both the morning and afternoon surveys, there was little overlap between species. The combined results from Day 1 and Day 2 are shown in Figure 5.

Figure 3. Results from the medium-scale sampling (1 m between samples) performed on Day 1 at Site A. Empty diamonds indicate the presence of *T. caespitum* workers; large filled circles indicate the presence of *M. minimum* workers; and smaller filled circles indicate the presence of *S. molesta* workers. Axes are the x and y coordinates within the 96 X 22 m plot (in meters).

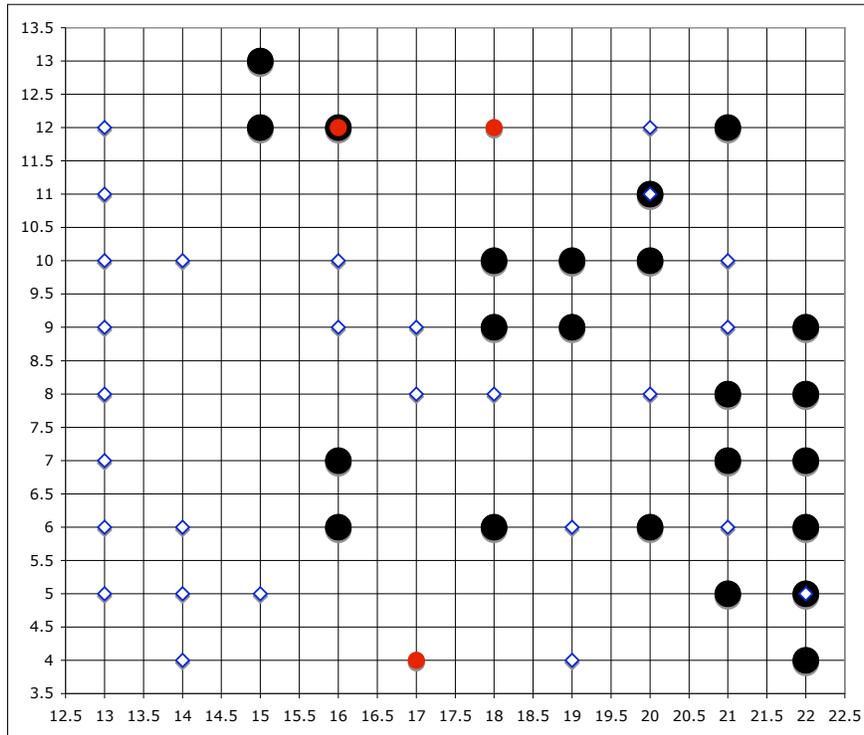


Figure 4. Results from the small-scale sampling (0.5 m between samples) performed on Day 2 at Site A. Results from the sampling started at 11:15 a.m. (a) and the sampling started at 1:25 p.m. (b) are shown. Empty diamonds indicate the presence of *T. caespitum* workers; large filled circles indicate the presence of *M. minimum* workers; and smaller filled circles indicate the presence of *S. molesta* workers. Axes are the x and y coordinates within the 96 X 22 m plot (in meters).

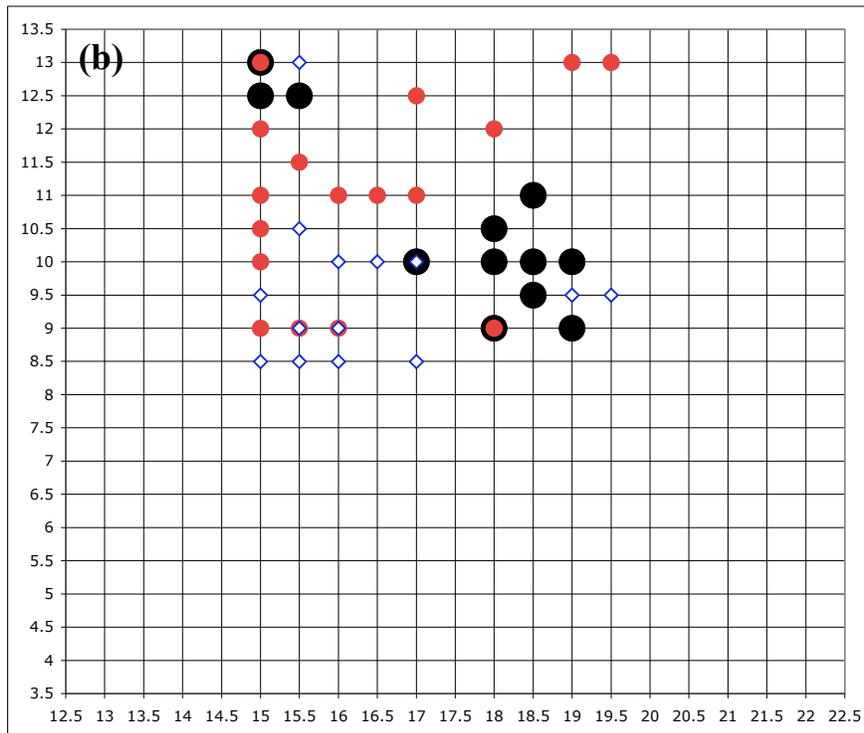
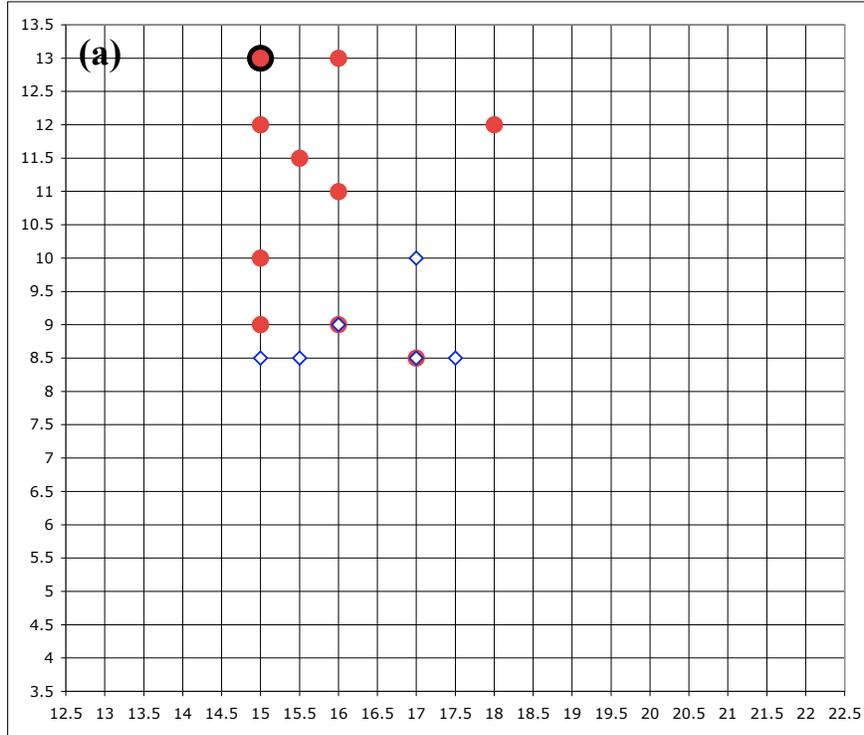
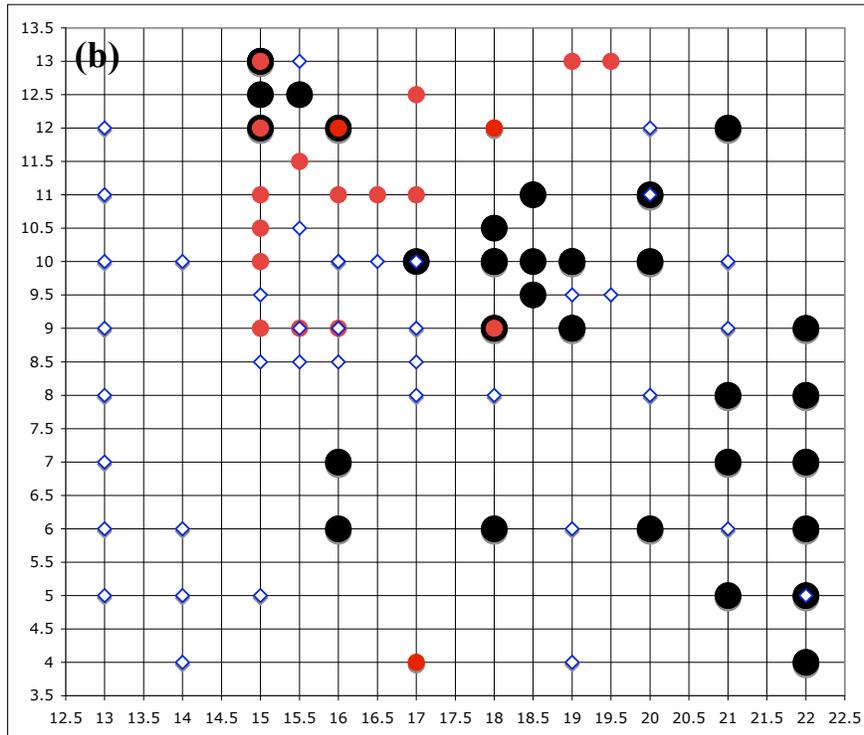
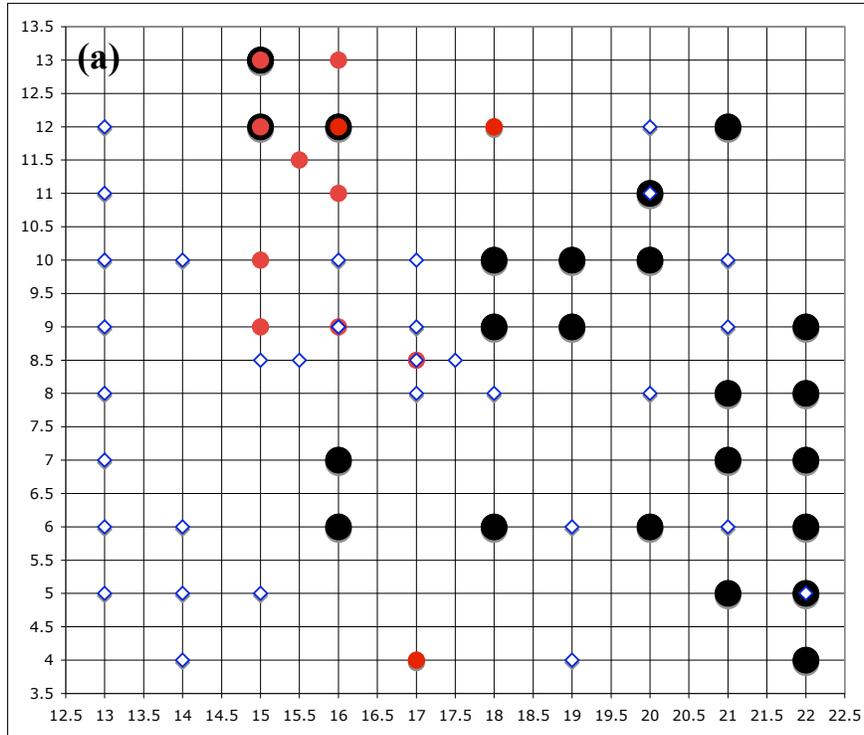


Figure 5. Results from the small-scale sampling (0.5 m between samples) performed on Day 2 at Site A overlaid on the results of the medium-scale sampling. Results from the sampling started at 11:15 a.m. (a) and the sampling started at 1:25 p.m. (b) are shown. Empty diamonds indicate the presence of *T. caespitum* workers; large filled circles indicate the presence of *M. minimum* workers; and smaller filled circles indicate the presence of *S. molesta* workers. Axes are the x and y coordinates within the 96 X 22 m plot (in meters).



The medium-scale survey at Site B was also dominated by *T. caespitum*, which occupied 55 out of 100 baits (Figure 6). *M. minimum* was also prevalent, occupying 35 out of 100 baits (Figure 6). *S. molesta* was distributed sparsely (4 out of 100 baits, Figure 6). There was some overlap between *T. caespitum* and *M. minimum* (12 sites) and between *S. molesta* and *M. minimum*, but no overlap between *S. molesta* and *T. caespitum*.

On Day 2, the morning and afternoon surveys exhibited similar patterns, with *T. caespitum* dominating the site, a few occurrences of *M. minimum*, and even fewer occurrences of *S. molesta* (Figure 7). Figure 8 shows the results from Day 2 overlaid with the results from Day 1.

Figure 6. Results from the medium-scale sampling (1 m between samples) performed on day 1 at Site B. Empty diamonds indicate the presence of *T. caespitum* workers; large filled circles indicate the presence of *M. minimum* workers; and smaller filled circles indicate the presence of *S. molesta* workers. Axes are the x and y coordinates within the 96 X 22 m plot (in meters).

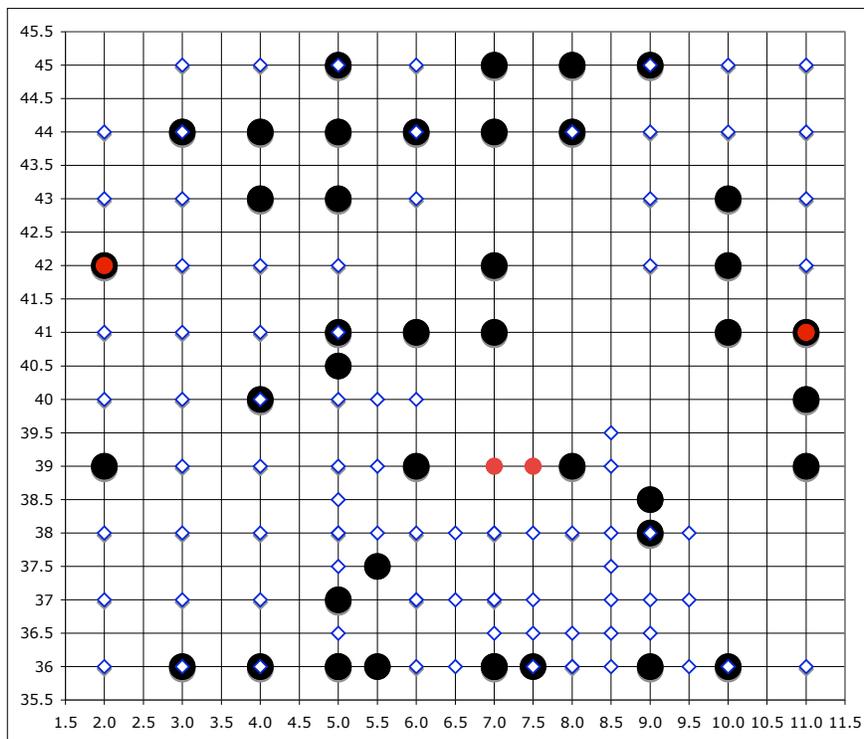


Figure 7. Results from the small-scale sampling (0.5 m between samples) performed on Day 2 at Site B. Results from the sampling started at 11:45 a.m. (a) and the sampling started at 2:00 p.m. (b) are shown. Empty diamonds indicate the presence of *T. caespitum* workers; large filled circles indicate the presence of *M. minimum* workers; and smaller filled circles indicate the presence of *S. molesta* workers. Axes are the x and y coordinates (in meters).

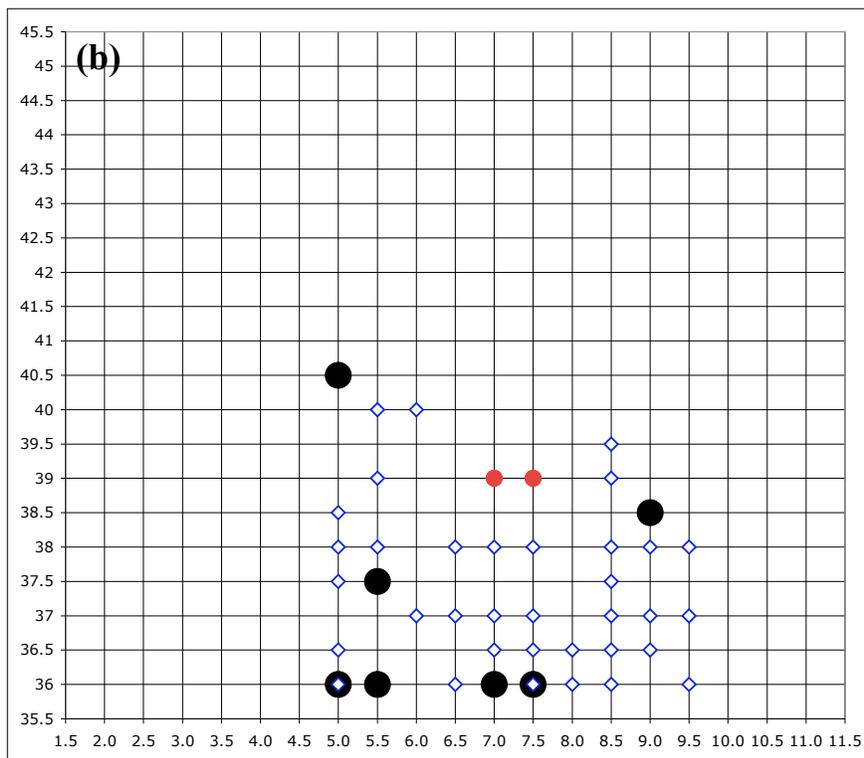
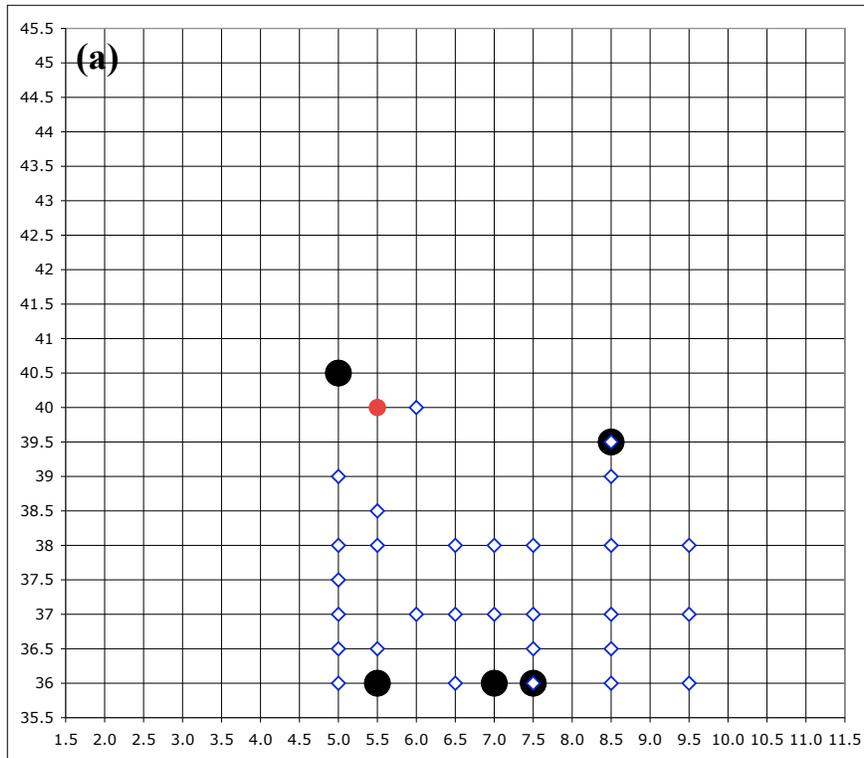
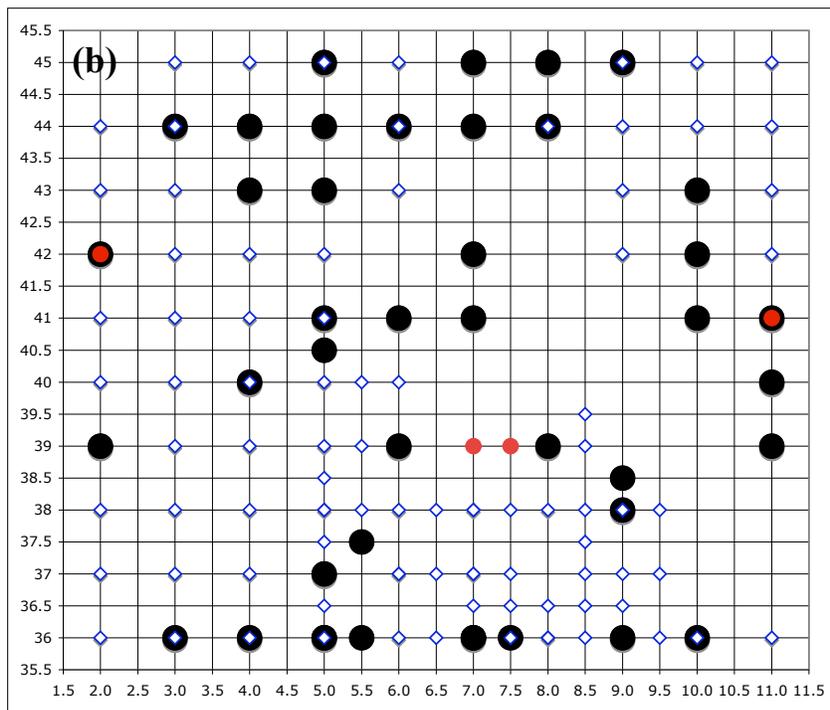
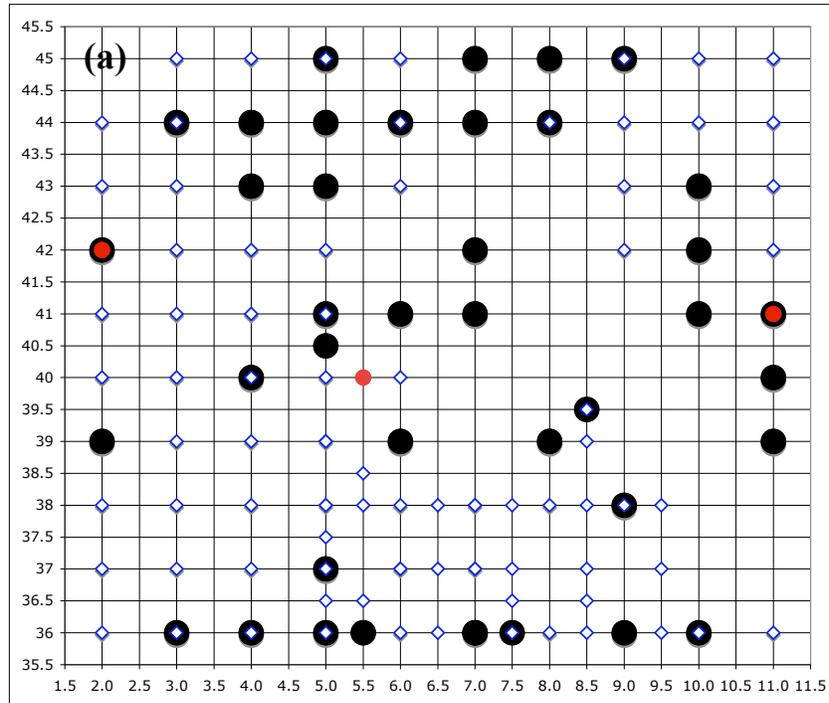


Figure 8. Results from the small-scale sampling (0.5 m between samples) performed on Day 2 at Site B overlaid on the results of the medium-scale sampling. Results from the sampling started at 11:45 a.m. (a) and the sampling started at 2:00 p.m. (b) are shown. Empty diamonds indicate the presence of *T. caespitum* workers; large filled circles indicate the presence of *M. minimum* workers; and smaller filled circles indicate the presence of *S. molesta* workers. Axes are the x and y coordinates within the 96 X 22 m plot (in meters).



DISCUSSION

The results from the medium-scale surveys (1 m between baits) and the smaller-scale surveys (0.5 m between baits) are largely concordant with the results obtained by Jackson et al. (2008) using 2 m bait spacing. The basic locations of the three ant species are similar to what was found in the previous study, with *T. caespitum* dominating Site B, *S. molesta* dominating the upper portion of Site A (at least in the survey performed on Day 2), *T. caespitum* dominating the bottom of Site A, and *M. minimum* being scattered without a clear relationship to the other species. The competitive interaction between *T. caespitum* and *S. molesta* is still apparent, with very little overlap occurring between these species compared to the amount of overlap between *T. caespitum* and *M. minimum*. These results indicate that the basic qualitative results obtained by Jackson et al. (2008) are relatively insensitive to sampling scale.

A suggestive, but as yet unsubstantiated, feature of the patterns that were apparent across the different spatial scales is that the pattern appears to be fractal, or self-similar, in nature. Fractal patterns look the same across multiple spatial scales, i.e., there is no natural scale at which to view the pattern. An example of this is the pattern of craters on the moon's surface. The moon is bombarded by particles from space that are of a range of sizes, so the surface of the moon has craters of a wide range of sizes. Therefore, it would be difficult to tell what the scale is of a photograph of the moon's surface (assuming that the photograph is framed tightly enough that nothing but the moon's surface is visible), as there is no way to readily discern what the actual size of any large craters in the photograph may be without any external reference (and likewise for smaller craters). A similar pattern can be seen when comparing the survey data taken at the large scale (Figure 1) to those taken at the smaller scales (Figures 5 and 8). In each case, there are multiple clumps of each species type, and the clumps are interdigitated. Without any external reference, it would be difficult to know if the plots are of the entire 96 X 22 m sample plot or of one of the smaller-scale plots. This sort of fractal pattern is closely related to the existence of power law scaling of clump-size distributions, but it goes beyond the results reported in Jackson et al. (2008) in that it suggests that the power law scaling observed at the larger scale (2 m spacing) extends to smaller spatial scales.

These results suggest that the scale of experience of the ants is no larger than, and is possibly smaller than, what can be resolved using the 0.5 m bait spacing. There is significant detail in the spatial distributions that is apparent at the finest sampling resolution that would be lost at coarser resolutions, which suggests that the ant colonies respond differently to two baits spaced 0.5 m apart than they would to one bait placed between these two locations. In other words, what is occurring at the scale of the 0.5 m-spaced baits alters the behavior of the ants, and therefore events at this spatial scale are clearly part of the scale of experience of the ants. From the perspective of an observer, then, additional information can be obtained by sampling at this finer scale.

Although changing the spatial scale of sampling in this study did not alter the qualitative results obtained by Jackson et al. (2008), these results are important in that they confirm our basic understanding of the competitive interaction between *T. caespitum* and *S. molesta* and the lack of a clear competitive relationship with *M. minimum* (but see MacDonald et al. 2008), as well as providing insight into the scale of experience of these ants. This information will provide

valuable background for future investigations as the invasion by the non-native species, *T. caespitum*, progresses.

ACKNOWLEDGEMENTS

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ANTS IN PLANTS AND ANTS IN SOIL, THE WORLD FROM AN ANTS EYE: THE ROLE OF EXOGENOUS FACTORS IN DETERMINING SPECIES DISTRIBUTIONS

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DAVE MARVIN, IVETTE PERFECTO

ABSTRACT

Patterns occur at all levels in nature. Many of these patterns, crystal structure, the spiral of a snail's shell, and the distribution of ant nests in a coffee plantation, for example have been proven to arise due to endogenous processes. In this project, we sought to examine whether exogenous factors were also playing a role in the observed spatial patterns of three ant species in an environment that was assumed homogeneous in previous studies. We found that both soil moisture and plant cover varied over the examined space. We observed patterns of ant distribution related to these factors. *S. molesta* were correlated with moister soils and both *T. caespitum* and *M. minimum* were found more frequently in drier soils. The only correlation with vegetation found was a negative relationship between *Rubus* and *T. caespitum*. These results highlight the importance of detailed measurement of environmental variables when searching for the causes of patterns in nature.

INTRODUCTION

The study of spatial patterns in natural systems is a large focus of the study of ecology. Finding patterns in nature and drawing conclusions as to the underlying mechanisms that explain them is the key to understanding and prediction of natural systems (Levin, 1992). Ecological patterns in space can be driven by exogenous or environmental cues including climate and topography, or soil moisture and vegetation cover, or they can be derived by endogenous factors like life history traits of individual species or species interactions. Many studies of observed patterns are completed on homogeneous landscapes so as to eliminate exogenous cues and to learn more about the endogenous factors (Possingham et al, 2005). For example, the arboreal ant species *Azteca instabilis* in Central America is found throughout the forests but any spatial patterns they create are driven by both the heterogeneity of the environment as well as their own life history and interspecific interactions. However, when they are found on a relatively homogeneous landscape such as the shade tree coffee plantation in Southern Mexico several underlying endogenous mechanisms of their non-random spatial distribution of nest-sites are elucidated such as interactions with parasitic phorid flies (Vandermeer et al, 2008).

Yet it is almost impossible to completely avoid the effects of a heterogeneous environment on spatial distribution of individual species. And it should be recognized that heterogeneity in the environment plays a very important role in species distribution, dispersal, and conservation (Fahrig et al, 2005 and Possingham et al, 2005) and because of this it should not be overlooked or avoided. Landscape heterogeneity is key to the

persistence of populations because it creates spatial patchiness providing sanctuaries for prey species (Fahrig et al, 2005). This theory was explicitly noted in the context of predator prey relationships but could be extrapolated to antagonistic relationships in which two species are competitively exclusive.

In this study we seek to understand the spatial distribution of three ant species in the E.S. George Reserve. This work is a continuation of a line of research at the E.S. George Reserve to determine the factors involved in the distribution of three dominant ant species in the field that is now called the ant field. The three ant species involved are *Monomorium minimum*, *Solenopsis molesta*, and *Tetramorium caespitum*. The first two ant species listed are native ant populations and the latter is an invasive species. Previous work done on the ant fields assumed the ant fields to be a homogenous environment due to the recent removal of the topsoil in 1988. Because of the assumptions about the homogeneity of the field, questions about ant distribution were directed towards endogenous factors such as competition between the three ant species (Jackson et al. 2008). The study saw that *S. molesta* and *T. caespitum* are exclusive and will not occupy the same location, while *M. minimum* is distributed randomly throughout the plot and does not appear to be competitive with either of the other two species. This study also determined that the distribution of *S. molesta* could be described by a power function, which means that this ant species exhibits a spatially constrained distribution. This constraint could be determined by competition with other ant species or by exogenous environmental cues, as we will be looking at in this paper.

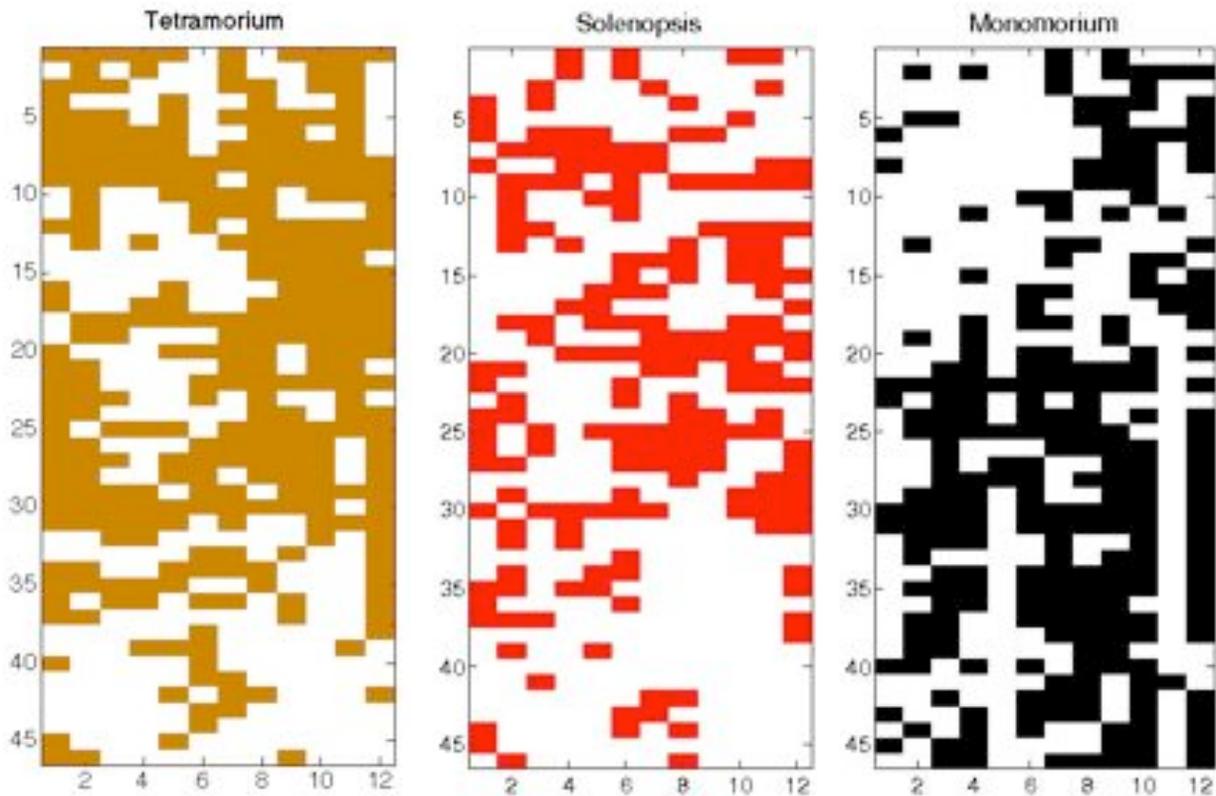
Using the distribution of ants as mapped by the Jackson et al. (2008) study we set out to determine if their distribution was solely a factor of competition or it was also dependent on exogenous factors such as vegetation and soil moisture.

METHODS

Study site

This study took place in the E.S. George Reserve in Livingston County, MI. Due to the series of studies on this particular system, the field has been titled the “ant field”. In 1988 the topsoil from this field was entirely removed and what we see there today is a field in a primary succession stage. A small hill, forested land, and experimental ponds border the ant field. The hill contributes to a small amount of topographical decline leading away from the hill. Here, a grid had been placed covering 92 X 22 meters with flags marking every 2 meters. Ant distribution in the fields had been previously mapped (figures 1a, 1b, 1c).

Figures 1a, 1b, and 1c respectively: 1a shows the spatial distribution in the ant fields of *T. caespitum* in tan. 1b shows the spatial distribution of *S. molesta* in red and 1c. shows distribution of *M. minimum* in black (Jackson et al, 2008).



Study design

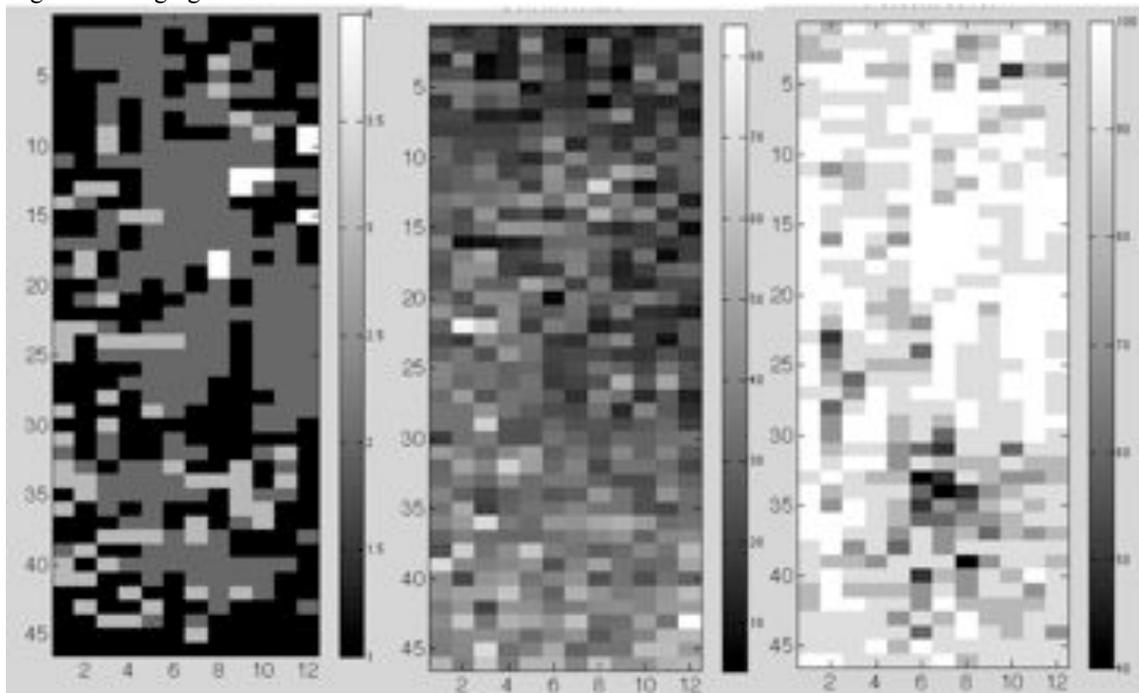
In order to determine vegetation cover, we grouped all vegetation into four categories: forbs, moss, grass and *Rubus*. The grass category was largely little blue stem (*Schyzachyrium scoparium*) and the *Rubus* was a trailing vine. At each flag we placed a 1 X 1 meter quadrant to the northwest and noted the two most dominant vegetation covers as well as the presence of any woody plants (*Eleagnus umbellata*, or *Rubus*). In each of those quadrants we also estimated by 10s the percent cover of vegetation. In the center of each quadrant soil moisture data was taken with a probe.

Previous ant distribution data (MacDonald et al. 2008) and only the most dominant vegetation type were used in our analysis. We compared vegetation type (Figure 2a) to soil moisture (Figure 2b), and then calculated differences in average soil moisture for each ant species. The likelihood that each ant species is associated with a particular vegetation type was found by comparing the expected and observed probabilities of each association. The dataset was then resampled 100,000 times based on the expected association probability, and the probability (reported p-values) that the observed association occurred more often than by chance was calculated.

RESULTS

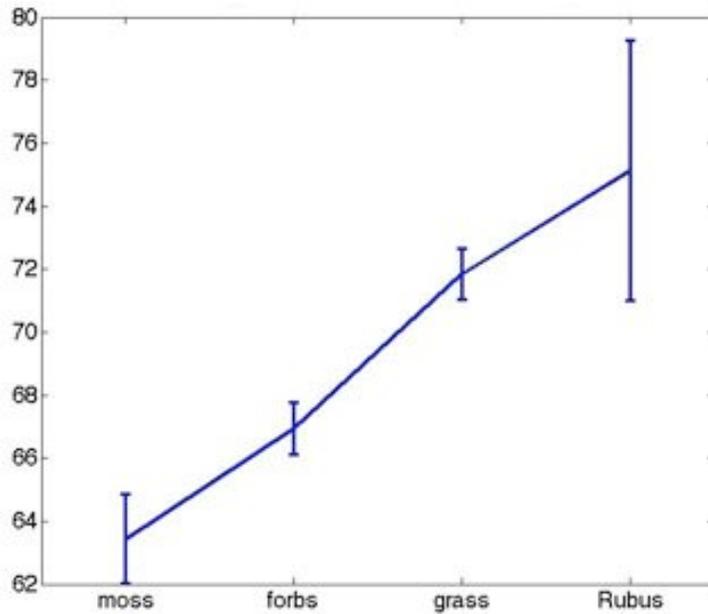
Grass was found to be the most frequently occurring dominant vegetation type (45.4%), followed by forbs (42.5%), moss (11.4%), and *Rubus* (0.9%). Soil moisture ranged from 16-96% with a mean of 68.15%. *M. minimum* was present across 36.9% of the study area, *T. caespitum* was present in 35.6%, and *S. molesta* in 27.5%.

Figure 2: Vegetation cover, soil moisture, and percent vegetation cover on the ant fields respectively. In 2a, areas shown in darker grey are dominated by grass. Areas shown in black represent those dominated by forbs, white is *Rubus* and light grey is moss. In 2b, white shows the wettest soils and black shows the driest with shades of grey for intermediate soil moisture. 2c shows percent cover where white is 100% covered by vegetation ranging to 40% cover in black.



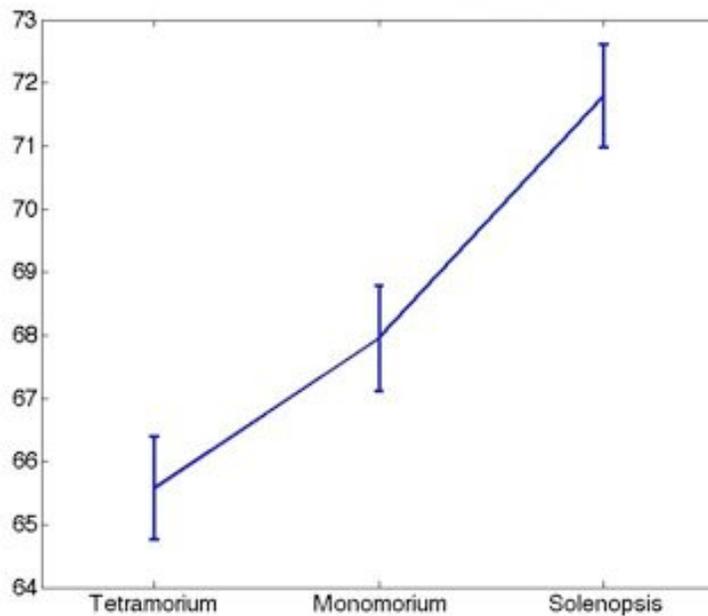
There was a significant difference between soil moisture and vegetation cover as measured by a one-way ANOVA, $F(3,695)=18.804$, $p<0.001$. A Hochbergs GT2 post-hoc test found that all vegetation types significantly differed in their soil moisture percentage (grass and forbs $p<0.001$, *Rubus* and forbs $p=0.015$, grass and moss $p<0.001$, *Rubus* and moss $p=0.006$) except for two combinations (*Rubus* and grass $p=0.355$, forbs and moss $p=0.812$). Both *Rubus* and grass were found in areas with higher soil moisture content, while forbs and moss were found on relatively drier soils (Figure 3).

Figure 3: Percent soil moisture (y axis) and dominant vegetation cover (x axis). Bars represent +/- 1 standard error.



The average soil moisture for each ant species (Figure 4) differed significantly as determined by a one-way ANOVA, $F(2,696)=13.026$, $p<0.001$. A post-hoc Gabriels Test found a significant difference in soil moisture between *S. molesta* and *M. minimum* ($p=0.005$) and between *S. molesta* and *T. caespitum* ($p<0.001$). There was no significant difference between *T. caespitum* and *M. minimum* in soil moisture content.

Figure 4: Percent soil moisture and ant species. Bars represent +/- 1 standard error.



The probability that a species of ant was associated with a particular vegetation type was calculated. There was no significant association between *S. molesta* and grass ($p=0.1835$), which was unexpected because both grass (Figure 3) and *S. molesta* (Figure 4) prefer soil with higher moisture content. Because *Rubus* and grass were both present in soils with higher moisture we decided to look at both of those vegetation types together with the distribution of ant species. However, there was no significant association found ($p=0.4039$).

We did see a significant association between *T. caespitum* and *Rubus* ($p=0.0271$) which elucidated the fact that *T. caespitum* is extremely unlikely to be found in *Rubus*. However, because *Rubus* is a low-lying ground cover that can often be hidden from view by taller plants, its abundance in a given location can easily be underestimated. Therefore, to look deeper into this connection we ran the *T. caespitum* and *Rubus* resampling again with *Rubus* as both the dominant and sub-dominant vegetation cover. This resulted in a higher significant association ($p=3.10E-04$) than before. There were no other significant associations between ant species and vegetation types.

DISCUSSION

The range of soil moisture and vegetation cover show that this field exhibits heterogeneity, contributing to the observed ant distribution in the field.

We observed in the ant fields that soil moisture and vegetation cover were strongly correlated which is unsurprising: soil moisture is a determining factor in plant species communities. We saw that grass and *Rubus* did not show a significant difference in soil moisture and both grow in the moister soils.

As shown in figure 4, the heterogeneity in the soil moisture contributed to ant distribution, which means that competition is not the only factor determining ant distribution. We see *S. molesta* preferring moister soils and both *T. caespitum* and *M. minimum* preferring drier soils. Even though *S. molesta* shows a preference for moister soils and these soils are correlated with the presence of grass, we did not see a trend between grass and *S. molesta*. However, by examining the figures, it appears as though *S. molesta* is associated with grass as dominant vegetation, which would make sense because *S. molesta* does show a preference for moister soils (figure 4), which is where grass is more likely to be growing (figure 3). The lack of statistical trend between *S. molesta* and grass could be due to the survey method in which we noted the two most dominant plant species. This was often times a judgment call as the two most dominant vegetation types were sometimes hard to determine which was more dominant. Our survey method did not take into account presence of any vegetation that was not dominant or woody either.

We did see that *T. caespitum* was extremely unlikely to be found anywhere that *Rubus* was found. This also makes sense when we look at the other analyses that show *Rubus* growing in soils with higher moisture content (Figure 3) and *T. caespitum* favoring drier soils (Figure 4). This could also be due to the fact that *Rubus* is more likely growing in moist soils and *S. molesta* is more likely found in moister soils and the two ant species have been documented as competitively exclusive (Jackson et al, 2008). It will be very

difficult to pull the variables apart in a field experiment and will likely need some sort of laboratory set up in order to control for more variables at a time.

If we see that *Rubus* is indeed excluding *T. caespitum* it may have various ecological implications. *Rubus* is sprawling into the field from the forested side and as succession on this field progresses we will likely see an increase in *Rubus* cover. *T. caespitum* is an invasive species and is currently possibly out-competing *S. molesta* (MacDonald, 2008). Because ants perform very important ecosystem functions such as soil aerations, seed dispersal, and sometimes pollinators, it is important to determine the relationship between *Rubus* and *T. caespitum*.

Since our results did show that the ant field is not spatially homogeneous it makes sense that the heterogeneity would contribute to the determination of ant distribution. What originally appeared homogeneous to our human eyes may, in the eyes of ants be quite heterogeneous. Fahrig et al (2005) noted that each species observes its own environment in different scales of space and time. Fahrig et al also argue the idea that no single mechanism can explain all spatial patterns observed and that a two-scale model will prove more accurate than one. It is clear from past experiments on the ant field that there are endogenous factors contributing to ant distribution (Jackson et al, 2008 and MacDonald et al, 2008) but it is also clear from the work we did that exogenous factors are also contributing to their distribution.

Considering that two of our species, *S. molesta* and *T. caespitum* are competitively exclusive (Jackson 2008), different landscape covers and patchiness may enhance species coexistence (Fahrig 2005). If we see our field as a grid of suitable habitat or non-habitat for each ant species, we can imagine that certain grids become barriers depending on the ant species. For example, if *T. caespitum* is excluded by *Rubus* as our results suggest than as the *Rubus* spreads throughout the field, this habitat may become a barrier for *T. caespitum* to forage and obtain food.

In the future, we recommend a lab experiment in order to determine whether the reason *T. caespitum* is not found with *Rubus* is due to the presence of *S. molesta*, soil moisture, or the plant itself. We also recommend re-looking at the ant fields and surveying the vegetation in finer detail, taking into account presence of all plant species. It would also be interesting to determine the vegetation cover of the entire plot. Our methods only encapsulated one quarter of the plot by using a 1 X 1 meter quadrant in 2 X 2 meter grids.

Also, mealy bugs have been documented to be present on grass roots and *S. molesta* is known to tend to these bugs so it would also be interesting to survey the grass roots in the area for these mealy bugs to see if they are determining the distribution of *S. molesta*.

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HOURGLASS ISLAND: AN EXCEPTION TO THE RED MAPLE PARADOX

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ABSTRACT

The red maple paradox is a phenomenon of transition in northern American forests. In forests traditionally dominated by hardwood species such as oak, the subcanopy is increasingly populated by red maple. This project sought to examine white oak regeneration in the absence of red maple. We found that without competition from red maple, white oak can regenerate under a range of conditions, including highly variable amounts of canopy cover. We found no significant difference between the growth rates of white oaks in a large plot with red maple and those in another plot lacking red maple.

INTRODUCTION

Across eastern North America, forests are undergoing a successional shift in canopy and understory species composition. Oak (*Quercus*) forests, once dominant in the northeastern United States, are being replaced by more opportunistic trees better suited to understory conditions (Abrams 1992, 1998). The most successful of these opportunistic trees is the red maple (*Acer Rubrum*). A species once confined to swampy areas pre-European settlement, the red maple has come to dominate the understory and sub-canopy of historically hardwood forests. As large hardwood trees continue to fall, the ubiquity of red maple in both the understory and overstory is expected to further increase, with possible repercussions on forest ‘value’ and forest dwelling communities (Rubbo & Kiesecker 2004, Mcshea 2006).

Changes in land use practices combined with certain ecological characteristics of both oaks and red maple have contributed to the transition seen throughout eastern forests. Factors such as increases in acorn predator populations combined with selective logging of mature oaks significantly reduced oak regeneration (Abrams 1998). However, the most critical factor resulting in the widespread disappearance of oaks has been post-European settlement fire suppression (Abrams 1992, 1998). Periodic burning eliminated red maple saplings ultimately confining the species to swamp areas which allowed the more fire tolerant oaks to dominate and regenerate (Abrams 1992, 2003). As a result of fire suppression practices, the shade tolerant, “super-generalist” red maple (Abrams 1998) has outcompeted oak species and come to dominate the understory of closed canopy oak forests. Moreover, the initial colonization of the understory and sub-canopy by red maple resulted in an increase in foliage density further reducing the competitive ability of shade intolerant oaks.

Though the relationship between historic oak savannas, systematic burning, and red maple colonization is well documented (Dyer 2006, Fei and Steiner 2007), few studies have attempted to disentangle oak regeneration capabilities from red maple competition. Thus, we sought to determine whether oaks can regenerate under a closed oak canopy in the absence of

both periodic fire and red maple competition. Hourglass Island in the E.S. George Reserve offers an ideal setting to address this question as previous surveys have found few red maples establishing under the oak and cherry dominated canopy of the island.

METHODS

Data Collection

On September 14, 2008, the tree community on the north lobe of Hourglass Island at the E.S. George Reserve was surveyed. Hourglass Island is comprised of two lobes and separated from the mainland of the E.S. George Reserve by a swamp. The primary canopy tree species on Hourglass Island include white oak (*Quercus alba*), black oak (*Quercus velutina*), and black cherry (*Prunus serotina*). Five transects established in 2007 in a 50 m _ 50 m plot were identified and re-surveyed. Each transect was 10 meters wide and 50 meters long. In the survey of 2007, any woody vegetation with a circumference greater than 10 cm at 1.3 meters from the ground was assigned a unique number by nailing aluminum tags to the trunk at breast height, tree species and x and y coordinates were recorded, circumference at breast height (CBH) of each tree was measured by using tailor tapes. In our survey, we re-measured the CBH of every tagged tree by using the same method and recorded abnormal changes (e.g. missing, falling, etc.).

In order to investigate how canopy cover affects the growth rate of little oak trees, we also measured the canopy cover percentage by using a vertical densitometer. Thirteen little oak trees were selected randomly from the 5 transects. Two observers each took four data points outside of each small oak's canopy, compared the image in densitometer and the standard canopy cover table, then estimated the canopy cover percentage. The average value from all eight readings was recorded as the canopy cover of the tree.

Analysis

All data were analyzed using Microsoft Excel 2003. Relative growth rate (RGR) was calculated by: $(CBH_{2008}-CBH_{2007})/CBH_{2007}$. Trees were mapped by graphing x- and y- coordinates, CBH of each tree were represented by bubble size and tree species were represented by different colors. The distribution of all small white oaks (CBH under 50 cm) within the plot was also mapped.

The estimated canopy cover around the 13 randomly selected little white oaks was plotted against their RGR. The linear trend line was generated and the linear correlation coefficient was calculated.

RESULTS

Ten tree species were documented during a 2007 survey of the north lobe of Hourglass Island. These species were measured again during our survey. The canopy of the surveyed area

was composed primarily of white oak (*Quercus alba*), black oak (*Quercus velutina*), and black cherry (*Prunus serotina*). The understory of the surveyed area was composed of small white oak trees and the invasive plant, autumn olive (*Elaeagnus umbellata*). Also present in small numbers were witch hazel (*Hammamelis virginiana*) and common serviceberry (*Amelanchier arborea*). Sassafras (*Sassafras albidum*) was present but limited to the edge of the plot near the swamp. Single individuals of american elm (*Ulmus americana*) and black walnut (*Juglans nigra*) were found (Figure 1 and Figure 2).

The relative growth rates of small white oaks did not vary spatially and thus did not exhibit dependence on spatially varying environmental factors. A seemingly random distribution of growth rates was observed (Figure 3). Canopy measurements around thirteen small white oaks did not reveal any significant influence of canopy coverage on relative growth rate (Figure 4). We extrapolated five year relative growth rates for white oaks on Hourglass Island in order to compare the average growth rate to relative growth rates of white oaks growing in the big plot, in the presence of maples. Due to high variance within the measurements on Hourglass Island, a seemingly large difference was not statistically significant (Figure 5).

Figure 1. Species composition and distribution of the North Lobe of Hourglass Island. Circle size is proportional to circumference at breast height.

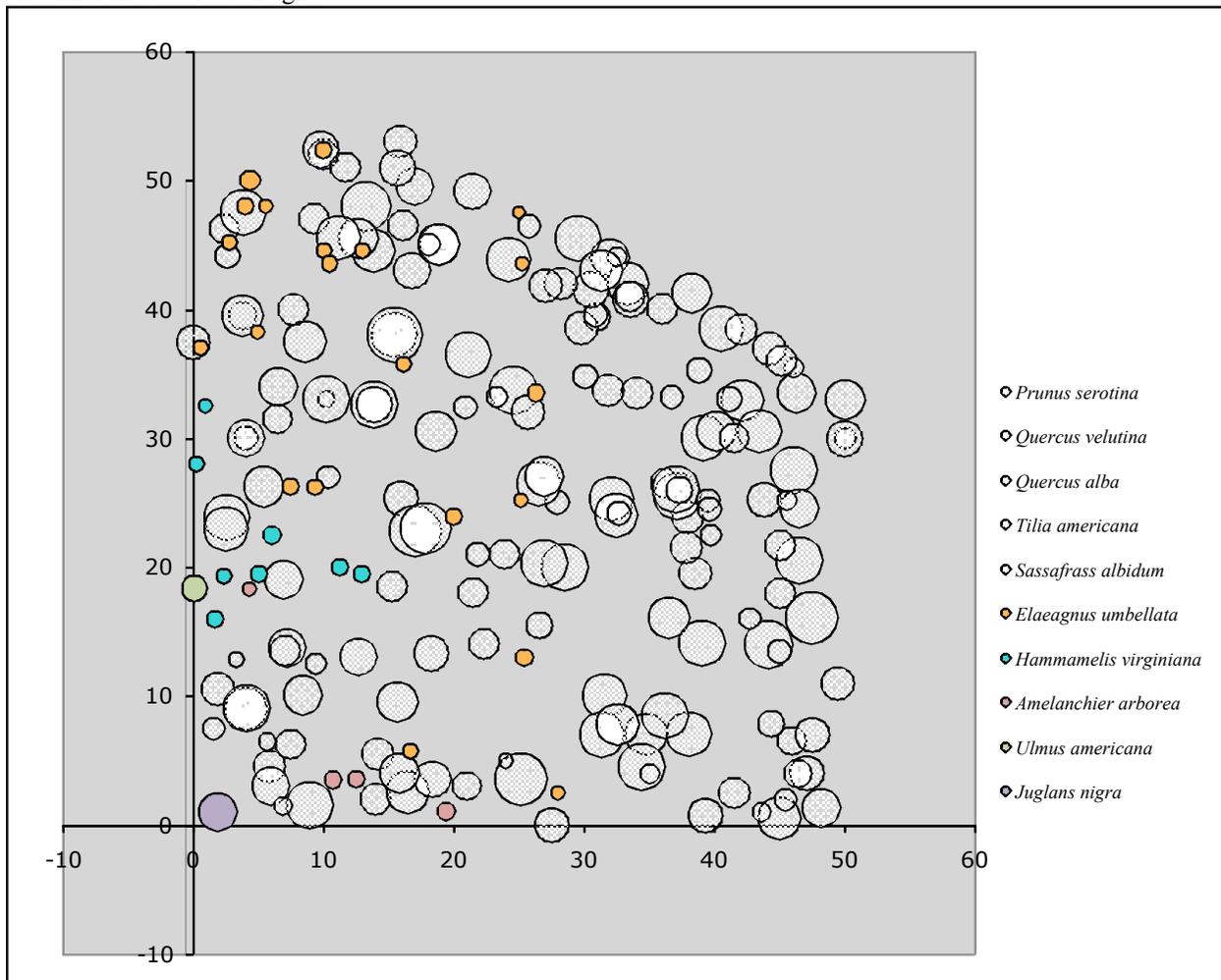


Figure 2. Percent of canopy and subcanopy occupied by each of the ten species surveyed. Canopy individuals were those 50 cm cbh or over and subcanopy individuals were those under 50cm cbh.

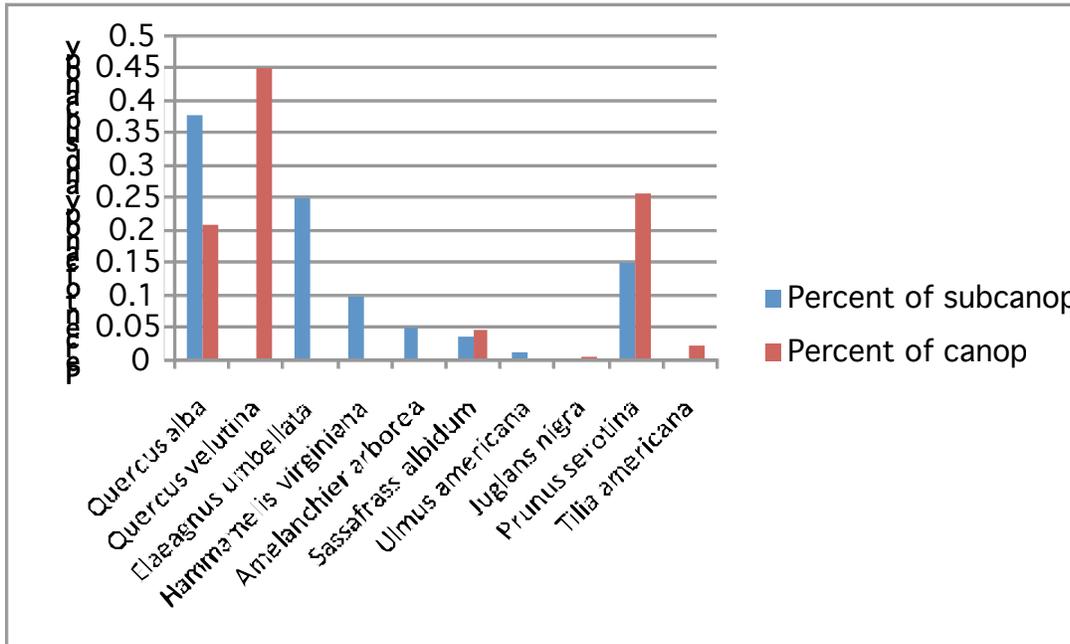


Figure 3. Relative growth rates of white oaks under 50cm cbh. Growth rates do not exhibit dependence on location specific factors such as nearness to the swamp. Figure does not include small white oaks from transect three due to missing data from 2007.

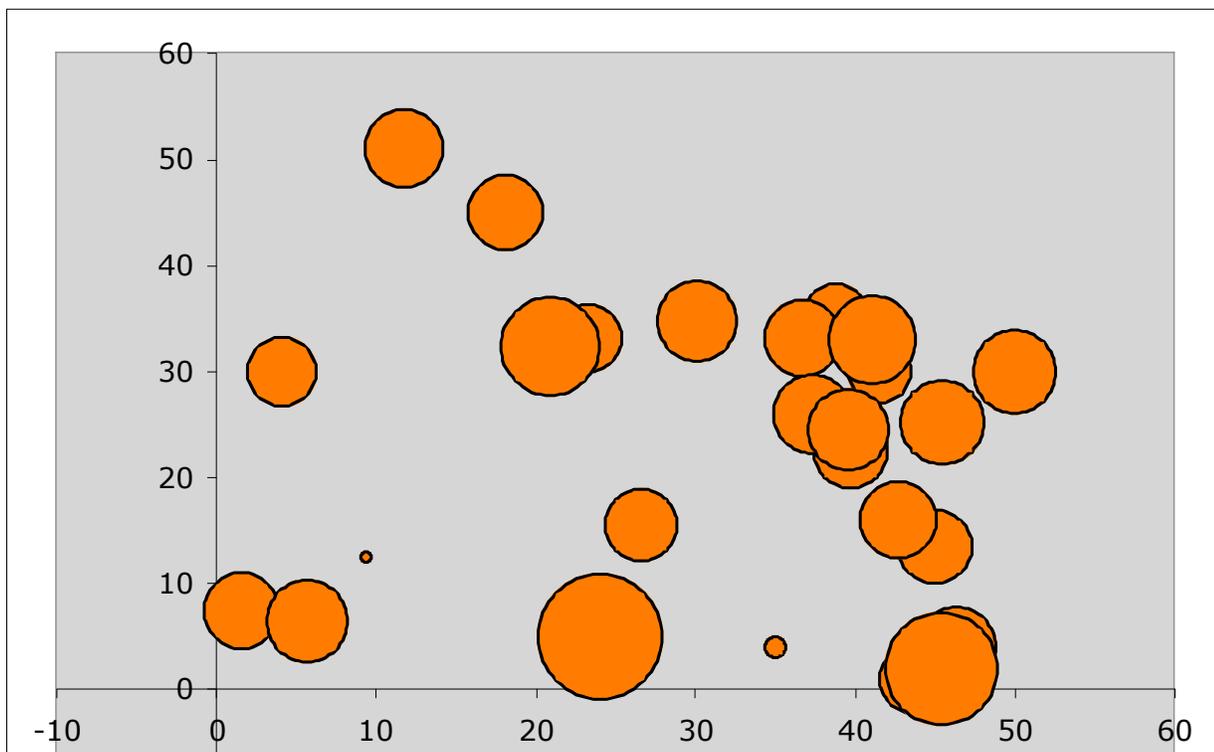


Figure 4. The relative growth rates of thirteen small white oaks did not vary significantly with the percentage of canopy cover under which they were growing.

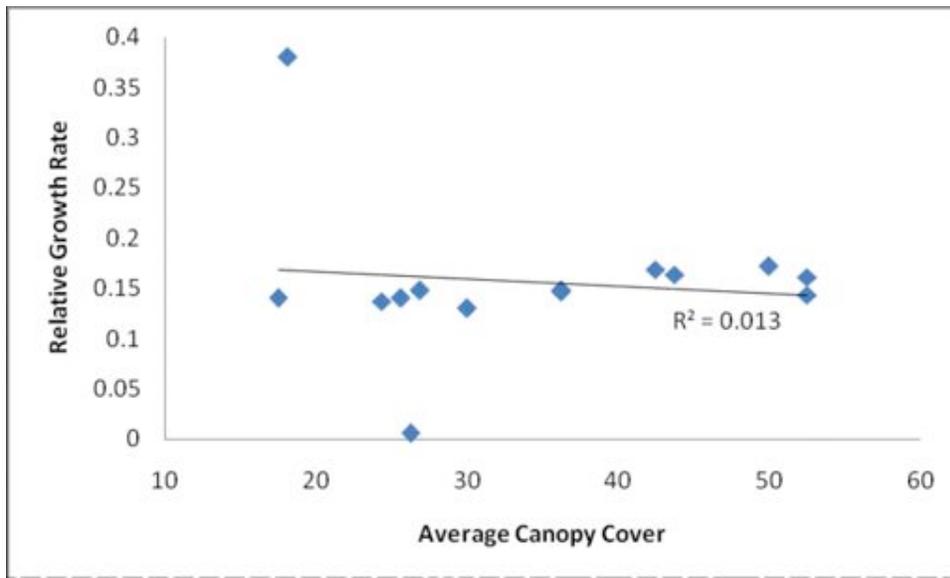
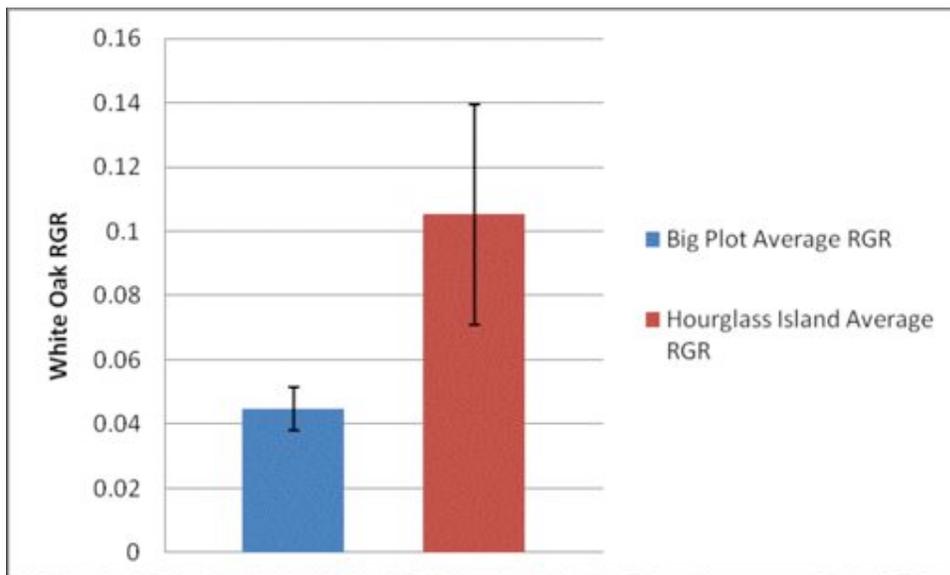


Figure 5. The average small white oak relative growth rates between small white oaks in the big plot and small white oaks on Hourglass Island were not significantly different (Student's T-test, unpaired, $p=0.12$). The high standard error in the plot on Hourglass Island demonstrated by the error bars eliminated any statistical difference between the two sets of data.



DISCUSSION

Our study demonstrated that white oaks were the primary canopy species regenerating in the absence of red maples on the north lobe of Hourglass Island. Although large black oaks were present, we found a greater abundance of white oak seedlings in the under-story. This result confirms that the dominance of white oaks is related to the high density of oak seedlings that enables under-story of small white oaks to become established (Runkle, 2005).

We found no significant correlations between the locations and relative growth rates of white oaks, demonstrating that abiotic conditions (e.g. water) did not play an important factor. There is strong evidence that eco-physiological properties of white oaks allow it to persist during drought periods (Abrams 2003). Long-term studies of climate change and relative growth rates of white oak species could confirm whether white oaks species are more tolerant to drought periods than other species. We also found no significant relation between small white oak growth rate and canopy cover, suggesting that even without a significant gap in the canopy, white oak may be capable of regenerating when red maple is not present. The average growth rates among white oaks in the big plot were not significantly slower than those of white oaks on Hourglass Island. This indicates that many abiotic factors suggested to account for the difference in demography of the two plots are not actually affecting oak growth.

While red maples were the dominant subcanopy species found on the main island (Big Plot), they remained largely absent from the north lobe of Hourglass Island. Three red maple species were found on the periphery of the island (John Vandermeer and Ashley, personal communication.) Although there is a seed source for red maples, seedling establishment appears to be limited. Dense ground cover might limit red maple recruitment if said ground cover were to differentially impact establishment of oaks and maples. The commonly found *Vaccinium Angustifolium* (low blue berry species) might be one such limiting factor for the recruitment of red maples due to toxic release in the soil (USDA 2008).

Hourglass Island seems to provide a snapshot of how white oak regeneration might occur if red maple were not present. White oaks are successfully establishing under a wide range of canopy cover in areas with varying access to water. Further investigation is needed to determine why red maples which are present on the south lobe of Hourglass Island have not yet colonized the north lobe of the island. It may be only a matter of time before the white oaks of the north lobe of Hourglass Island fall victim to the red maple paradox.

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USING FUNCTIONAL TRAITS AS A PREDICTOR OF FOREST COMMUNITY COEXISTENCE

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ABSTRACT

Theoretical ecologists develop demographic models as a means of predicting tree species coexistence in forest communities. Such models are limiting in that life history traits such as mortality, fecundity, and growth rate require large, long-term data sets. A current focus attempts to create criteria for plant community coexistence based on functional traits such as specific leaf area. We applied a demographic model of Adams *et al.* (2007) to a community of tree species in Southeast Michigan, using functional traits as proxies for demographic characteristics. The Adams *et al.* model evaluates community dynamics based on species competition for light. We modified the model by making many demographic traits constant across species, and looked at whether the remaining varying traits were able to predict coexistence. Specifically, we considered coexistence by examining the specific leaf area of six tree species as a function of crown transmissivity. Results predict stable coexistence between hickory and red maple at medium light, and stable coexistence between Black Cherry and Red Maple at low light. While our model is limited in its applicability to natural systems, our results offer valuable insights into the limits of the Adams *et al.* model and provides a basis for the creation of a more comprehensive forest community model based on functional attributes of individual species.

INTRODUCTION

Plant community ecologists have for a long time sought to understand processes maintaining multispecies coexistence in forest ecosystems. The availability of essential resources such as light, nitrogen, and phosphorus is inherently limited in natural plant communities. By the principle of competitive exclusion, one would expect certain species to dominate ecosystems. In forest communities, it has been suggested that coexistence mechanisms are largely related to trade-offs in life history and functional characteristics (Adams *et al.* 2007; Poorter 2007). According to niche theory, such trade-offs should give rare species a competitive advantage; thus promoting forest diversity (Adams *et al.* 2007). While it could be argued that neutral models neglect trade-offs in community dynamics, Adams *et al.* (2007) suggest that neutral theory should also incorporate trade-offs in order to explain coexistence of tree species with variable life history traits. Ecosystem-level gradations in environmental characteristics such as climate and topography also foster trade-offs (Adams *et al.* 2007).

Theoretical models attempt to derive forest tree species coexistence by examining these life history tradeoffs. Adams *et al.* (2007) formulate a method for predicting the outcome of interspecific competition in a forest community competing for light.

$$(Adams \textit{ et al. } 2007) \quad z_i(L) = H_i \left(\frac{G_{D,i}(L)}{\mu_{D,i}(L)} \ln \left[\frac{2\pi\alpha_i^2 F_i G_{L,i}^2}{\mu_{L,i}^2} \right] \right)^\beta$$

Light is considered a unidirectional resource in forest communities and competition for light among species is inherently asymmetric (Poorter 2007). Taking into account the growth and mortality of individual species in the understory and canopy, the rate of reproduction, and height allometry parameters, the Adams model examines the canopy height ($Z_i(L)$) that a monoculture of species ‘i’ would reach if its understory light level is ‘L’. It predicts that species ‘j’ will invade species ‘i’ only when it outcompetes species ‘i’ in the light environment created by ‘i’. Stable coexistence will thus occur when species ‘i’ and species ‘j’ are able to invade each other. The Adams model presents multiple limitations when applied to actual forest communities. For example, it assumes a homogenous physical environment and ignores species-specific pathogen and herbivore effects (Adams *et al.* 2007). In addition, life history traits such as mortality and fecundity require a large, long-term data set. A current goal of forest models is to create a comprehensive criteria for multispecies coexistence based on more easily obtainable plant functional traits.

Functional traits are plant characteristics that relate to the establishment, growth, survival, reproduction, and ultimately fitness of the individual (Poorter 2007). Such traits are important in determining the distribution of species along environmental and successional gradients (Poorter 2007). For instance, tree species vary in their ability to tolerate vertical gradients in light from the forest floor to the canopy (Poorter 2007). Tree height is considered one of the most important determinates of functional trait variation (Poorter *et al.* 2007, Porter 2007). Height plays an important role in forest gap dynamics. In the beginning of a successional sequence, short light tolerant species are gradually replaced by taller shade tolerant trees (Poorter 2007). It has been suggested that in early-successional species may show a negative relationship between light demand and height, whereas later species that establish and grow in shaded conditions may show a positive relationship (Thomas and Bazzaz 1999). A second functional trait, specific leaf area (SLA), measured as leaf area per unit biomass, indicates the efficiency of biomass investment for light capture (Poorter 2007).

Using functional traits such as height and specific leaf area, it becomes possible to create a more applicable theoretical model of forest tree community dynamics. We applied an oversimplified version of Adams model to a Michigan forest community, using functional traits such as specific leaf area as proxies for life history variables defined in the model in order to obtain preliminary predictions of coexistence. Specifically, fecundity, mortality, diameter growth rate of canopy trees, a crown radius parameter, and two height allometry parameters from the model were held constant. This creates a model in which growth rate of understory tree species is compared as a function of crown transmissivity. Understanding understory growth rate as the product of specific leaf area, nitrogen assimilation rate, and leaf to mass ratio, a coexistence model based on

function traits becomes possible. Our simplified model assumes NAR and LMR to be constant across tree species, leaving the specifications of coexistence as:

$$SLA_j(L_i) > SLA_i(L_i)$$

In order for coexistence to occur, species 'j' must obtain a higher SLA than species 'i' in the light level created by 'i'. By evaluating the specific leaf area of different tree species at varying light levels, we examined whether the oversimplified model provided sufficient information to predict trends of species coexistence in the Oak-Hickory forest.

METHODS

Field measurements were completed at the E.S. George Reserve in southeastern Michigan. The forest canopy of the ESGR is dominated by oak (*Quercus Sp.*) and hickory (*Carya Sp.*) with a red maple (*Acer Rubrum*) and black cherry (*Prunus serotina*) subcanopy.

Tree height and bole height were determined using a clinometer, in which distance away from the tree was measured and height extracted. Average adult ($H < 20\text{m}$) tree height across all species was considered to be the canopy height, Z^* . Bole height was the difference between height at the tallest branch and height at the lowest shade-providing branch. Canopy transmissivity, L_i was evaluated using the average bole height per species. For all height measurements, it was assumed that the viewer was at a 45° angle from the ground and the tree was at a 90° angle from the ground.

The crown was assumed to be a circular shape for all trees. Measurements of crown radius were assessed as the average of the longest diameter of tree branches and the perpendicular axis as viewed from below.

Measurements of tree diameter at breast height were used to infer diameter growth rate of canopy and understory (see Adams *et al.* 2007).

To simplify the Adams *et al.* 2007 model, all field measurements were held constant for all species. Surface Leaf Area (SLA) data and light transmission data for trees on the ESGR were obtained from Jeffery Lake. Canopy transmissivity was inferred from tree heights such that a canopy tree is exposed to high light and a medium tree to medium light and a low tree to low light. Shade tolerances were determined using a scale developed by Jeffery Lake and correlated with canopy depth and surface leaf area.

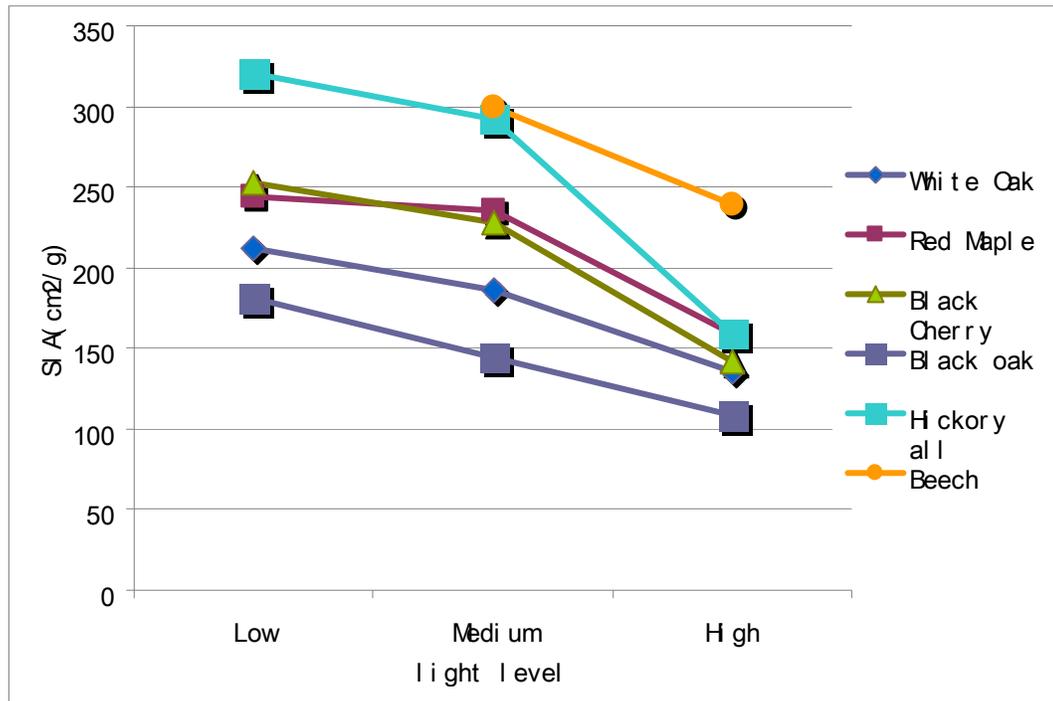
RESULTS

We measured a total 59 trees from six species in the Big Plot: *Acer rubrum* (red maple), *Carya sp* (two species of hickory, which we clump together in our analysis), *Prunus serotina* (black cherry), *Quercus alba* (white oak), *Quercus velutina* (black oak), and a single *Fagus grandifolia* (american beech). While our measurements included individuals from both the canopy and the understory, our analysis was limited to canopy level trees ($>20\text{m}$).

Result from comparing SLA of different species under different light conditions show that in general SLA decreased as light level went from low to high (Figure 1). Two slight

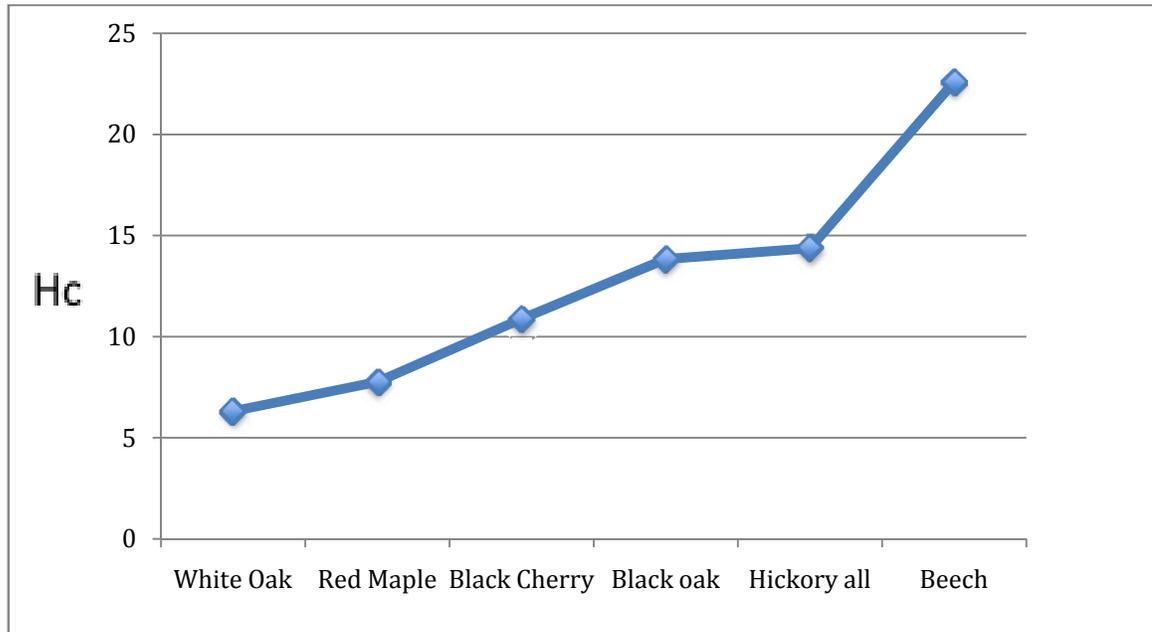
crossovers were apparent, the first between red maple and hickory from high to medium light, and the second from black cherry to red maple from medium to low light.

Figure 1. A comparison of SLA as a function of crown transmissivity for the six dominant tree species in the Big Plot.



We also compare the crown depth (H_c) between the six dominant species (Figure 2). Increasing crown depth corresponds marginally to shade tolerance rank (intolerant – tolerant: black cherry, white oak, black oak, hickory, red maple, beech).

Fig 2. A comparison of crown depth (Hc) for the six dominant tree species in the Big Plot.



DISCUSSION

Overall, specific leaf area increased from high to low light levels for all six of the tree species measured. This is most likely a function of the decreased photosynthetic rates present at low light levels. Two slight crossovers were observed in the graph predicting coexistence. The first occurred between hickory and red maple transitioning from high to medium light. At high light (high crown transmissivity), hickory species had a smaller SLA, and thus a lower understory growth rate, than red maple, while at medium light hickory have a higher SLA. As Hickory also has a higher Hc (a deeper crown) than Black Cherry, by the stable coexistence should occur between hickory and red maple, as hickory is outcompeting black cherry in its own light environment (Hastings per comm).

A second crossover was apparent between black cherry and red maple moving from medium to low light. According to the modified model, black cherry has a higher SLA than red maple at low light, and therefore also a higher growth rate. As Black Cherry also has a higher Hc (a greater crown depth), it is doing better in the light environment created by red maple at medium light, thus out surpassing it at low light and stably coexisting.

In general, canopy depth of a species increased with shade tolerance rank. This is logical, as species with a greater tolerance to low light should foster a deeper depth in their canopy. It is important to note that while black cherry is noted as having a very low shade tolerance, though this species is often observed in the understory.

The modification Adams *et al.* model predicts that species with a higher crown transmissivity should have a lower SLA. In biological terms, this implies that species with a higher light in its understory must be outcompeted by other species in its understory, so it must have a lower SLA at that light level. The other species must have a higher SLA at that light level so that it can grow faster there. Interestingly, this is the opposite of what is observed in forest ecosystems. In general, shade intolerant species have a higher crown transmissivity and a higher SLA (Hastings per comm.). This observation makes sense only in the context of disturbance. In the presence of a light gap, shade intolerant species must be able to establish and grow quickly in the environment created by the light gap. Multiple studies have emphasized the importance of functional trait variations at the seedling level in shaping plant community dynamics (Poorter 2007, Pearson et al. 2003). Poorter (2007) argued that this regeneration niche had a strong and lasting effect on leaf traits and community structure. A major limitation of the Adam et al. model is that it basically ignores forest gap dynamics.

The scope of our analysis was extremely limited by the short data collection period. Our variation of the Adams *et al.* model assumes many variables, such as mortality and net assimilation rate are constant. Clearly, this is not going to be the case in a forest ecosystem in which individuals vary on an individual, species, and population level. None-the-less, our simplified model provides a background for altering forest demographic models to include functional traits.

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PSEUDANTHONOMUS HELVOLUS (CURCULIONIDAE) SEED PREDATION OF
HAMAMELIS VIRGINIANA (HAMAMELIDACEAE) WITHIN A TEMPERATE NORTHERN
HARDWOOD FOREST

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ABSTRACT

The weevil *Pseudanthonomus helvolvus* Boheman (formerly *P. hamamelidis* Pierce) frequently oviposits upon witch-hazel (*Hamamelis virginiana*) seeds. This study investigated the relationship between the frequency of seed predation and overall witch-hazel clump size and density of witch-hazel individuals within a clump. Ten solitary individuals outside of the clumps were also sampled to determine the frequency of seed predation compared to trees within clumps. A positive correlation exists between greater numbers of fruits per tree in areas of canopy transparency; however, after correcting for light, no difference exists between the number of fruits in clumps and solitary individuals. The solitary trees exhibited a lower percentage of parasitized fruits than clump trees, and while not significant, the trend suggests a Janzen-Connell effect. Further investigation is recommended to include more solitary individuals to observe whether a Janzen-Connell effect exists, as well as an analysis of estimated weevil population relative to witch-hazel fruit harvest the previous growing season.

INTRODUCTION

Angiosperms have developed numerous methods for seed dispersal to ensure propagation. The multitudinous, miniscule comose seeds of the eastern cottonwood (*Populus deltoides*) dispersed by wind strive for success by dispersing large amounts of seed far and wide. The black walnut (*Juglans nigra*) produces relatively few (compared to the cottonwood) large globose nuts walnut, relying upon mammals such as fox squirrels to disperse and bury them for later consumption with the requirement for survival being a poor memory of the squirrel. Numerous methods have evolved to increase reproductive fitness and minimize the adverse effects of seed predation.

Witch-hazel (*Hamamelis virginiana*) has developed a rather self sufficient method of seed dispersal; the plant mechanically ejects two black lustrous seeds from mature fruit. While this method ensures a higher rate of success that the seed will fall into suitable habitat (the mother tree is certainly alive there), one may argue that this short distance dispersal method may leave local populations susceptible to herbivory or infestation by a disease. Of several more generalist herbivores that consume fruits or leaves of witch-hazel, one insect in particular has chosen witch-hazel as its only host (De Steven 1983): the curculionidean weevil *Pseudanthonomus helvolvus* Boheman (formerly *P. hamamelidis* Pierce, Integrated Taxonomic

Information System; www.itis.gov). This method of seed dispersal results in a highly patchy distribution of witch-hazel, including some dispersal out of patches animals resulting in solitary individuals. The highly patchy distribution of witch-hazel and seed predation by the host-specific weevil provides a perfect opportunity to investigate the potential manifestation of the Janzen-Connell effect. The Janzen-Connell effect in this type of scenario essentially hypothesizes that the probability of seed destruction would decrease as distance from the parent tree increases.

P. helvolus seed predation of witch-hazel has been well documented by De Steven (1981a, 1981b, 1982, 1983) on the E.S. George Reserve since the late 1970s. This study particularly focused on the *P. helvolus* seed predation frequency and the areal size of witch-hazel clumps and density of witch-hazel individuals. The investigators predicted that as witch-hazel clump size increased, seed predation by *P. helvolus* would increase as large micro-populations would be easier to find, as well as exhibit larger populations of the weevil as there may be an accumulation within the clump. Similarly, the investigators predicted seed predation would increase as density within a clump increased. Conversely, the investigators expected that solitary individuals removed from a larger clump would have lower predation percentages as suggested by Janzen (1970) and Connell (1970), where the probability of seed destruction decreased with the increase in distance from the parent tree. While this study did not investigate the survivorship of witch-hazel seedlings, the authors postulate that discrete individuals would suffer less predation as would discrete seeds.

NATURAL HISTORY

Hamamelis virginiana

Witch-hazel is a small tree often occupying the understory of dry-mesic northern hardwood oak-hickory forests within southeastern Michigan (Barnes 2004; Voss 1985). Several clonal trunks grow together, reaching a height of ten meters and rarely a diameter greater than 12 cm (Barnes 2004). Abnormal to temperate woody species, witch-hazel flowers in autumn, typically from September through and November; the flowers often persist after the leaves have fallen (De Steven 1983). The flowers are born in clusters of 3, are perfect (trees monoecious), and exhibit four narrow, twisted, bright yellow petals (Barnes 2004). Of greater novelty, while the flowers are insect pollinated in the fall, fertilization itself does not occur until the spring of the following growing season (De Steven 1983). Literature differs on if witch-hazel flowers are in fact self-pollinating and self-compatible (Anderson 2002; De Steven 1983). The fruits produced are two seeded capsules, grown to full size by August. The two black ovoid seeds mature and are dispersed in autumn, typically in October, through ejection after the capsule dries and becomes woody (DeSteven 1982). Seeds travel approximately one to three meters. Though not a dominant means of dispersal, seeds have been apparently been dispersed by small mammals such as the fox squirrel and cottontail rabbit (De Steven 1982; Sweetman 1944). Once dispersed, the seed remains dormant through two winters prior to germination (Shoemaker 1905; Sandahl 1941).

Pseudanthonomus helvolus Boheman

The *Pseudanthonomus* genus comprises a group of small weevils whose larvae typically consume fruits or flower buds (De Steven 1983). Regarding witch-hazel seed predation, the reviewed literature refers to *P. hamamelidis* Pierce; however, as previously noted the Integrated Taxonomic Information System recognizes *P. helvolus* Boheman as the current nomenclature. Witch-hazel is the only known host for this particular weevil, and weevil population densities vary year to year as a function of the amount of fruits produced and percent fruit parasitized (De Steven 1983). Oviposition occurs in mid-June, with typically a single egg hatching a larva which burrows into the fruit. The larvae consume both seeds, pupates within the fruit, and emerges in late-August, early-September. Adults are believed to hibernate within the litter layer of the forest floor (De Steven 1983).

METHODS

The study was conducted on September 27, 2008 at the E.S. George Reserve, a 464 ha tract of forests, wetlands, and old fields, located within Livingston County, MI. This study area was located within an 18-hectare oak-hickory plot locally referred to as Big Woods (Figure 1). Every living woody plant within Big Woods with a circumference of 10cm at breast height (1.37m above grade) has been identified, tagged with a circular aluminum numbered disc, and plotted onto a grid system. Five clumps and 10 solitary individuals were evaluated (Table 1).

Figure 1. a) 18 ha. Big Woods Plot with *H. virginiana* in black; b) *H. virginiana* isolated from other trees with clumps outlined.

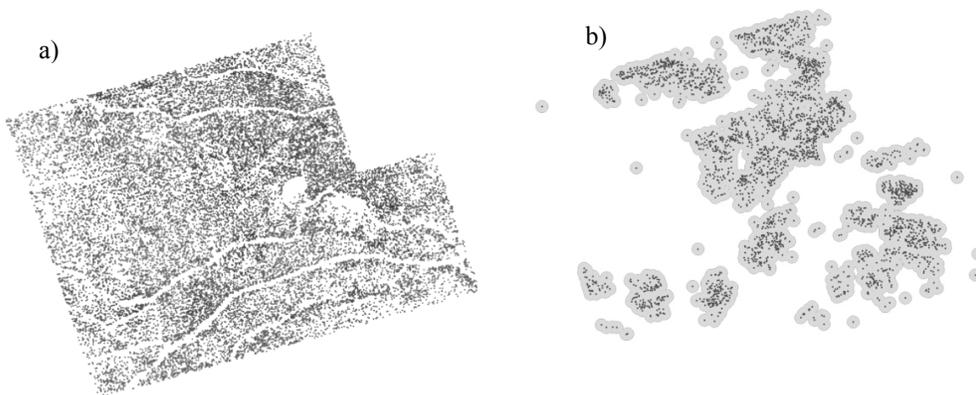


Table 1. Clumps with individual witch-hazel and area identified.

Clump	Witch-hazel individuals	Area (m ²)
1	235	3103
2	112	865
3	4	8
4	1131	15892
5	12	414

Two methods were used to evaluate witch-hazel seed predation: transect specific survey within a clump and random meander survey within a clump. Both methods collected the same information: number of healthy fruits, number of fruits with oviposited, number of fruits with only one seed parasitized, number of fruits completely parasitized, and the tag number of the individual if present. The transect specific survey was conducted by laying a 50 m tape in random orientation within a plot. Each witch-hazel trunk within 1.5 m from the transect line was investigated, noting the lateral distance along the transect and the distance perpendicular to the transect line. The transect specific survey added an additional measure of canopy transparency using a densitometer, the random meander survey sought to evaluate every witch-hazel individual within a clump. It must be noted that not all witch-hazel individuals were able to be evaluated as some were too tall and fruits were out of reach. The random meander survey was conducted to gather as much documentation of fruits as possible since the transects may not yield sufficient numbers because of sporadic fruiting and the fact that some trees were too tall to sample.

RESULTS

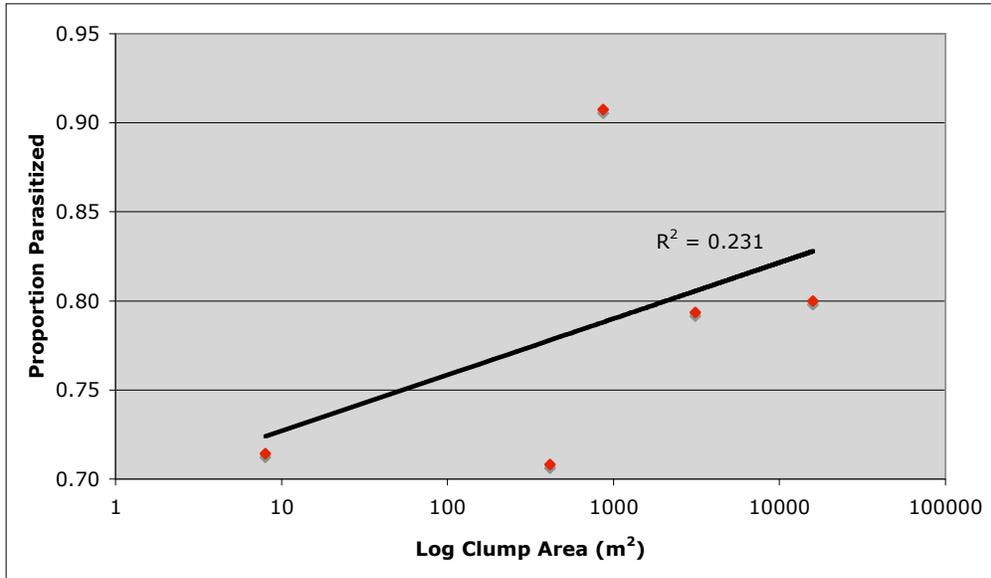
A total of 96 *Hamamelis virginiana* trees and saplings were surveyed among five clumps and ten solitary individuals. Fruits categorized as oviposited, half-dead, or dead were considered parasitized. We found that 76% of all fruits in the sample showed some evidence of parasitization. Parasitization rates within the clumps were explored to determine what clump attributes, if any, affected *P. helvolus* activity. In trees from the random sample method, no significant correlation between proportion of fruits parasitized and either clump area ($R=0.158$, $p= 0.400$) or clump density ($R= -0.334$, $p= 0.291$) was found using Pearson's Correlation Coefficient (Figure 2). When all data were pooled (from random and transect sampling; Figure 3), again no significant correlation was found between proportion of fruits parasitized and either clump area ($R= -0.298$, $p= 0.313$) or clump density ($R= -0.564$, $p= 0.161$). If pooled witch-hazel clumps are compared to isolated individual trees, we find that isolated individuals suffer much less parasitization than clumped individuals ($t(8)= 1.502$, $p= 0.086$; Figure 4).

Average fruits per tree were compared for the pooled data. No significant correlation was found when comparing average fruits per tree and clump size ($R= 0.144$, $p= 0.409$). However, there exists a possible negative correlation between the average fruit produced by a tree and clump density ($R= -0.726$, $p= 0.083$; Figure 5)

Canopy openness data gathered for the transect sample was compared to the average fruits per tree to determine whether levels of light impact fruiting abundance of witch-hazel (Figure 6). Trees found in more open areas of the forest were positively correlated with a higher average number of fruits per tree ($R= 0.513$, $p= 0.03^*$). However, a t-test of the residuals (Figure 7) revealed no significant difference between the isolated individuals and clumped trees in the average fruit per tree while controlling for light exposure ($t(12)= -0.144$, $p= 0.888$).

Figure 2: Proportion of fruit parasitization from the random sample compared with a) clump area and b) clump density.

a)



b)

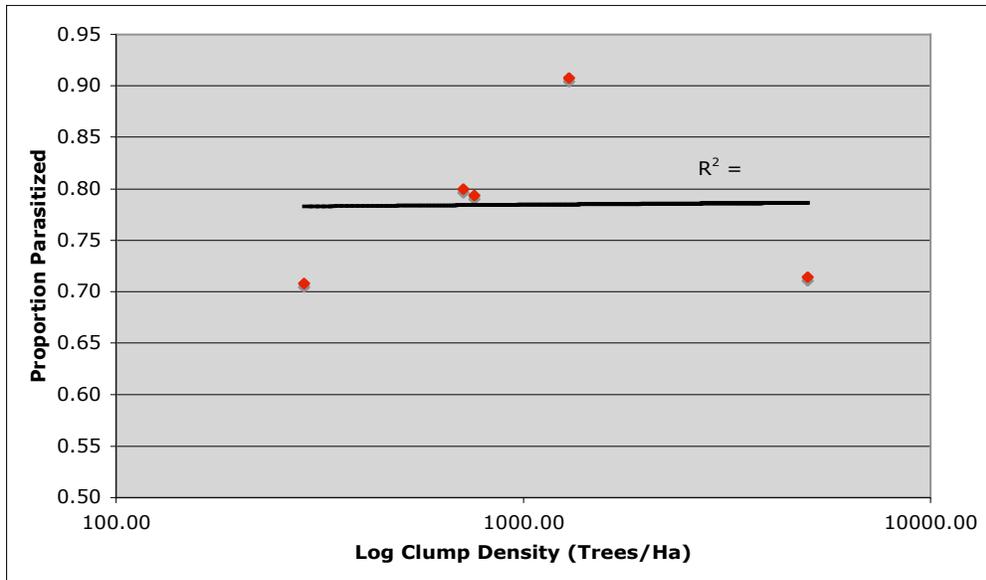
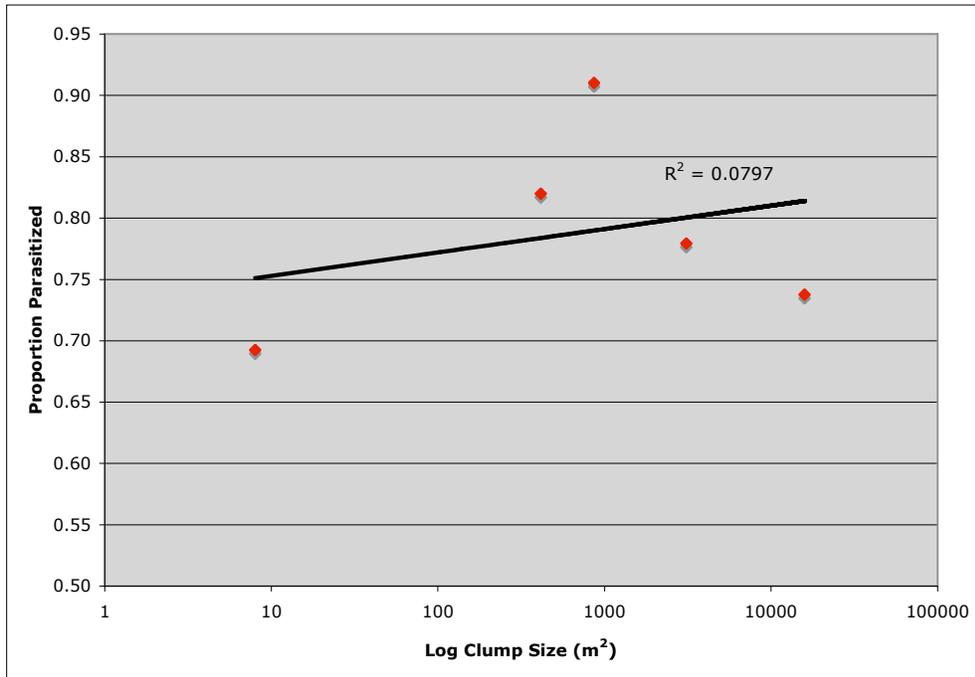


Figure 3: Proportion of parasitized fruit from the pooled data (random and transect samples) compared to a) clump size and b) clump density.

a)



b)

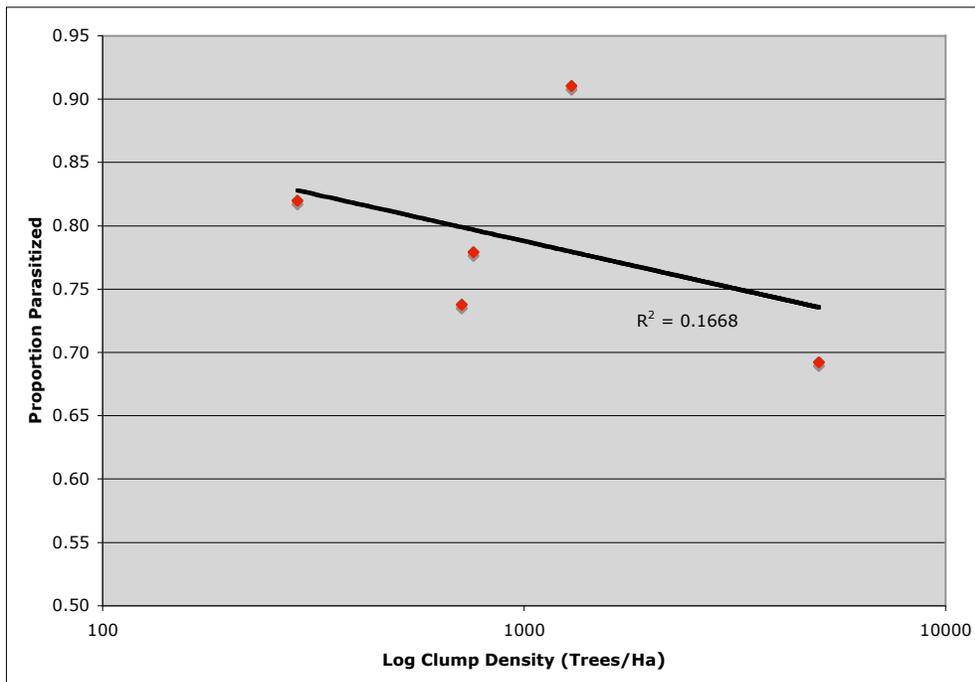


Figure 4: Mean proportion of fruits parasitized between isolated individual trees and clumped trees. Error bars represent ± 1 SE.

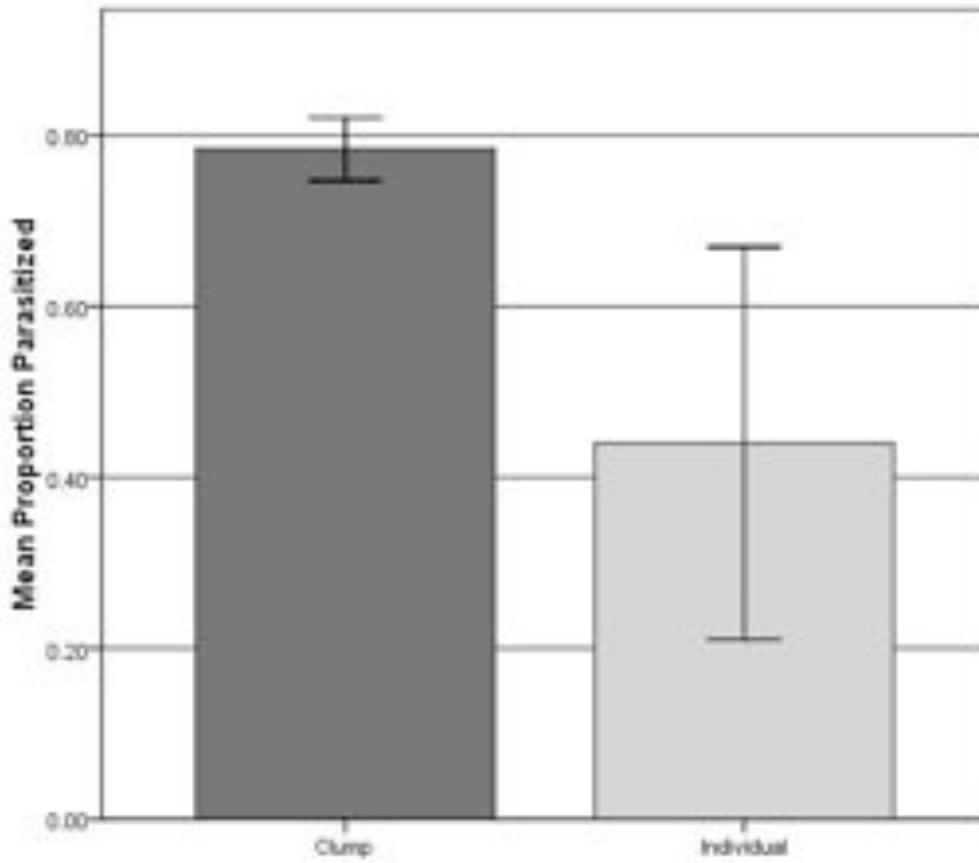


Figure 5: Average fruit per tree as a function of clump density for the pooled samples.

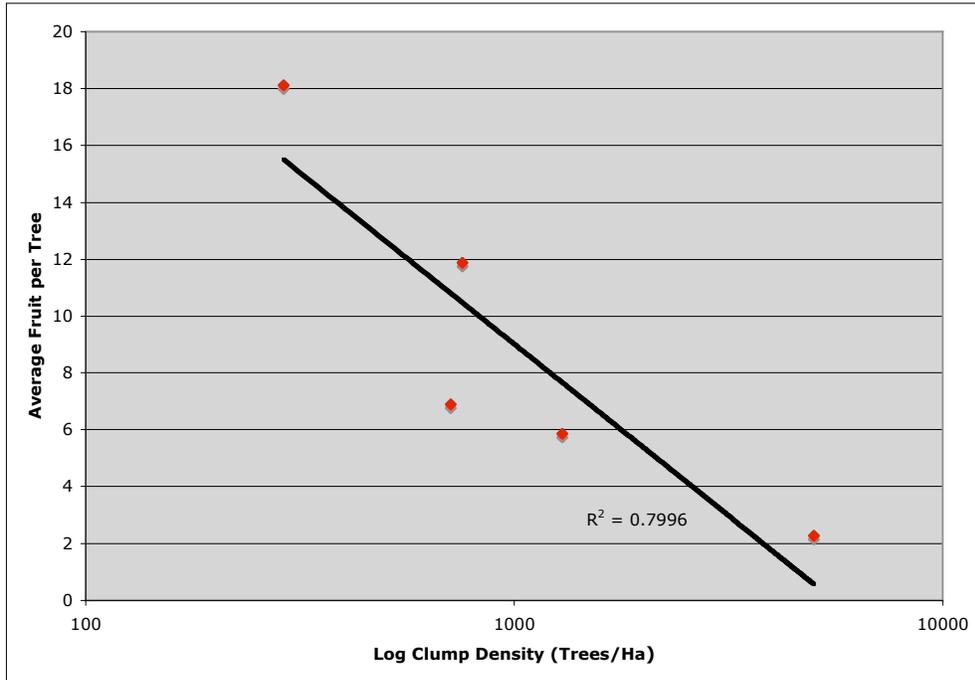


Figure 6: Average fruit per tree with varying canopy openness for both isolated individuals and clumped trees.

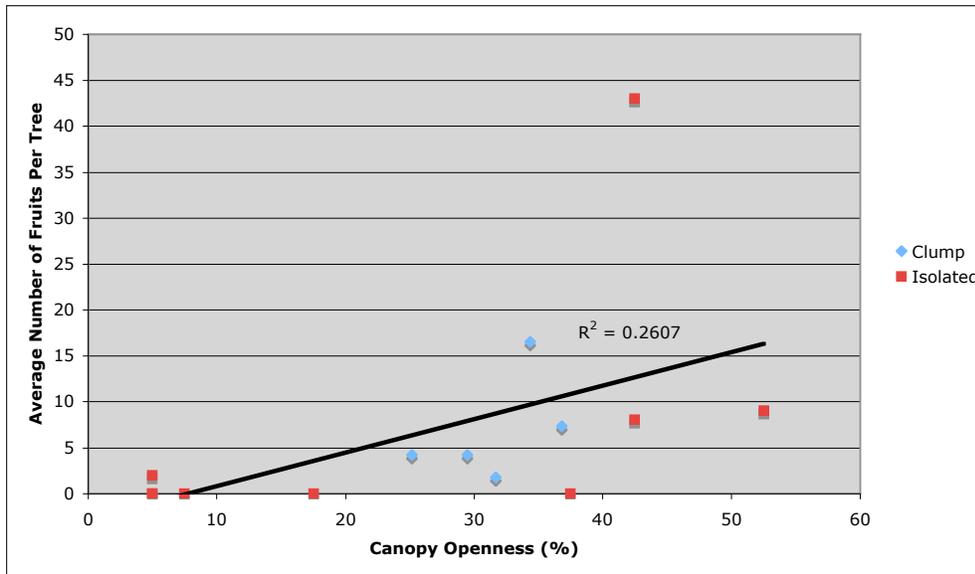
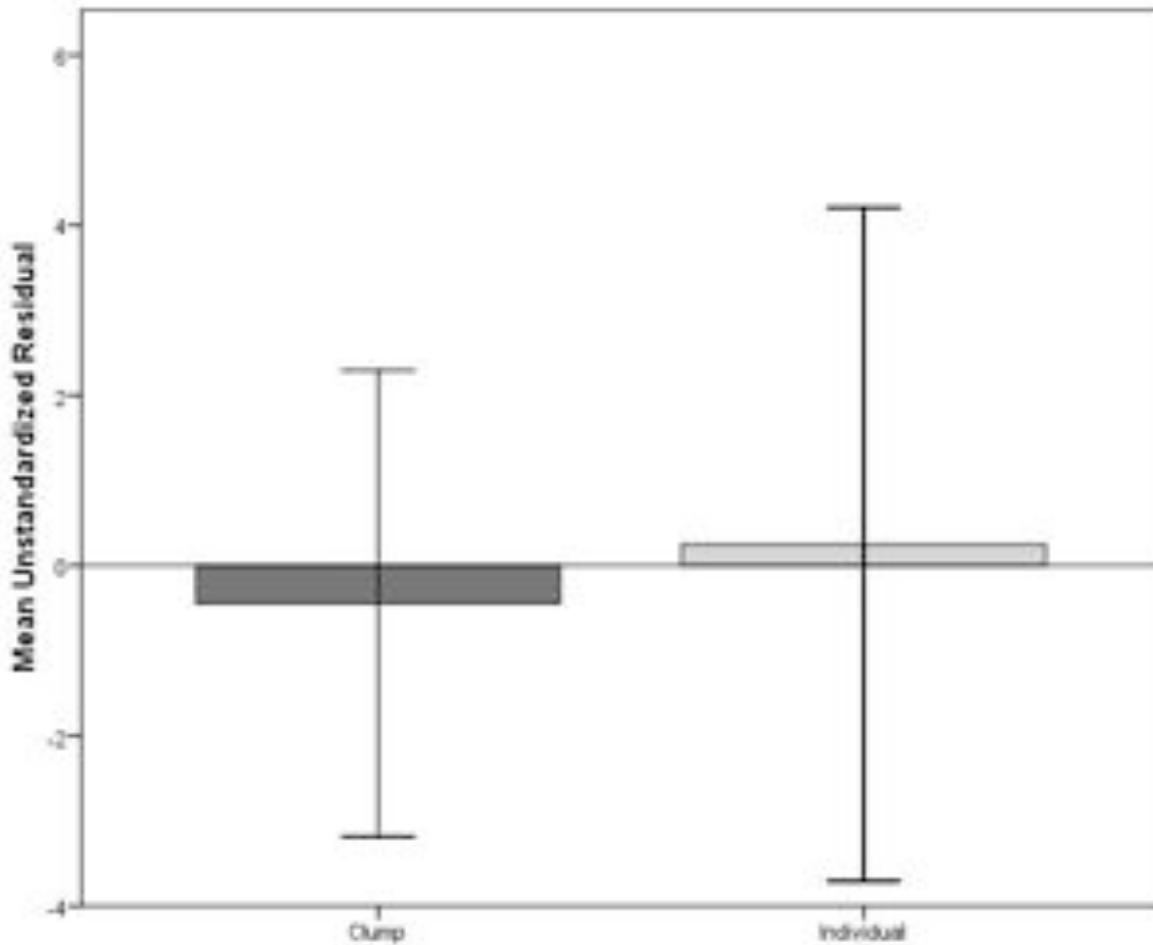


Figure 7: Residuals plot for canopy openness and average fruit per tree. Error bars represent +/- 1 SE.



DISCUSSION

No significant correlation was found between the frequency of seed predation by *P. helvolvus* and clump size or density within clumps. No significance was found between the amount of parasitism within clumps and the solitary individuals; however, there appears to be a notable trend towards less parasitism of fruits within the solitary trees. Although technically not statistically significant ($p=0.086$), a strong suggestion exists that solitary trees are significantly less parasitized than individuals within clumps. As distance from the clump (i.e. parent tree) increased, the seeds avoided predation and grew into mature, reproductive adults. Just as the seeds further away from the clump had less predation as predicted by the Janzen-Connell effect, the fruits on the solitary witch-hazel individuals also exhibited a lower frequency of parasitism.

The relationship between weevil parasitism and distribution of witch-hazel individuals becomes very importance when considering the reproduction and expansion (or lack thereof) of the witch-hazel population. The weevil population has a direct relationship with the amount of viable fruit produced by witch-hazel; i.e. the weevil population is low the year following a low fruiting year. Some evidence exists that witch-hazel mast years provides predator satiation,

allowing for greater survival of seeds during those years (De Steven 1983) and thus witch-hazel population expansion. Based upon the seemingly low fruiting year (personal estimation) and the relatively high parasitization, one would expect a masting year in the next growing season or two. This inference may be incorrect, however, as last year evidently had an even lower fruiting year (J. Vandermeer and D. Allen, personal communication). Although this year's parasitism rate appears high (76%), 24% of the healthy fruits will have the ability to disperse; this year may in fact be a mast year with weevil seed predation satiation.

Future investigation must pursue the dynamic relationship between fruit production and weevil population. This analysis combined with the natural dispersal mechanism of witch hazel will help determine the limiting factors of the spread of witch-hazel. Further investigation on the alternative dispersal mechanisms, presumably mammalian, resulting in solitary individuals may help understand the spread of new discrete witch-hazel clumps.

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COMPARING ADULT TREE AND SEEDLING RELATIVE DENSITIES AS A TEST OF COMMUNITY CONSTRUCTION MECHANISMS

HANNAH FOSTER, RACHEL HESSLER, DOUG JACKSON, HUIJIE GAN, DANA THOMAS

ABSTRACT

Seed dispersal and establishment are considered critical stages for most plant species, and many factors are involved in determining the next generation of plants in a community. Ideas like the Janzen-Connell effect, the regeneration niche, and Hubbell's neutral theory, help to describe the patterns observed in plant communities. Seeking to better understand the underlying mechanisms promoting the establishment of trees in forest ecosystems in order to predict the future of the Big Woods plot at the E.S. George reserve, we compared seedling density to adult density in four different forest habitats. Our results appear to support both the Janzen-Connell effect and the regeneration niche, but not Hubbell's neutral theory.

INTRODUCTION

Seed dispersal and establishment are considered critical stages for most plant species (Torres et al. 2008). The success of an individual seed in a particular environment is related to a number of abiotic and biotic stress factors that directly, and indirectly, affect plant survival. For instance, dispersal may occur in sites in which shade, light, or water stress conditions limit or prevent establishment (Torres et al. 2008). In addition, the presence of established neighboring plant individuals may impact seedling establishment through competition for resources or through influencing predation or pathogen abundance (Torres et al. 2008). Many theories have been put forth to explain the patterns found in plant communities, including the Janzen-Connell effect (Janzen, 1970; Connell, 1984), the regeneration niche, and Hubbell's neutral theory (Hubbell, 2001). All of these theories attempt to make sense of the patterns we see in forest ecosystems, as well as predict what future forests will look like. This is particularly important in a time of changing climate and ecosystems. Its importance can be seen, for instance, in the Red Maple Paradox. In this particular case, Red Maples are going against all prediction and taking over forest environments (Abrams, 1998). In order to understand why this is happening and preserve the biodiversity in forests, we must understand the mechanisms behind the distribution of trees in ecosystems.

The diversity of tree communities in the tropics is often attributed to the Janzen-Connell effect, which suggests that variations in seed dispersal can affect early seed and seedling survival by altering the incidence of predation and parasitism. Predator and parasite consumption has negative effects on plant recruitment at greater seed densities, which suggests that seedling survival increases with increasing distance between the seedling and the adult tree (Takeuchi and Nakashizuka 2007). Additionally, the adult tree shades the seedlings, competes for water, and may host predators or parasite

communities. This allows seedlings of different species the opportunity to take root in the spaces created around the adult species, avoiding what might otherwise end up as a monoculture, and creating a more diverse community. Although Janzen and Connell both found evidence for this phenomenon in the tropics (Janzen, 1970; Connell, 1984), a synthesis of studies on density dependence in seedlings by Hyatt (2003) showed little to no evidence supporting Janzen and Connell's ideas either in temperate or tropical climates.

Plant community ecologists have traditionally applied the concept of niche specialization as a means to explain the establishment and distribution of species in a community (Pearson et al 2003). Grub (1977) first defined the concept of the regeneration niche as the biotic and abiotic requirements of a species needed to replace adult individuals. A species' regeneration niche is often viewed in respect to the environmental conditions in the early part of the life cycle of the plant (Poorter 2007). Early environmental requirements coupled with high seedling mortality will determine whether an individual species will regenerate (Poorter 2007). The idea of the regeneration niche is closely related to understandings of forest successional changes (Poorter 2007). A shade intolerant plant species, for example, will establish in the environment created by a light gap. Inherently, an individual plant's response to environmental factors will change with age, as the aboveground portion of the tree will encounter variable light, humidity, and wind conditions as it grows from the herbaceous layer to the canopy (Collins and Good 1987). Poorter (2007) observed the regeneration phase, however short-lived, to have a strong effect on a plant species in a community.

Hubbell's (2001) neutral theory has, in recent years, been put forth as an alternative mechanism of forest species coexistence. Neutral theory assumes that all individuals have the same probability of birth and death, and they also have the same limited dispersal ability, in that they are simply more likely to disperse to neighboring areas (Jabot et al. 2008). This would mean that, from generation to generation, the proportion of each tree species in an ecosystem would remain approximately the same. Plant community ecologists tend to attempt to dichotomize niche and neutral theories of plant community assembly, when, in actuality it is possible for both models to interplay in a single system. For instance, Jabot et al (2008) proposed a neutrality model in tropical forests that takes into account establishment limitations in a local community. They suggested that tree species are not equivalent at the regional scale, due to differential environmental constraints for establishment, though neutral dynamics are still assumed at the local scale (Jabot et al 2008).

In this study, we examined the distribution of seedlings and saplings of dominant tree species in a mid-successional forest in Southeast Michigan. Comparing seedling and sapling distribution to adult tree distribution across multiple environments, we sought to predict underlying mechanisms promoting the establishment of plants in the forest community. If the Janzen-Connell effect has the greatest influence on distribution, one would expect that the seedlings closest to the adult trees would be of different species. Similarly, if niche regeneration is at work, we would expect to see habitats changing and new tree species, better evolved for the new habitat, taking over. On the other hand, if Hubbell's neutral theory is at work in the forest, one would expect to find that the seedlings surrounding the adult trees would be of the same species. We hypothesized that

we would find the forest exhibiting more closely the Janzen-Connell effect and the idea of the regeneration niche than Hubbell's neutral theory.

METHODS

Four different habitats were chosen within the Big Woods Plot in the George Reserve: the north and south slopes off Esker road, a swamp habitat, and a mesic habitat. For each habitat, two transects, each 50 meters in length, were laid out. We recorded the adult canopy trees and their seedlings within one meter on either side of the transects. We did not include any record of understory trees in our data.

We used a Chi-Square value to compare seedlings composition between different habitats. We used resampling to determine whether the seedling composition in each habitat was significantly different from what would be expected based on the surrounding adult communities. From census data that had been collected in 2003, we extracted the identities of the adult trees located in a swath extending 50 m perpendicularly from each transect; only adults of the species that we recorded in our survey were included. For some transects near the edge of the plot sampled during the 2003 census, it was not possible to extract data on 50 m of each side of the transect, so an alternate but similarly-sized area was used.

The probability that the observed seedling/sapling community could arise through random recruitment from the adult communities was determined by generating 100000 seedling populations drawn randomly from the adult communities' species distributions. The proportion of these randomly-generated seedling populations that had an equal or more extreme number of each tree species compared to the observed seedling/sapling population gave the probability that the observed distribution could arise through random sampling of the adult population. For example, if a hypothetical adult community has 10% red maples, and a sample of 100 seedlings was found to have 15 red maples, we would generate 100000 randomly-drawn seedling populations of size 100, with each individual in these populations having a 10% chance of being a red maple. The proportion of these 100000 populations with 15 or more red maples gives the likelihood that the observed population could be drawn from the given adult community.

RESULTS

We encountered 691 seedlings in the eight transects. Red Maple seedlings were found to be dominant on the N Slope and Mesic habitat, while seedlings of Hickory and White Oak were found to be dominant in S Slope and Swamp respectively (Table 1).

Table 1 Seedling compositions of different habitats.

Seedlings	N Slope	S Slope	Swamp	Mesic	Total
Red Maple	123	46	27	14	210
Black/Red Oak	13	22	3	10	48
White Oak	28	21	61	9	119
Hickory	51	90	15	12	168
Black Cherry	9	34	34	13	90
Elm	14	13	20	2	49
Sassafras	0	1	0	2	3
Ash	0	1	0	0	1

Basswood	0	0	3	0	3
Total	238	228	163	62	691

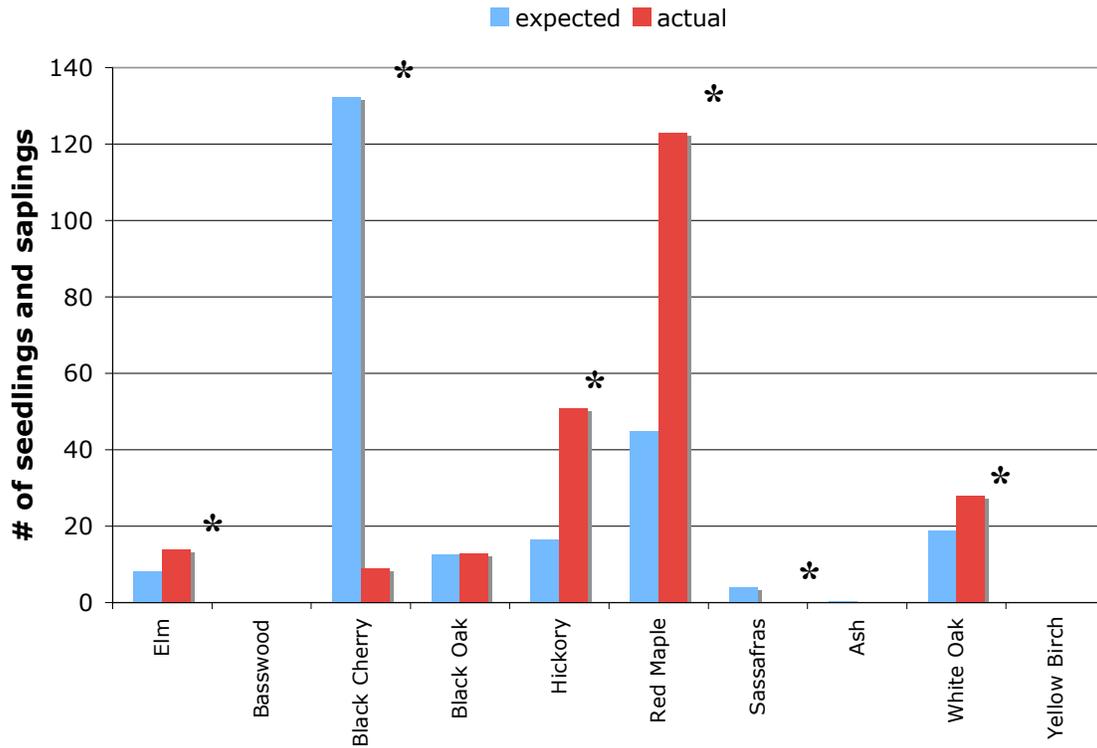
Chi-Square values show that there are significant differences in the seedling composition among all the habitats, except the North slope and Mesic habitats (Table 2).

Table 2. Chi-Square tests for the seedlings compositions between different habitats. For all pairs, df=17. The upper half of the table is the Chi-Square value; the lower half corresponds to the P values. * indicates that there are significant differences of the seedling compositions between different habitats.

	N Slope	S Slope	Swamp	Mesic
N Slope	0	65.6	103.5	45
S Slope	<0.0001*	0	90.7	14.5
Swamp	<0.0001*	<0.0001*	0	38.5
Mesic	0.0002*	0.631	0.002*	0

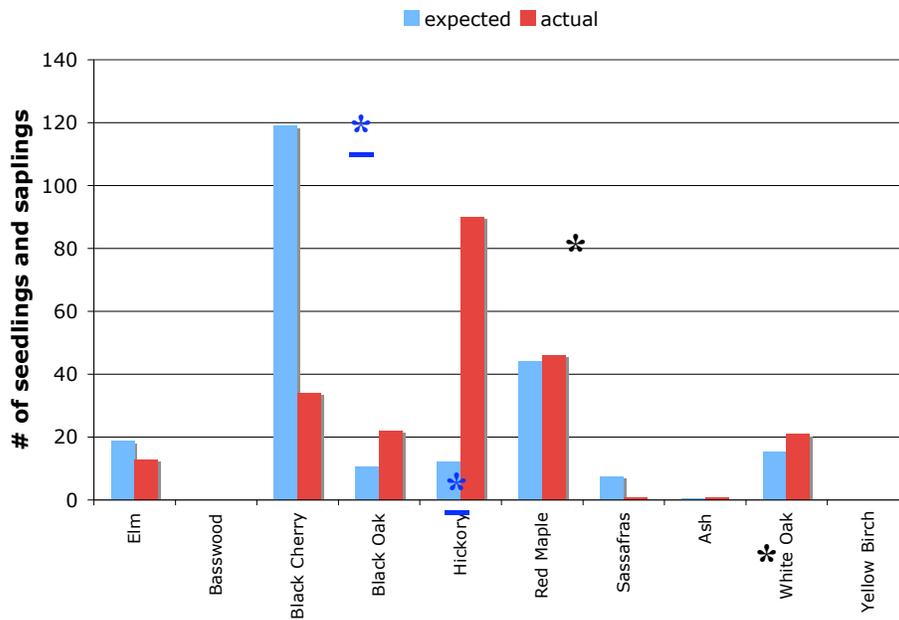
Figures 1-4 show the resampling results. For each tree species in each habitat, the expected (based on adult trees) and observed seedling counts are shown, with asterisks designating those species with observed frequencies significantly different ($P < 0.05$) from the expected frequencies. In the north slope habitat, 60% of the trees species showed significant differences in the number of seedlings compared to the expected number of seedlings (fig. 1).

Figure 1. Expected and actual counts of seedlings and sapling in the north slope habitat. Expected counts are based on the adult community surrounding the transects. Significance was determined via resampling.



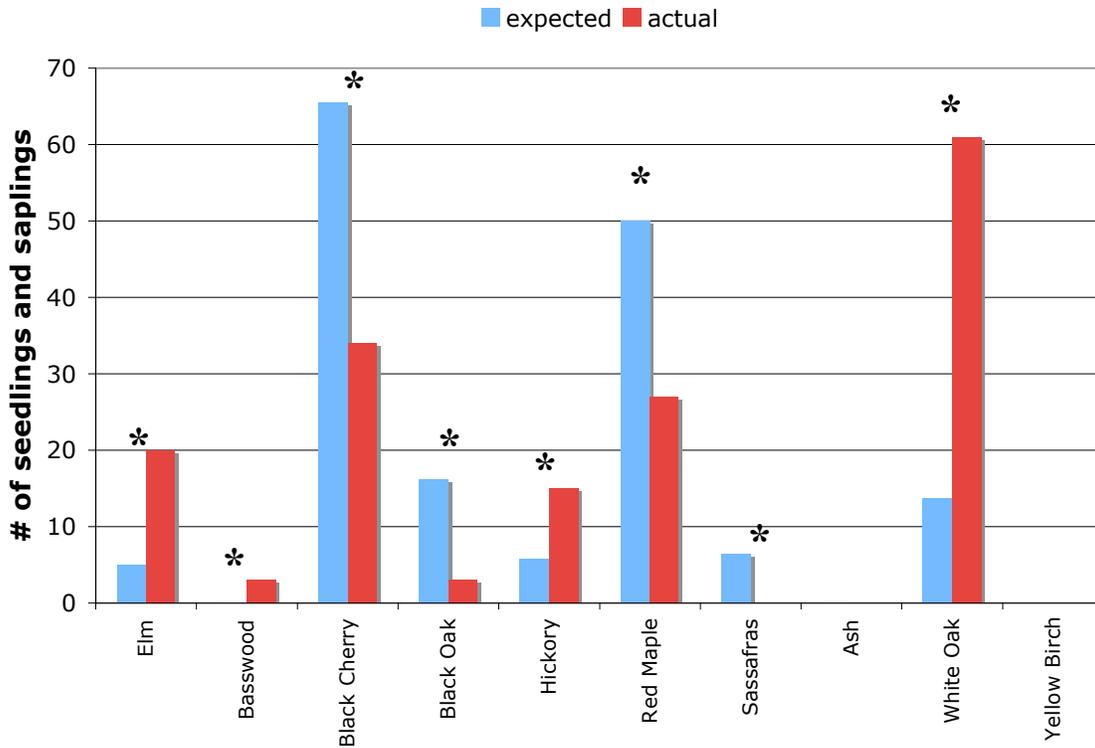
We saw significant differences in the expected number of seedlings to actual number of seedlings in 40% of the tree species in the south slope habitat (fig. 2).

Figure 2. Expected and actual counts of seedlings and sapling in the south slope habitat. Expected counts are based on the adult community surrounding the transects. Significance was determined via resampling.



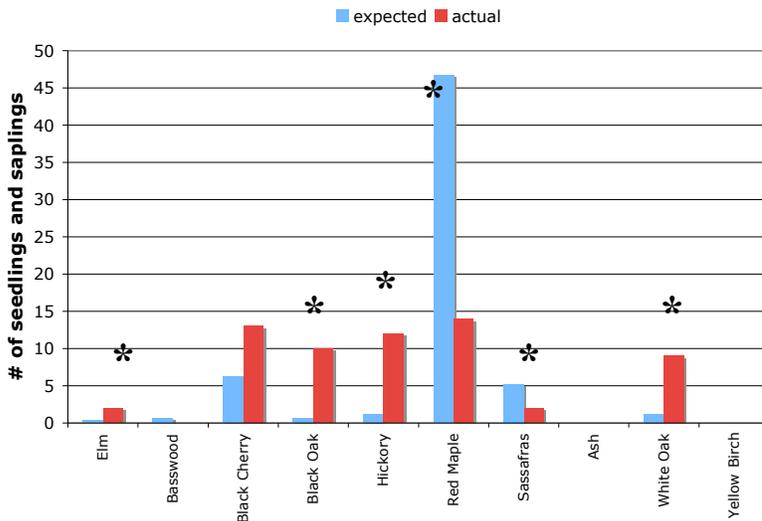
80% of trees in the swamp habitat showed significant differences in the number of seedlings compared to the expected number of seedlings.

Figure 3. Expected and actual counts of seedlings and sapling in the swamp habitat. Expected counts are based on the adult community surrounding the transects. Significance was determined via resampling.



In the mesic habitat, 60% of tree species showed differences in the expected number of seedlings compared to the actual number of seedlings.

Figure 4. Expected and actual counts of seedlings and sapling in the mesic habitat. Expected counts are based on the adult community surrounding the transects. Significance was determined via resampling.



DISCUSSION

Overall, we saw distinct differences between the proportion of adult trees of a species and the proportion of seedlings of that species in each habitat. Additionally, our results showed major differences between the expected number of seedlings (based on the number of adult trees) and the actual number of species in each habitat. The swamp habitat showed, by far, the greatest difference. This might be explained by the process of succession, which is supported by the fact that black cherry is often considered a pioneer species and red maple is frequently thought of as being accustomed to growing in swamps. The number of trees we found of each of these species in the swamp habitat was well below what we would have expected. This is evidence that the swamp habitat in the E.S. George Reserve may be experiencing succession.

The south-facing slope appeared to be changing the least of the four habitats, as only four out of ten tree species showed a significant difference in the expected number of seedlings and the actual number. A possible explanation for this is that the south-facing slope receives the greatest amount of sunlight and is thus able to meet the light requirements of a broader range of tree species. This may allow some of the light-loving tree species to persist even as other trees take root in the habitat.

The significant differences we found between the proportion of adult tree species compared with the proportion of seedling species as well as between the expected number of seedlings and the actual number of seedlings appear to support the Janzen-Connell effect in addition to the idea of niche regeneration. We see great diversity in the seedlings surrounding the adult trees, which could signify that the seed success of the established adults may decrease closer to the parent tree and increase further away, just as Janzen and Connell put forth (Janzen, 1970; Connell, 1984). We may be seeing niche regeneration throughout the forest, but in particular, in the swamp habitat, where the habitat may be changing and creating a more favored environment for new tree species to take root.

Our results, at first glance, appear to go against the Hubbell's neutral theory, since, if the neutral theory were true in this case, we would expect to see a similar proportion of seedlings to adult trees in terms of species. Obviously, we saw precisely the opposite of this, but there are many things that must be taken into consideration before ruling out the neutral theory:

First of all, we must look at what Hubbell was trying to do in creating the neutral theory. Hubbell himself says that the neutral theory was intended to offer the simplest possible explanation for the patterns we see in plant ecology. It was meant as a big picture theory, or a loose approximation and was not intended to be absolutely precise (Hubbell, 2005). Our study took place in a very small area, with only a few trees, and these are, perhaps, not the conditions for which Hubbell intended his theory. Had we looked at the entire Big Woods plot or the entire E.S. George Reserve, we may have seen a more similar composition of seedlings to adult trees. Additionally, if we consider the neutral theory to be, in fact, an approximation, it allows quite a bit of room for concepts like the regeneration niche and succession.

Another factor we must take into account before coming to any conclusions about these theories is the size of the trees we recorded. We did not differentiate between

seedlings and saplings (we considered both to be seedlings), which could significantly skew our results since many seedlings do not survive to sapling age, and many saplings have been in the same place for years waiting for the right conditions in which to grow. This means that, theoretically, all the saplings we found may have belonged to the adult tree species in that habitat and all the seedlings to other species. Conceivably, these intruding seedlings might be destroyed before they reach the sapling stage, leaving the seedlings of the adult trees to become the next generation. Not only did we not account for seedling age, but we also did not take into account the age of the adult trees and whether or not they were reproducing, which could also have an effect on our results.

Without further, more in depth study, including larger plots of forest, we cannot to come to any certain conclusions about any of the aforementioned theories. Although our results seem to indicate that the neutral theory does not apply, I believe it is possible for all the three theories to co-exist comfortably. On the small scale, we may be able to use the Janzen-Connell effect to understand the patterns we see directly beneath adult trees. On a larger scale, we can use niche theories and succession to predict the future of smaller plots of forest. Hubbell's neutral theory may be used on a grand scale to loosely describe what we see in forest communities. Therefore, we must not be so quick to dichotomize all these theories since each one was meant for a different purpose, with a different situation in mind. We must view each one as a piece of the greater puzzle of community and ecosystem ecology.

ACKNOWLEDGEMENTS

We would like to thank David Allen and Chris Dick for their assistance with this project.

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MODELING THE EFFECTS OF CLIMATE CHANGE ON TREE RECRUITMENT USING A GRADIENT OF SOIL MOISTURE AND LIGHT

ASHLEY LARSEN, JINGCHUN LI, ANDY MACDONALD, EMILY SLUZAS, SENAY YITBAREK

ABSTRACT

An increasingly problematic result of accelerating climate change is the shifting of species' natural ranges. This is of particular concern for terrestrial plant species given the slow migration rates among the majority of terrestrial plant species. Tree recruitment and the identification of bottlenecks in the recruitment process are therefore becoming more and more important to understanding species survival and conservation. The purpose of this experiment was to achieve some understanding (through field observation and modeling) of the way tree recruitment is modified under conditions of rapid climate change. Of particular interest in this study were gradients of both soil moisture and penetration of light, as they will likely play a key role as dynamic factors affecting the success rates of tree recruitment in the future. Utilizing a Hierarchical Bayesian Model, our data did not predict a reduction in overall biomass due to decreasing soil moisture as expected. An increase in biomass was predicted with increasing penetration of light as expected, however light penetration did not vary directly with soil aridity as predicted. Based on data collected, a significant bottleneck seems to occur between seedling and sapling stages in tree species present. More in depth (i.e. much larger sample sizes over much more variable gradients of light and soil moisture) studies should be undertaken in order to more fully understand the effects of climate change on tree recruitment. This should yield predictions about changes in forest composition, tree species conservation, and carbon storage moving forward.

INTRODUCTION

The acceleration of human-induced climate change will result in the rapid loss of biodiversity around the world (IPCC, 2002). Changes in the climate have already begun to alter ocean surface temperatures, precipitation patterns, sea levels, and the intensity of El Niño events. Furthermore, climate forecasts have predicted that changes in ecosystems will force species to migrate poleward (Gitay 2002).

The threat of climate change to biodiversity will most significantly impact terrestrial ecosystems due to shifting patterns of species ranges. In the near future, species will exhibit different migration rates as they move through fragmented landscapes that in turn will influence the composition of ecosystems (Gitay 2002).

Plant migration can provide us with a useful framework for forecasting the impact of climate change on species ranges (Clark 2001). Although the majority of seeds are dispersed close to the plant, migration of plant species is driven by rare long distance dispersal events. Dispersals commonly occur via wind or animals. Wind dispersals are generally more predictable since short distances take place under fair weather conditions while longer distances are often associated with storm occurrences under severe weather conditions (Neilson 2005).

It's widely recognized that predicting biodiversity under future global climate scenarios remains a challenging task (Ibáñez 2006, Neilson 2005). However, the underlying assumptions of this complexity does not shed any light on viable mechanistic studies that attempt to understand the effects of climate change on species distribution at varying geographical scales

(Thuiller 2008).

Substantial increases in temperatures in the coming century will substantially impact species composition on a global scale. For example, in the state of Michigan climate models have predicted that by 2030 the region will become much drier due to increased evaporation and transpiration, closely resembling current summer temperatures of Ohio (Union of Concerned Scientists 2003). Therefore, increased arid regions in the state of Michigan will drastically alter forest composition, soil moisture, topography, and dispersal events (Ibáñez 2008). Species may not be able to survive in habitats were the underlying habitat conditions have changed and will therefore be forced to migrate to higher latitudes.

This study provides a mechanistic understanding of how tree species recruitment is differentially impacted by climate change. We assessed the impact of climate change modeled using environmental gradients of soil moisture and light will affects tree biomass. We also examined bottleneck occurrences at the seedling, sapling, and adult stages under varying environmental conditions. We used a hierarchical Bayesian modeling approach (Ibáñez 2008) to estimate parameters.

METHODS

This study was conducted on Saturday, October 4th at the ES George Reserve. Ten plots, ten by ten meters each were set up on a large slope. The approximate locations of the transects are shown in orange on the map of the ESGR below.



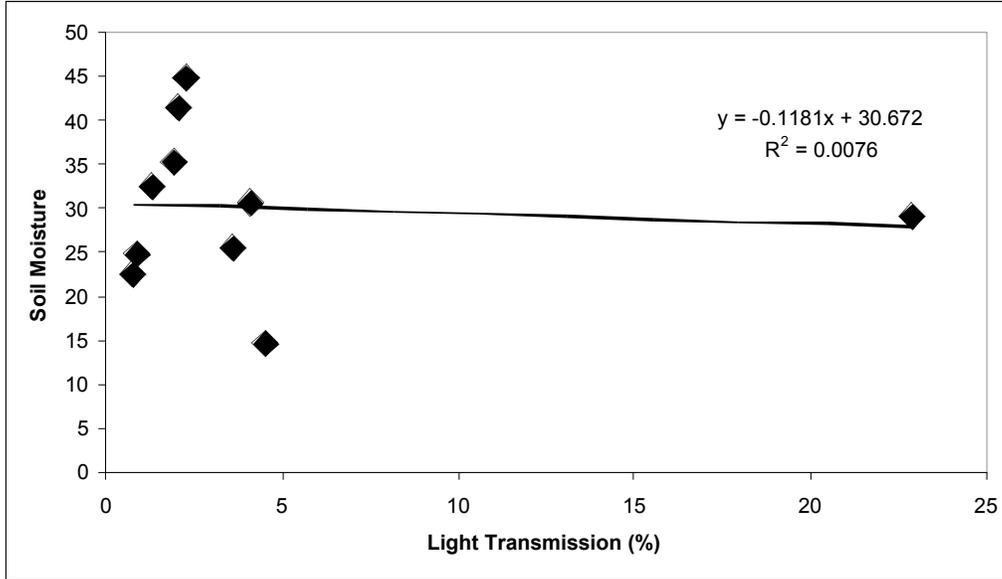
Plots were selected at varying points along the slope in attempt to obtain a gradient in the soil moisture content of the plots. In each plot, we measured the diameter at breast height (DBH) of all adult trees, counted the number of saplings, and counted the number of seedlings in one fourth of the plot. We measured soil moisture in ten locations within each plot using an M3000 soil moisture meter (Aquaterr Instruments Inc., Costa Mesa, CA) and took ten light transmission measurements per plot using an LAI-2000 analyzer (LI-COR Inc., Lincoln, NE).

We used a hierarchical Bayesian model to analyze our data. We used this model to estimate the number of seedlings (λ) at time i as a function of soil moisture and light in relation to the number of adults in each plot and estimate the number of saplings as a function of soil moisture and light in relation to the number of seedlings in each plot. The structure of the model was $\text{Log}(\lambda_i) = \alpha_1 + \alpha_2 * \text{cm}^2 \text{bai} + \alpha_3 * \text{soilmi} + \alpha_4 * \text{light}_i + \epsilon_i$ where α_1 is the intercept, $\text{cm}^2 \text{bai}$ is basal area of adult plants, soilmi is soil moisture, light_i is light, and ϵ_i is error.

RESULTS

The relationship between soil moisture degree and forest light transmission from the same site were investigated (fig.1), no significant correlation was detected.

Figure 1. Soil moisture is independent of light.



Based on the Hierarchical Bayesian Model, the effects of adult tree basal area (represent the effect of adult tree), soil moisture and light transmission on the abundance of seedlings were estimated. The effect coefficients of those parameters were represented by the Mean Value (table 1). Similarly, environmental effects on saplings were also estimated (table 2).

Table 1. Parameter affecting seedling abundance.

Parameters	Mean	Std. Error	Lower Limit	Upper Limit	Trend
Seedling Intercept	5.07	0.08	2.62	7.38	
Effect of Basal Area	0.00	0.00	0.00	0.00	None
Effect of Soil Moisture	-0.03	0.00	-0.11	0.04	Negative
Effect of Light Transmission	0.07	0.00	-0.03	0.20	Positive

Our data shows that the adult trees have no significant effect on the growth of seedlings. While the increasing of soil moisture degree shows slightly negative effect on seedlings and the rising light transmission shows somewhat positive effect. However, all the trends are not significant enough to indicate a strong relationship.

Table 2. Parameter affecting sapling abundance.

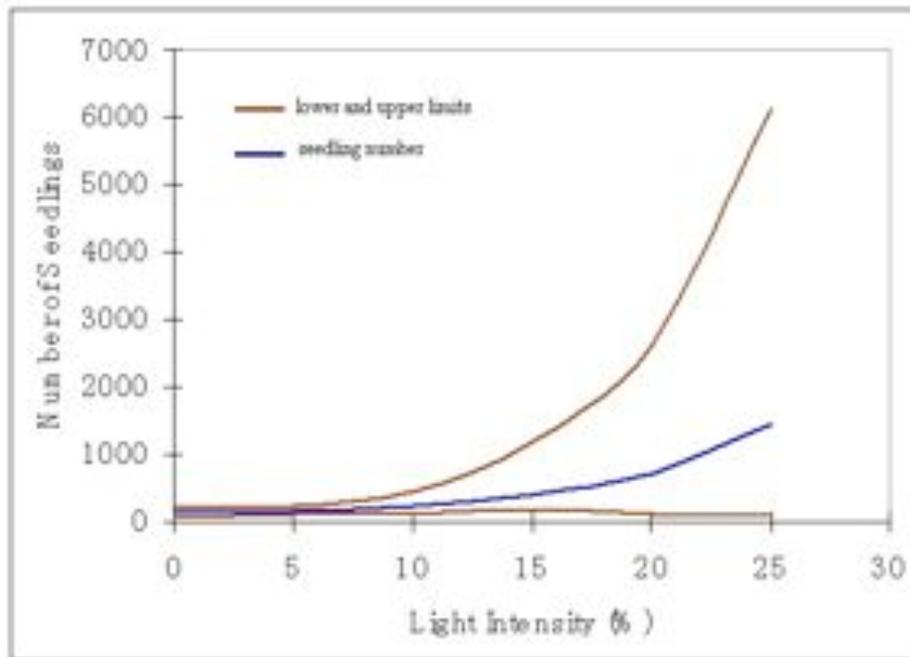
Parameters	Mean	Std. Error	Lower Limit	Upper Limit	Trend
Sapling Intercept	3.10	0.13	-0.62	7.30	

Effect of Basal Area	0.00	0.00	0.00	0.01	None
Effect of Soil Moisture	-0.04	0.00	-0.18	0.07	Negative
Effect of Light Transmission	-0.06	0.00	-0.25	0.15	Negative

In terms of saplings, the adult trees also don't show any great effect on the saplings, but the increasing soil moisture and light transmission both have negative effects on the grow of saplings, though not significant.

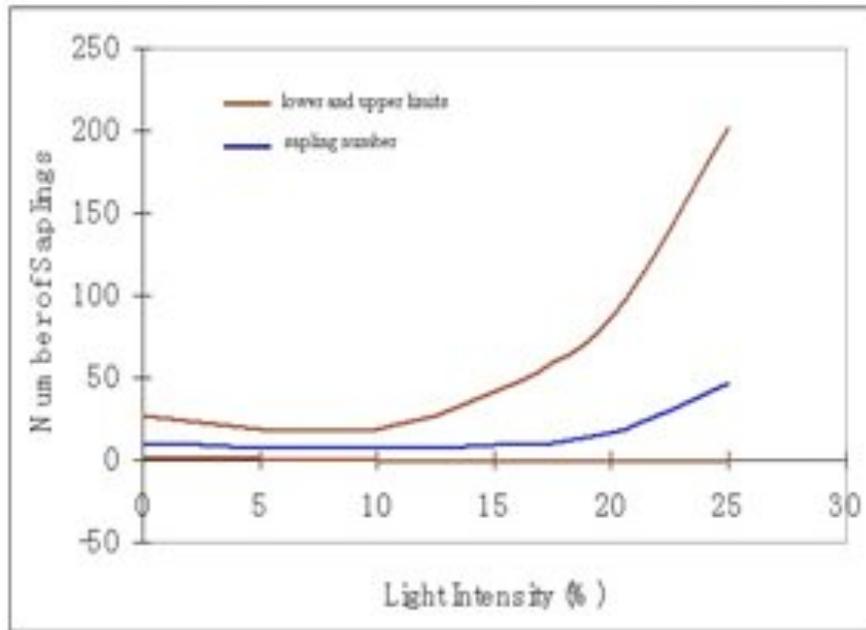
By inputting those coefficients calculated from our data back to the functions, we were able to predict the growth trend of seedling or saplings under given environmental conditions (fig. 2, 3, 4,5).

Figure 2. Number of seedlings per plot increases with light intensity (canopy light transmissions).



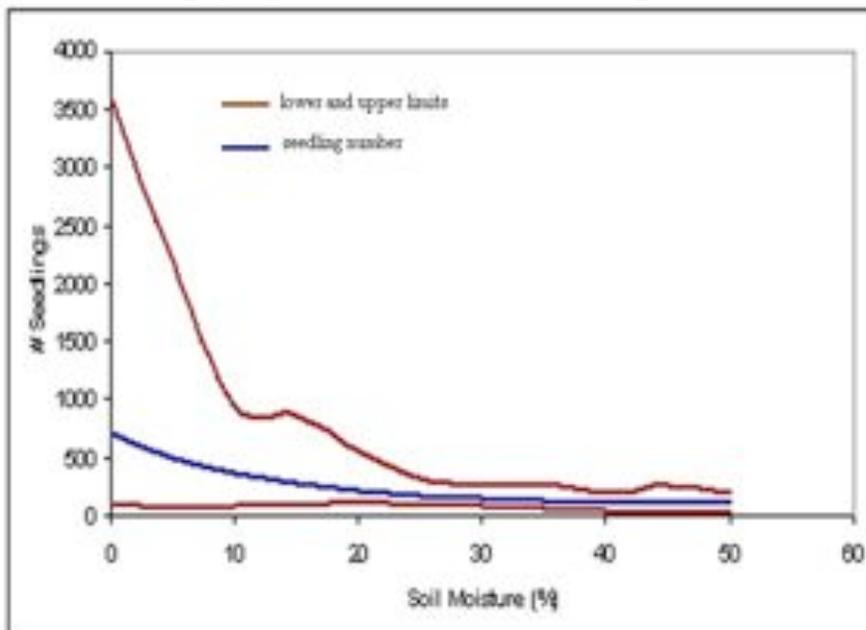
From our model, with the light intensity increasing from 5% to 25%, the seedling abundance should increase accordingly.

Figure 3. Number of saplings per plot increases with light intensity (canopy light transmissions)..



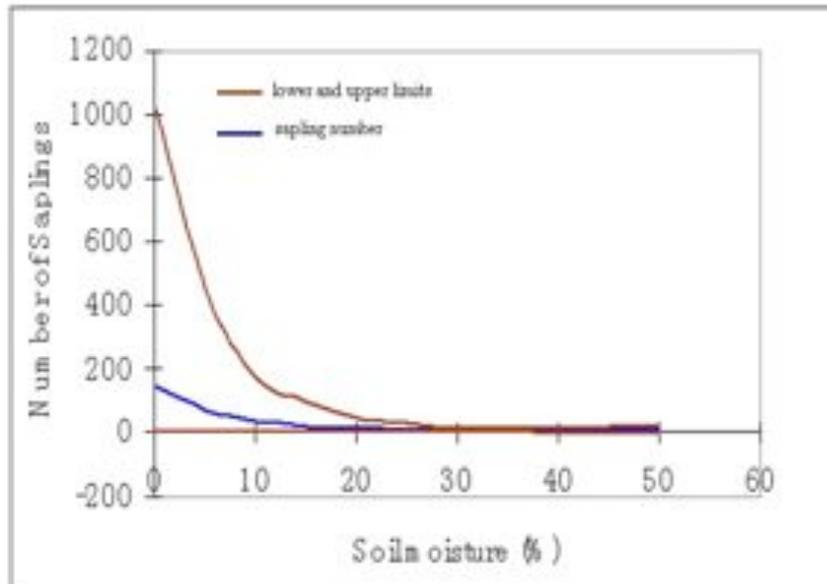
For the sapling model, the increasing of light intensity from 5% to 25% should also result in the growth of seedling abundance.

Figure 4. Number of seedlings per plot decreases with increasing soil moisture.



Since the soil moisture has a negative effect on seedlings with the increasing of soil moisture percentage, the number of saplings should decrease rapidly.

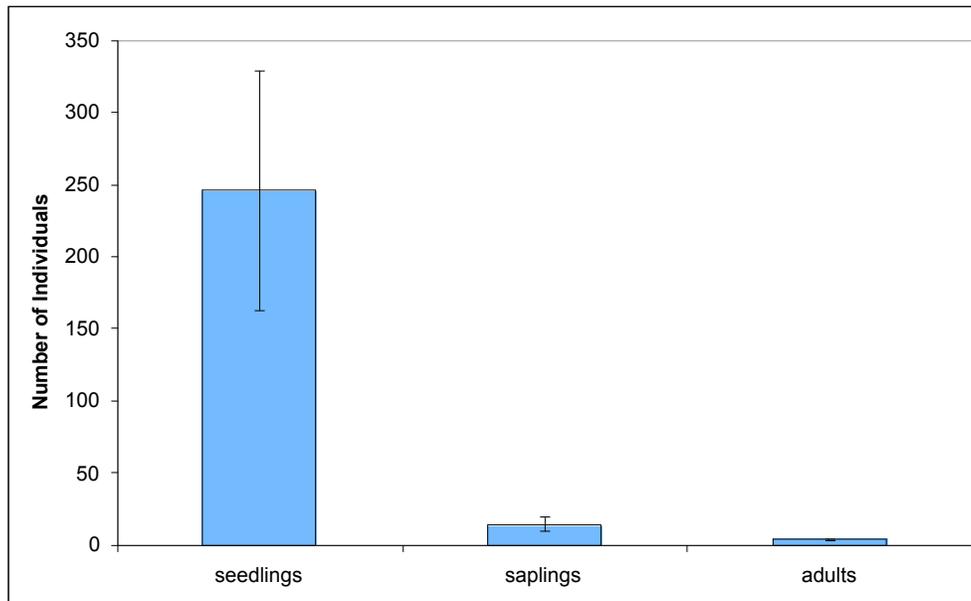
Figure 5. Number of seedlings per plot decreases with increasing soil moisture.



The same pattern was seen for saplings, with the increasing of soil moisture percentage, the number of saplings should decrease rapidly.

We also compared the total numbers of seedlings with saplings and adults (fig.6). The amount of individual seedlings is significantly larger than the other two.

Figure 6. Number of individuals in each life stage.



DISCUSSION

Our primary purpose in this study was to look at how climate change, modeled using a gradient of soil humidity and light penetrance, will impact the overall biomass (modeled using abundance of seedlings and saplings) of trees. Our model predicts that aridity will not drive a reduction in tree abundance as expected, but instead will promote an increased overall biomass. Abundance of both seedlings and saplings did increase with increased light availability, but light penetrance did not vary directly with soil aridity as predicted.

It is important to note that soil moisture, light penetrance, and adult biomass variables were not significant predictors in our model. Though it is possible soil moisture and light availability are not fundamental drivers of tree regeneration, it is unlikely adult biomass bears no significant relationship to future tree abundance. These results are likely an artifact of experimental design and small sample size.

Modeling aridity using a soil humidity gradient requires a more even distribution of sampling at a finer scale gradient than that used for this experiment. Furthermore, soil conditions were largely unpredictable with the least arid sites located at the most elevated sampling locations. Light measurements were taken systematically at 10 points. Since eight of the 10 points were along the edge of the quadrant, light measurements may not have accurately represented the average conditions present in the plot.

Models predicting impacts of climate change require a large sample size followed over a long period of time (Ibáñez *et al.* 2008, Guisan & Thuiller 2005). Previous models incorporating soil humidity, adult biomass, and light availability have predicted tree biomass to decrease with reduced humidity and reduced adult biomass (Ibáñez *et al.* 2007, 2008).

Future studies should incorporate a greater sample size over a larger gradient of soil moisture and light values. In addition, studies should focus on factors influencing the survival probability from seedling to sapling since that appears to be the most significant bottleneck. Incorporating tree species into this model may also be important factor because the rate of carbon sequestration varies among species (Bachelet *et al.* 2001). Currently northern forests are experiencing a shift as hardwoods are replaced by red maple (*Acer rubrum*) and invasive shrubs, such as autumn olive (*Elaeagnus umbellata*). As the community composition shifts, the value of woody biomass in terms of carbon storage may change dramatically. More research is needed before the affect of climate change on forest composition and carbon storage can be adequately predicted.

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Measuring Woody Biomass and Above-ground Carbon Storage in Four Habitats Types on the E.S. George Reserve.

Dana Thomas, Huijie Gan, Leiling Tao, Andy MacDonald, Ashley Larsen,
Dr. Kathleen Bergen

ABSTRACT

Forests are dynamic ecosystems that provide a number of important ecosystem services including habitat structure and carbon sequestration. Recently, carbon sequestration has become a hot spot of ecological research as scientists struggle to understand the various carbon sinks, and how climate change will affect and be affected by those sinks. Since above-ground biomass is directly related to carbon storage, quantifying woody biomass lends insight into how forests are retaining carbon. Using biomass allometry equations, we investigate the distribution of biomass and stored carbon among closed forest, lowland forest, swamp and old field habitats, and examine whether tree species richness relates to woody biomass in the different habitats. We find the lowland forest stores the most carbon, followed by the closed forest, the swamp, and the old field. There was no relationship between tree species richness and biomass. ()

INTRODUCTION

Plant ecologists have for decades been interested in estimating the biomass of individual tree species (Ter-Mikaelian and Korzukhin 1997). Allometric equations relating traits such as diameter at breast height (DBH) and total height to aboveground biomass have been created for many species. Such equations are often developed in studies of forest production and forest fuel estimation, and require destructive sampling (Ter-Mikaelian and Korzukhin 1997). The use of existing equations in biomass estimations offers a sustainable alternative to destructive methods. Ter-Mikaelian and Korzukhin (1997) present a useful synthesis of biomass equations for North American tree species. By providing a review of equations created across various studies and geographic regions, they allow for a better approximation of aboveground woody biomass. In recent years, allometric biomass equations have extended beyond single-stemmed trees to include multi-stemmed individuals such as *Elaeagnus angustifolia* (Zhou et al. 2007).

Quantifying above-ground woody biomass gives ecologists insights into ecosystem services such as habitat structure and biodiversity and carbon storage. A current focus of remote sensing is the creation of maps defining the locations of known species occurrences, as well as the potential locations of these species based on similarities in habitat characteristics (Bergen et al. 2007). Bergen et al. (2007) are working to model multidimensional habitat space of bird species in Northern Michigan. Their research suggests that models including forest and landscape structure parameters

such as vegetation type, spatial neighborhood descriptions, and biomass are more accurate in predicting bird species habitat (Bergen et al. 2007).

Measurements of biomass in forest ecosystems can be used as a proxy for estimating carbon stored in above-ground wood mass. Carbon is commonly extracted as 50% of total biomass. The capacity of temperate forests to store carbon has received considerable attention in recent years (Gough et al. 2008). Forest carbon storage is an important ecosystem service, locking up carbon that might otherwise exist as carbon dioxide, a potent greenhouse gas (Gough et al. 2008). In the Northern hemisphere, forests are estimated to sequester up to 7×10^8 metric tons of carbon annually, or nearly 10% of current global fossil fuel carbon emissions (Gough et al. 2008). Gough et al. (2008) have observed forest carbon to occur primarily in wood mass and soil organic matter, with above- and belowground pools containing 42% and 58% respectively of the 180 metric tons of carbon per ha stored in ecosystems.

Variations exist in the capacity of individual forest ecosystems to take up and store carbon. The amount of carbon stored in a particular region will be influenced by factors such as climate change, disturbance, and forest age, and forest type. Increased atmospheric carbon dioxide, elevated nitrogen deposition, and intensified forest management is expected to reduce annual carbon storage in temperate forests (Hyvonen et al. 2006; Gough et al. 2008). Significant disturbance has also been shown to have a negative impact on forest carbon storage (Gough et al. 2008). Forest age and type play a noticeable role in carbon storage (Pregitzer and Euskirchen 2004). Old growth forests for example have been shown to act as carbon sinks (Luyssaert et al. 2008). Douglas fir forests on average store 100 tons of carbon per hectare in living aboveground biomass, while Eastern Oak-Hickory forests store on average 75 tons of carbon per hectare (Potter et al. 2008).

Obtaining an estimate of above-ground woody biomass in a particular region is thus important for making predictions of habitat structure and biodiversity, as well as estimating carbon pools and predicting the carbon budget in response to climate change, land use, and forest management (Wang et al. 2008). Our study provides a basic measurement of woody biomass and carbon distribution in four different habitat types on the E.S. George Reserve. Using biomass allometry equations developed for different tree species, we examined at how woody biomass and carbon are distributed on the George Reserve, the proportion of biomass occurring in the canopy, and whether any relationship exists between tree species diversity and woody biomass within each habitat.

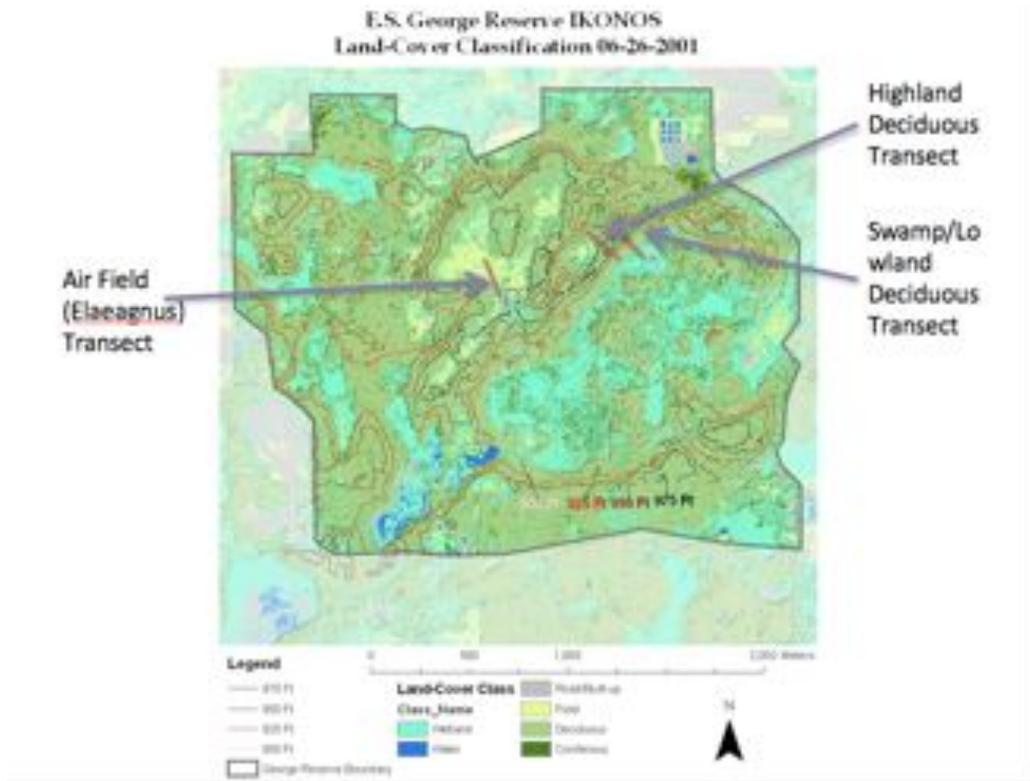
METHODS

Study site

Our study was conducted inside the E.S. George Reserve, a 1500-acre fenced preserve located in Southeastern Michigan. We completed ground-truth measures of biomass in four habitat types across the Reserve. Ground-truthing is an important part of biomass mapping with remote sensed imagery. Forest stands are sampled using a standardized

plot-transect method, and observed measurements are compared to mapped images. We selected a total of three transects encompassing four distinct habitat types. Transect 1 represented the upland deciduous forests, transect 2 represented both swamp and lowland deciduous forest, and transect 3 an open old field dominated by *Eleagnus umbellata*. Each transect was initiated along a particular azimuth (325°, 145° and 320° respectively) (Figure 1).

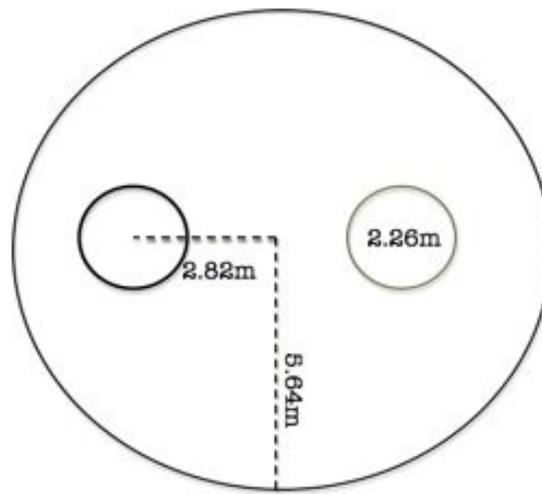
Figure 1. Locations of the three transects within the E.S. George Reserve.



Field Sampling

Within each transect, 2 to 5 plots were established at 25 meters intervals. Individual plots encompassed both a “large plot “ (100 m²) and two “subplots” (16m² each), with radius of 5.64m and 2.26m respectively. The center of the large plot was 2.82 m away from the center of the subplots (Figure 2). Within the larger plots, the diameter at breast height (DBH) of over story trees (DBH>9cm) was measured. In subplots, only the DBH of understory trees (DBH 3-9cm) was measured. When measuring multiple-stemmed individuals (*Eleaganus umbellata*), three DBH measurements were taken for each tree: one at the main trunk and two at the largest branches.

Figure 2. Diagram of plot layout.



Biomass and Carbon Estimation

For upland, lowland and swamp deciduous forests, allometric equations for calculating the biomass of different tree species followed the basic format:

$$M=aD^b.$$

Where M corresponds to total biomass, D stands for DBH, and a and b are allometric parameters for acquired species (Ter-Mikaelian and Korzukhin 1997). For multi-stemmed *Eleaganus umbellata*, biomass was estimated using a cost-saving preferred method (Zhou et al. 2007). The cost-saving preferred method takes into account both trunk and stem measurements and follows the format:

$$M_T=0.3019D_{10}^{1.733}$$
$$M_B=5.067 \times 10^{-2}(\text{sum}D_{ij}^2)$$
$$M=M_T+M_B$$

Where D stands for DBH, M_T corresponds to trunk biomass, M_B to stem biomass, and M to total biomass (Zhou et al. 2007). Biomass measurements for each habitat type were standardized by area. Above-ground carbon within each habitat was estimated as 50% of the total biomass.

RESULTS

Biomass estimated varied greatly between the four different habitat types (Figure 3). The lowland Forest has the largest biomass per area (kg/ha) while Old Field has the least biomass (kg/ha) (Figure 3). The biomass of the swamp, measured just 25 meters away from the lowland forest plot, was only about 10% of that of the lowland forest (Figure 3). The carbon storage distribution shows similar pattern. Carbon estimates correspond closely to previous studies suggesting the Eastern Oak-Hickory forests to on average store 75 tons/ha of carbon (Potter et al. 2008). The proportion of biomass allocated to the overstory and understory was similar among closed forest, lowland forest and swamp, with the percentage of overstory biomass over 90% (Figure 4). In old field, only 50% of the biomass came from the overstory.

Figure 3. Distribution of biomass within the E.S. George Reserve (kg/ha).

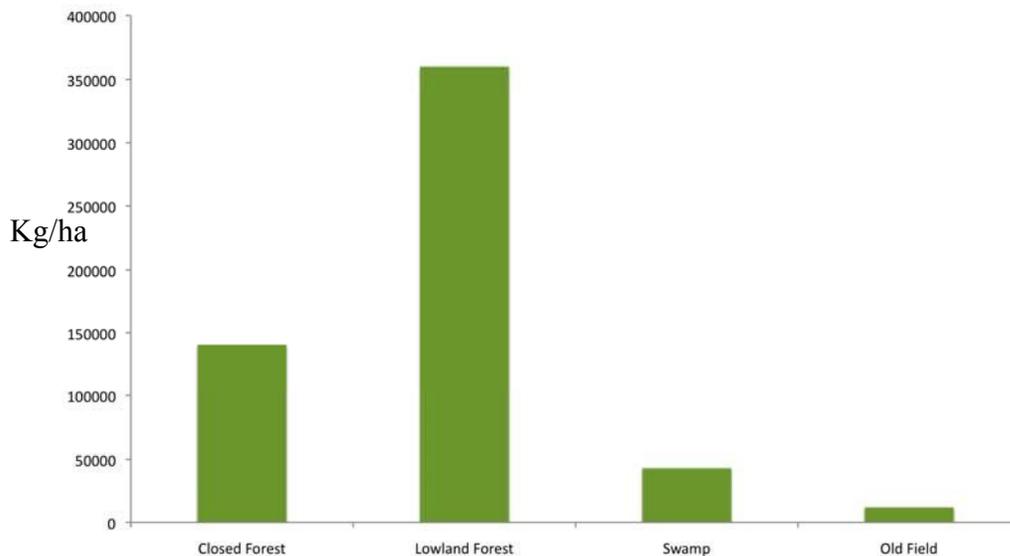
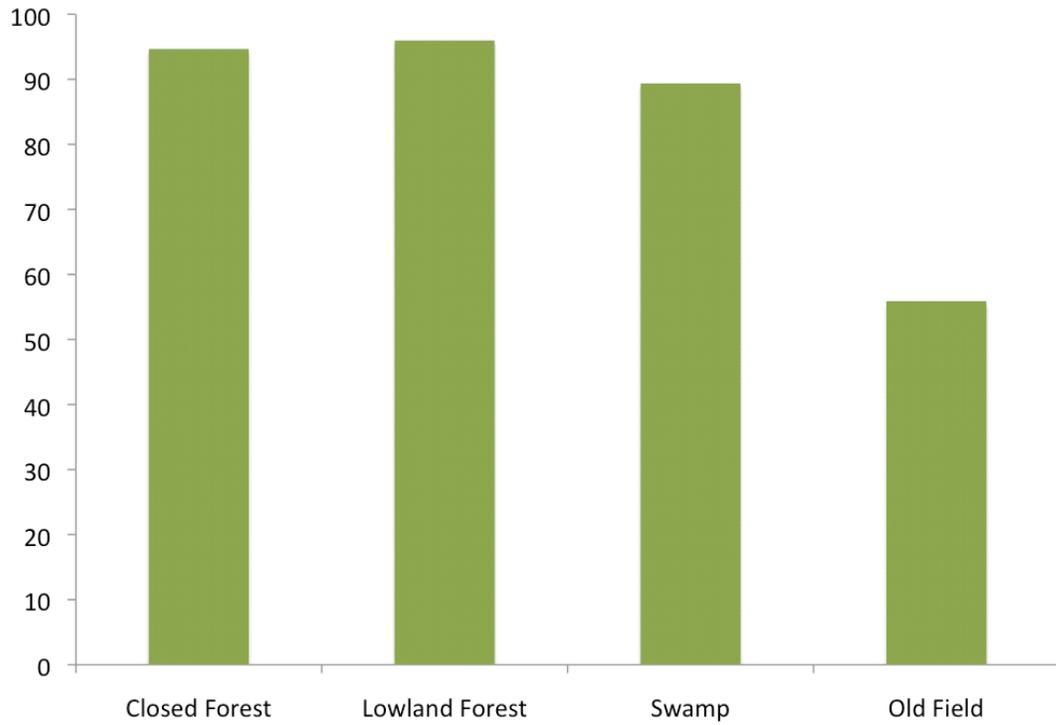
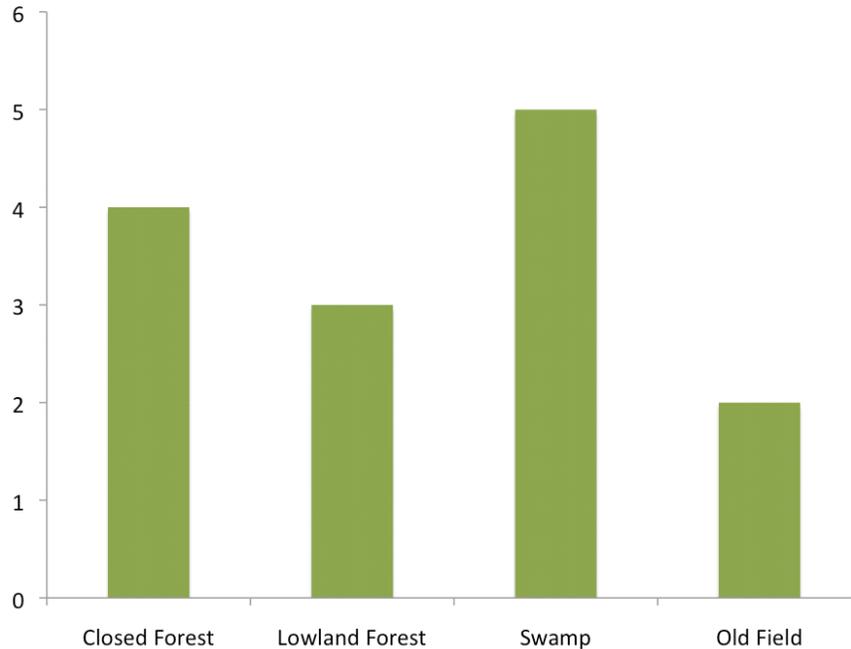


Figure 4. Proportion of above-ground biomass present in the overstory as opposed to the understory within each habitat.



Tree species richness in each of the four stands was fairly similar, with the highest of 5 species occurring in swamp and a low of 2 species in our plot survey in the old field (Figure 5). There was no clear observed trend between the distributions of species richness and biomass.

Figure 5. The number of tree species occurring in each of the four habitats.



DISCUSSION

Our results suggest the moist lowland forest plays an important role in above-ground carbon storage within the E.S. George Reserve. The total carbon stored in the lowland forest sampled in this study more than doubled that of all other habitat types sampled. Neither an increase in species richness nor a change in allocation to overstory biomass was observed within the habitat, suggesting some other mechanism(s) are contributing to this observed increase in biomass and carbon storage.

For example, over story stem-density may have a much greater impact on carbon storage potential than does species richness or diversity. Density is likely a product of a number of factors such as tree species present, soil moisture, and soil type. The lowland forest sampled had, based on observations, a much higher soil moisture level than did the old field and closed forest, which could explain the higher levels of carbon storage in the lowland forest sample. The shift in species present in the swamp as soil moisture increases and type changes could account for the observed drop in carbon storage levels in that particular habitat type.

A small sample size was a limiting factor in this study. A larger, more comprehensive sample both within and among the four habitat types would have produced much more certainty in our results. In order to compare ground truth measurements to remotely sensed images and extract a better biomass estimate, it would be necessary to increase the sample size in order to encompass a larger area and consequently to produce a more accurate picture of the habitat types sampled in general.

Standard ground-truth plot-transect methods typically sample 5 transects, each containing 8 large plots, within each stand.

A large-scale estimation of carbon storage potential for various habitat types within the E.S. George Reserve has important implications for conservation. Knowledge of carbon distribution within and among different forest habitats would offer valuable insight into future management practices within the Reserve. As temperate forests provide a potential carbon sink in the face of increased atmospheric carbon dioxide emissions (Gough et al. 2008).

The application of remote sensing techniques to other facets of forest dynamics, such as net primary productivity (Bergen and Dobson 1999) could, in conjunction with allometric equations for biomass and ground-truthing, provide a better understanding of carbon storage and distribution among habitat types and environmental conditions. For instance, including more comprehensive measurements of conditions such as soil moisture, soil type, and canopy cover could be particularly useful given expected shifts in environmental conditions under climate change.

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A PRELIMINARY ANALYSIS OF LIGHT HETEROGENEITY AND FOREST GAP DYNAMICS WITHIN AN OAK-HICKORY FOREST

DANA THOMAS

ABSTRACT

A major question in forest ecology is how light gaps influence ecosystem processes and promote coexistence and biodiversity among plant community. A large body of research suggests the importance of niche specialization among resource gradients created in gaps in maintaining coexistence. Recent work has illuminated the potential for neutral processes, maintained by factors such as light heterogeneity and recruitment limitation, in promoting coexistence. Advance regeneration, or recruitment of seedlings and saplings that survived the disturbance leading to gap formation, has received attention as a key determinant of forest gap composition. I investigated sapling abundance as a function of crown transmissivity in an Oak-Hickory forest on the E.S. George Reserve in Southeast Michigan. Due primarily to fire suppression, the understory of the forest is becoming dominated by Red Maple and Black Cherry saplings, which will eventually replace the Oak-Hickory canopy. Results suggest variation in sapling abundance in relation to canopy openness. Specifically, Red Maple saplings appear most often at intermediate canopy density. This study offers preliminary insight into the processes influencing the distribution of saplings in the forest understory.

INTRODUCTION

Light gaps are ubiquitous in temperate and tropical forest ecosystems. Gaps are created when one or more trees die, leaving a space in the forest floor (Brokaw and Busing 2000). While large canopy gaps often occupy less than 10% of a forested area, understory gaps, or those that do not allow significant amounts of light through, can occupy over 50% (Boudreau and Lawes 2005). Both canopy and understory gaps are known to influence forest community dynamics. Light gaps increase microclimate heterogeneity, promote coexistence and diversity, and alter forest biogeochemical processes (Brokaw and Busing 2000; Scharenbroch and Bockheim 2008). For instance, tree fall gaps in general have greater soil moisture, soil temperatures, and incoming solar radiation (Scharenbroch and Bockheim 2008). Gaps store less carbon, and contain as much as 75% less leaf litter than a closed understory (Scharenbroch and Bockheim 2008). This in turn impacts organic matter decomposition and nitrogen mineralization (Scharenbroch and Bockheim 2008). Interestingly, gaps tend to be aggregated in forests, showing a tendency to form adjacent to preexisting gaps (Pagnutti et al. 2007). Cluster and size distributions of gap formations and closures in Barro Colorado Island have been shown to follow a power law function (Pagnutti et al. 2007).

Many plant species depend on light gaps for regeneration (Brokaw and Busing 2000). If resources such as light and soil vary predictability within and among gaps, competition could lead to niche specialization on different levels of these resources (Brokaw and Busing 2000). Niche specialization within light gaps is commonly put forth as a mechanism of tree species coexistence (Brokaw and Busing 2000). In a review of forest gap dynamics, Brokaw and Busing (2000) point out that many plant species do perform differently involving establishment, growth, and survival in light gaps. Traditional gap theory assumes that shade intolerant species are best adapted to exploit the high light environment created by canopy gaps (Dietze and Clark 2008). Recent research has suggested that, in most ecosystems, tree fall gaps are in fact not dominated by shade intolerant species (Dietze and Clark 2008). Diversity in light gaps is more often determined by advance regeneration, or recruitment coming from seedlings and saplings that survive disturbance (Dietze and Clark 2008). Persistence of live damaged trees increases understory shade, generates fine scale environmental heterogeneity, and moderates ecosystem response to damage (Dietze and Clark 2008). In a survey of light gap regeneration in southern Appalachian forests, Dietze and Clark (2008) observed recruitment from sprouts to constitute 26 to 87% of early gap regeneration, forming the dominant pathway of regeneration for some plant species. Differences in sprouting ability were large and consistent across different sites. Specifically, *Quercus* and *Carya* species tended to exhibit low sprout recruitment, while *Acer rubrum* occurred primarily through advance regeneration (Dietze and Clark 2008). Variations in sprouting ability suggest the importance of non-neutral processes in determining gap dynamics. However, Brokaw and Busing (2000) suggest that trees species do not show enough differences in distribution or behavior to support that coexistence of many species is maintained by niche partitioning alone.

A growing body of work suggests that canopy gaps might play a neutral role in maintaining species richness, promoting whatever diversity and mix of trees that are locally present in the community (Brokaw and Busing 2000). Chance events can both limit niche partitioning and promote diversity in gaps (Brokaw and Busing 2000). Advance regeneration has been argued to actually reduce gap partitioning, in that regrowth in light gaps will simply be dominated by the tallest advance regenerators (Brokaw and Busing 2000). Recruitment limitation, or the limited ability of tree seedlings to disperse to and establish in gaps, may allow them to be filled by chance assortment of what ever is nearby (Brokaw and Busing 2000). All gaps will inherently experience some degree of light heterogeneity over both short and long time periods. Newly established trees thus must be broadly adapted to cope with this variability, reducing the probability of definite niche specialization to different light levels (Brokaw and Busing 2000). The long held view of the positive correlation between gap size and plant diversity has recently been observed to often actually just be a function of greater stem densities in larger gaps (Brokaw and Busing 2000). It is quite possible that coexistence and diversity in forest communities are determined by a combination of niche and neutral processes (Brokaw and Busing 2000).

The influence of forest gap dynamics and light heterogeneity on sapling abundance, growth, and mortality in was examined in an Oak-Hickory forest on the E.S.

George Reserve in Southeast Michigan. Due to reduced fire intensity, the dominant tree species composition in the forest is shifting to a Red Maple-Black Cherry demography. Ecologists are thus interested in under what conditions Red Maple saplings are able to survive and grow under the Oak-Hickory canopy. The current study asks:

1. How is the abundance of Red Maple, Black Cherry, and Witch Hazel saplings affected by canopy openness?
2. How are the growth rates and mortality of Red Maple, Black Cherry, and Witch Hazel saplings affected by canopy openness?
3. Does the size of the open space influence the abundance of saplings?

METHODS

A 500 meter transect was set up along a 260 degree azimuth on the North Slope of the Big Plot (Figure 1). Data was not collected from the first 50 meters of the transect, but instead the initial section was used to develop an optimal mode of data collection. From 50 meters to 500 meters, a densitometer reading was taken every two meters. A crown transmissivity chart was used to record the relative openness of the canopy (1%=canopy gap; 100%=closed canopy). Every ten meters, the tag of the nearest tree was recorded.

Figure 1. Map of the E.S. George Reserve showing the approximate location of the 500 meter transect located in the Big Plot.

In order to obtain the distribution of saplings along the transect, the coordinates of each tagged tree were recorded referencing the master Big Plot data file. Data could then

be extrapolated for all saplings under 20 meters within a 5 meter radius of the entire transect.

The abundance of Red Maple, Black Cherry, and Witch Hazel saplings was plotted as a function of canopy openness. Abundance distributions were then compiled for high light (1-25% canopy cover), medium light (26-50% canopy cover), and low light (51-95% cover). A Chi-Square Goodness of Fit was performed to look for differences in abundance at various light levels. Average relative growth rate and frequency of mortality was compiled for each crown transmissivity level and a regression analysis performed to observe growth rate and mortality as a function of canopy openness.

RESULTS

A total of 387 Red Maple, 124 Black Cherry, and 332 Witch Hazel saplings were included in the analysis. Abundance of each species varied significantly between low, intermediate, and high canopy openness ($p= 4.90 \times 10^{-12}$; Figure 2). Preliminary analysis suggests that, while Black Cherry saplings do not appear to be more abundant at particular degrees of canopy openness (Figure 3), Red Maple saplings occur at a greater frequency at intermediate openness (Figure 4) and Witch Hazel at low-intermediate openness (Figure 5).

Figure 2. Distribution of the abundance of Red Maple, Witch Hazel, and Black Cherry saplings at low, medium, and high canopy openness.

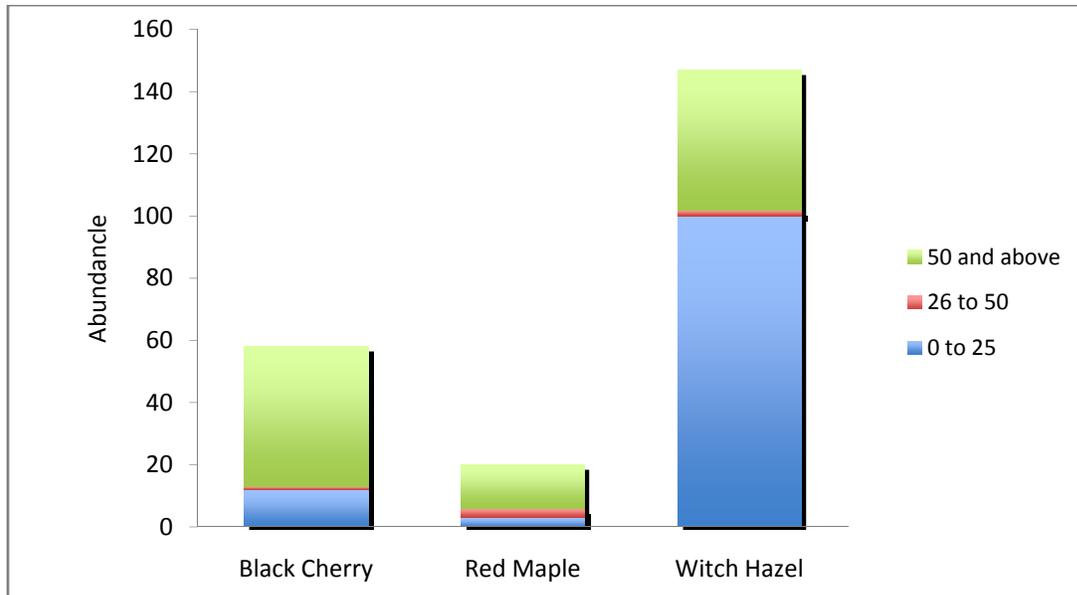


Figure 3. Abundance of Black Cherry saplings at varying degrees of canopy openness (100=closed canopy).

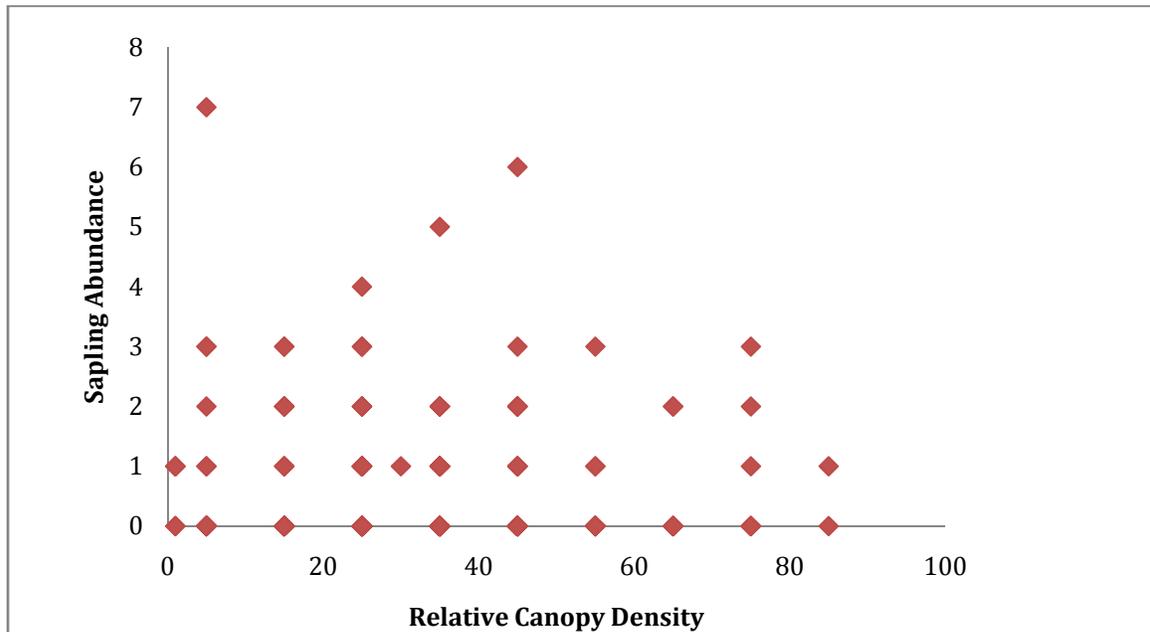


Figure 4. Abundance of Red Maple saplings at varying degrees of canopy openness (100=closed canopy).

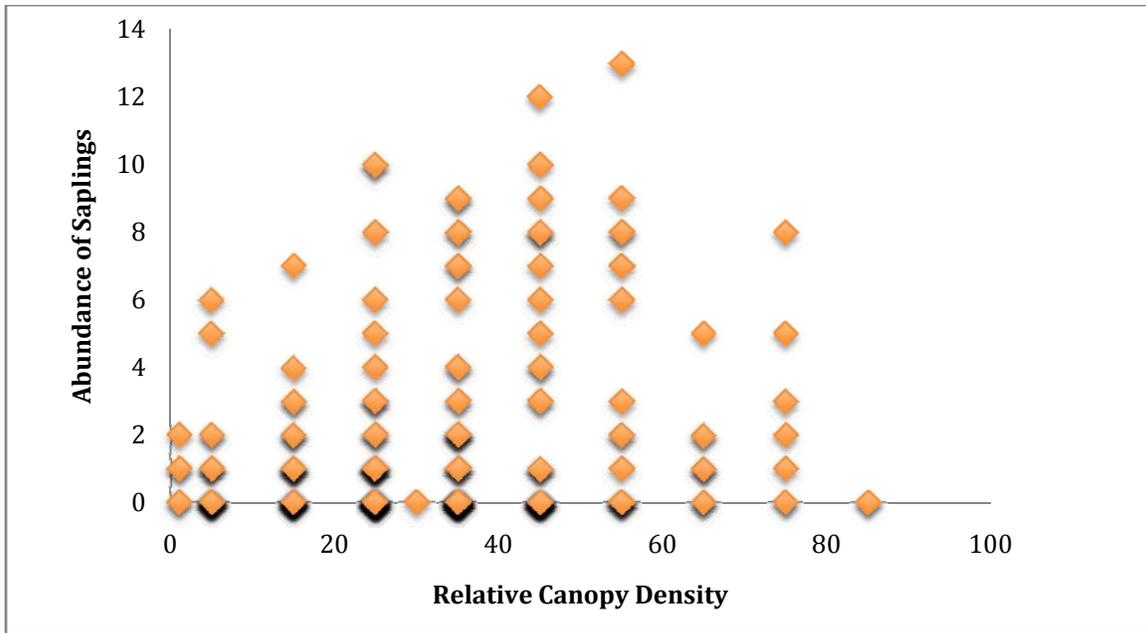
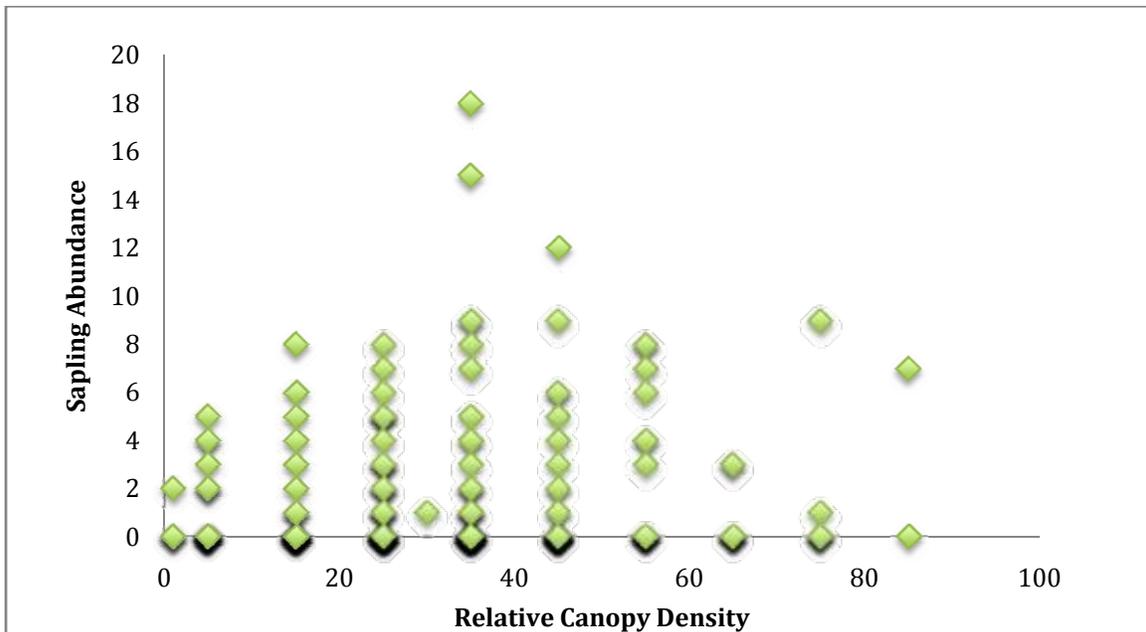


Figure 5. Abundance of Red Maple saplings at varying degrees of canopy openness (100=closed canopy).



Strong trends were not observed for average relative growth rate (Figure 6) or mortality (Figure 7) of saplings at varying levels of canopy openness. No trend was observed for stem density per area as a function of gap size (Figure 8).

Figure 6. Average relative growth rate of saplings at varying relative canopy densities.

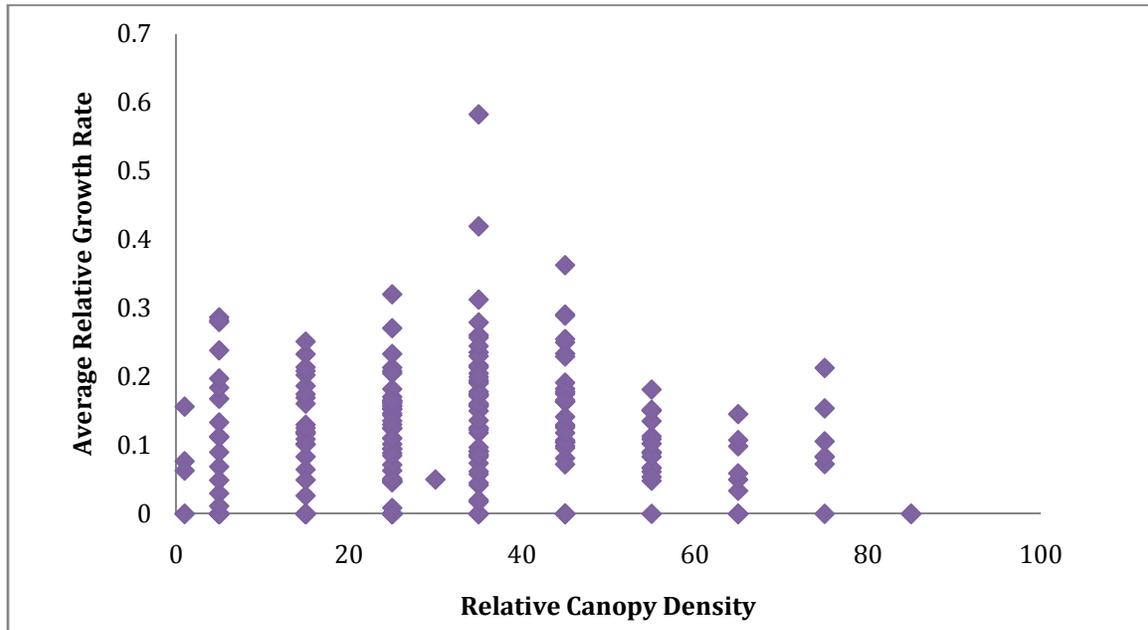


Figure 7. Average proportion of saplings that died in 2008 at varying canopy densities.

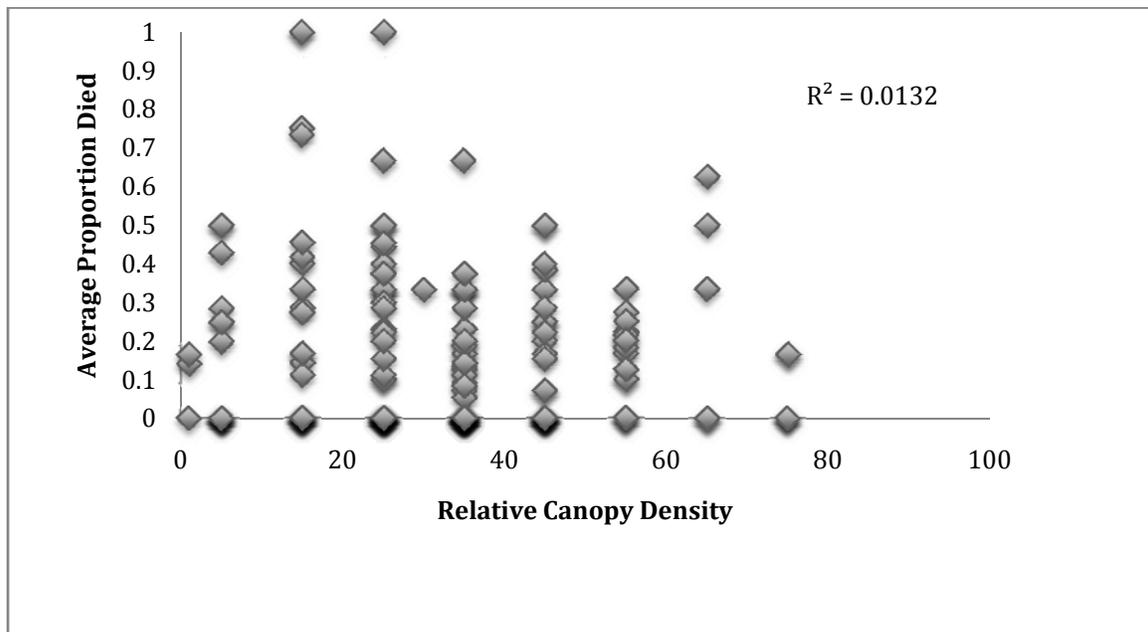
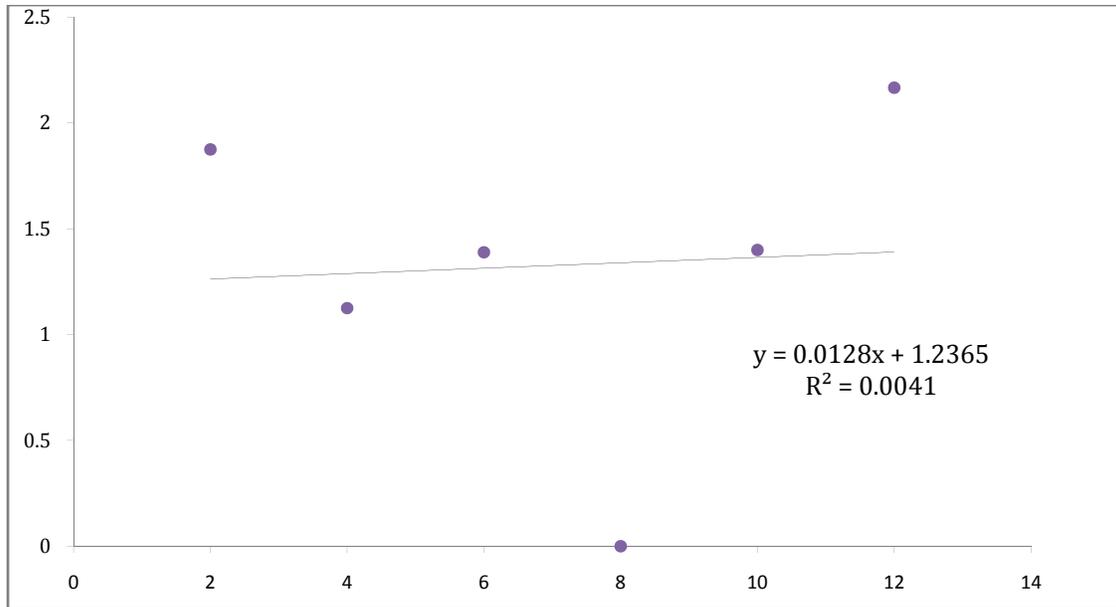


Figure 8. Average sapling abundance per gap area plotted against gap area.



DISCUSSION

While few concrete conclusions can be inferred from the present study, results suggest that saplings in the Big Plot do respond differentially to variations in canopy openness. This suggests that exogenous factors such as light heterogeneity might play a role in influencing sapling distribution. Red Maple, a species commonly classified as ‘shade tolerant’ appears to do best under intermediate canopy openness. It is possible that open, high light understory conditions could favor the establishment of opportunistic shrubs such as *Berberis thunbergii*, while closed canopy conditions do not allow for adequate resources for seedlings to grow. Black Cherry and Witch Hazel, two less ‘shade tolerant’ species, appear to be less partitioned according to canopy openness and thus able to regenerate under a greater variety of conditions. The general intermediate openness of the understory of the Big Plot thus might provide an optimal condition for regeneration of Red Maple in addition to fire suppression.

It is important to note that a densiometer serves as only an approximation of both light heterogeneity and canopy openness. The north slope of the Big Plot was sampled in order to minimize variations in daily light intensity, though, inherently, densiometer measurements do not begin to fully capture understory light levels. Often light coming in from an angle could not be counted as a gap, as the above canopy was still extremely dense. It would be extremely beneficial to actually measure light coming into the understory.

Results show that saplings show some variation in their abundance under varying canopy densities, suggesting at least some degree of niche partitioning as a function of light heterogeneity. In order to truly gain insight into whether sapling abundance is controlled by niche or neutral processes (or a combination of the two), it would be necessary to consider the spatial distribution of forest gaps in relation to adult trees and saplings. Thus, the transitioning tree demography within the Big Plot offers ample future opportunity to examine gap dynamics in the forest.

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NO DIFFERENCE FOUND IN LEAF LITTER ARTHROPOD COMMUNITIES ACROSS THREE FOREST TYPES IN THE ES GEORGE RESERVE

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HUIJIE GAN, IVETTE PERFECTO

ABSTRACT

Arthropod community diversity in forest leaf litter layer was examined in E. S. George Reserve, located in Livingston County, Michigan. Three different habitats were studied, including predominantly oak forest, old red pine plantation forest and mixed forest comprising cherry, maple, oak, and hickory. The purpose of our study was to examine relationships between the forest leaf litter type and arthropod diversity. Arthropods were collected within one day, from nine sampling sites. For our sampling method we used sifting bin to collect arthropods from leaf litter. We also recorded the environmental parameters of each sampling sites, including ambient temperature, the average soil depth and soil PH. We obtained a total number of 140 specimens belonged to 65 morphospecies in 15 orders. The most abundant arthropods groups are ants, spider and beetles. We found no differences in species richness among the three different leaf litter types. But our results suggest that sampling sites shared same forest type and close locations tend to have more similar composition of arthropods species.

INTRODUCTION

In temperate forests, the top few centimeters of soil and the accumulated leaf litter is a compressed region of intense biological activity. Leaf litter and its decomposition are a vital part of ecosystem function. It plays two important roles in forest ecosystems: firstly, litter fall is an inherent part of nutrient and carbon cycling, and secondly, litter forms a protective layer on the soil surface that also regulates microclimatic conditions (Sayer, 2006). Arthropods are the most speciose animal group on earth, they consists approximately 75% of all currently known living and fossil organisms. Arthropods are also ubiquitous components of forest leaf litter, acting as predators and prey, contributing to decomposition of organic matter, and to the turnover and transport of chemical elements to the soil–litter interface (Peterson and Luxton, 1982). Small changes in arthropod communities may have major effects on local nutrient dynamics (Heneghan & Bolger 1998).

E.S. George Reserve (ESGR), located about 25 km northwest of Ann Arbor, was forested mainly by oak woodlands. Other vegetation covers also includes pine, hickory and cheery, etc. However, the forests are undergoing a successional shift in species composition. Parts of the oak forests are being colonized by more opportunistic tree species like red maple and invasive autumn olive. Before European settlement, oak was the dominant genus in the forests throughout much of what is now the eastern United States. Among the oaks, white oak (*Quercus alba*) reigned supreme (Abrams 1998). Red maple was generally limited to swamps and other areas sheltered from fire because it is much more sensitive to fire than is red oak and therefore would have been less common

on uplands. After 1900, the shade tolerant red maple quickly expanded out of the protected areas and started to dominate most forest understories throughout its range because the suppression of understory burning (Abrams 1998, 2003). In consequence, the composition of forest leaf litter layer is influenced by such transition, which might potentially affect the diversity of leaf litter arthropods community and nutrient cycling.

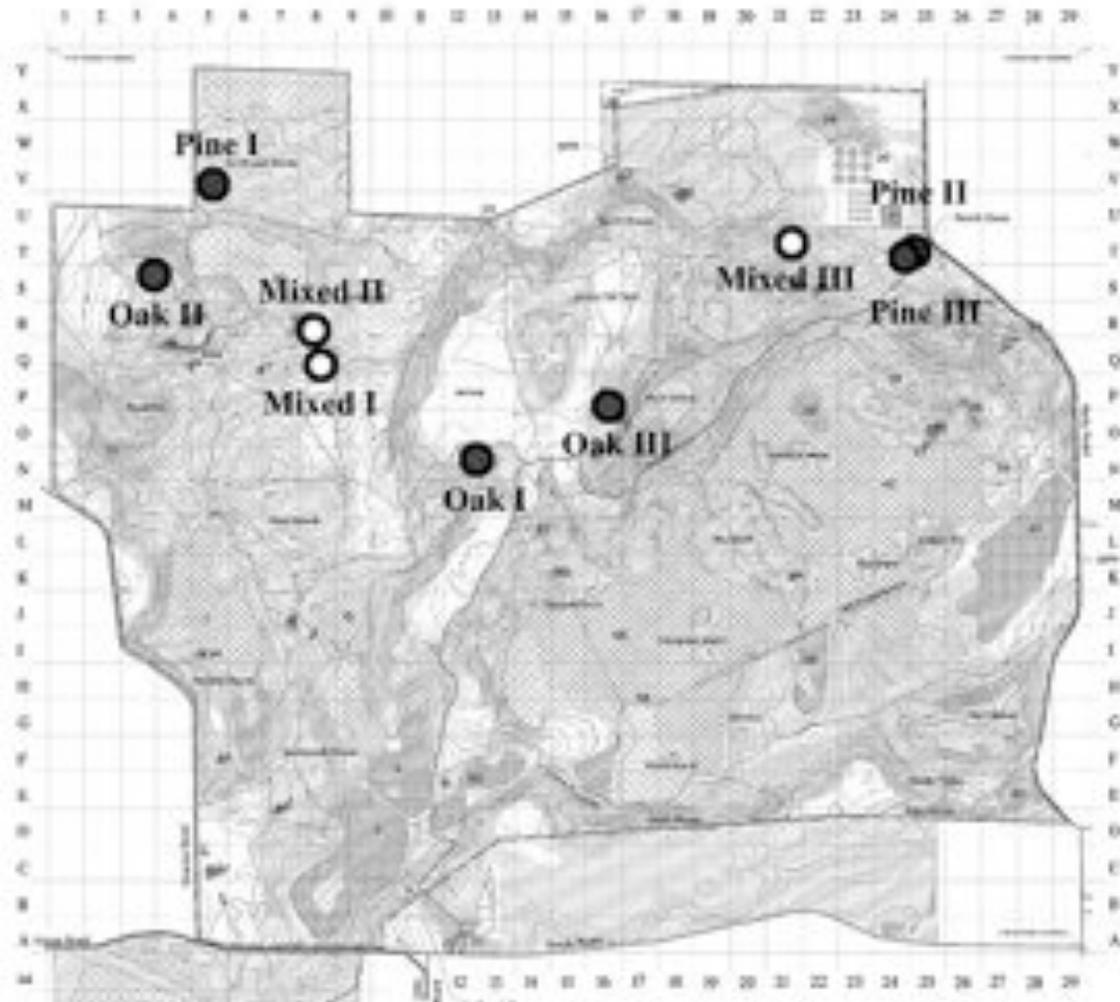
In the George reserve, arthropod assembles in leaf litter have not been well studied in recent years, let alone surveyed in different vegetation types and successional stages of forest. In this study, we investigated the arthropod diversity in different leaf litter types and examined its relationship with vegetation cover types. We chose three forest types as our study sites. One was white oak forest, which represents the characters of the old forest in North America. The other was a mixed forest mainly comprising cherry, maple, oak, and hickory, which is more characteristic of the new plant community. We also picked a pine plantation site which was specifically planted with pines. We expected to find difference in terms of the leaf litter arthropods composition across different forest types. Specifically, we assume that the mixed forest (mainly) will have higher arthropods diversity because of higher leaf litter diversity, and the pine plantation will have the least because of the nature of its leaf litter. We also compared arthropod diversity based on different geographic locations. We expected that communities with in closer ranges would have similar arthropods diversity share more species in common.

METHODS

Study Site

The ESGR is a 525-hectare fenced preserve located in Livingston County, Michigan, about 25 km northwest of Ann Arbor (approximately 42° 28' N, -84° 00' W). The climate is a humid type characterized by low thermal efficiency and by rainfall throughout the year. The forested areas in ESGR are all second-growth, chiefly oak and hickory, but also consist of numerous other tree species, including red maple, autumn olive, pine, cherry, etc. Nine different sites were selected for this study. Three sites were from predominantly oak forest, three from old red pine plantation forest and three from mixed forest comprising cherry, maple, oak, and hickory.

Figure 1. Sampling sites in E. S. George Reserve



Sampling

Data was collected on September 27, 2008, prior to 99.9% of autumn leaf fall, from the nine different sites. Sampling was done from three random, half-meter quadrants placed within a 20 meter radius under the mature forest canopy. The quadrants were determined by placing a half square meter frame on the leaf litter. Each site resulting in three samples, thus 9 samples were obtained from each forest type totaling 27 samples.

In each quadrant, the environmental parameters were measured, including ambient temperature, the average soil depth and soil PH. The average soil depth was calculated from depths measured at the four corners and center of the square. Then, the leaf litter was dissected along the inner edge of the frame and the surface of the litter was pounded to stimulate activity and compromise any dwelling cavities. The leaf litter down to the soil surface was quickly collected within a sifting bin and the bin was shaken continuously until the leaf litter was well separated. The remaining large particles of litter were sorted on a large white drop plastic cloth into three categories: non-decomposed or

identifiable leaves; decomposed or unidentifiable leaves; nuts and twigs. Each category was weighed.

The fine leaf litter which passed through the grate was searched for five minutes for arthropods. Any arthropods discovered were collected in 70% ethyl alcohol in a vial per quadrant. The fine leaf litter was weighted and collected in a site specific bag for further analysis.

Taxonomy

All samples collected were examined under dissecting microscope in the laboratory in GSER. The arthropods were identified at morphospecies level and sorted to order. Every morphospecies and individual number was recorded.

Data analysis

We used total catch per sampling site and per vegetation type for statistical analysis. Site character data and there relationship with arthropods diversity was analyzed using Microsoft Excel 2003.

The species richness was estimated by computing the species accumulation curves using EstimateS 8.0.0., with 95% confidence intervals, using the analytical formulas of Colwell et al (2004). Sample order randomization for estimators was run for 50 times. Species accumulation curves for whole sampling pool and each forest type were generated.

The Classic Jaccard index (Magurran 1998, 2004) computed by EstimateS 8.0.0 was used to reflect species similarity. The shared species between each nine sampling sites was compared, generating total 36 sites pairs. The nine sampling sites were further divided into three groups based on geographic location (Group 1: Pine I, Oak II, Mixed I, Mixed II; Group 2: Oak I and Oak III; Group 3: Pine II, Pine III and Mixed III). Sites pair shared same forest type were indicated by “T”, shared same location were indicated by “L”, others are indicated by “N”. Shared species between three forest types are also calculated.

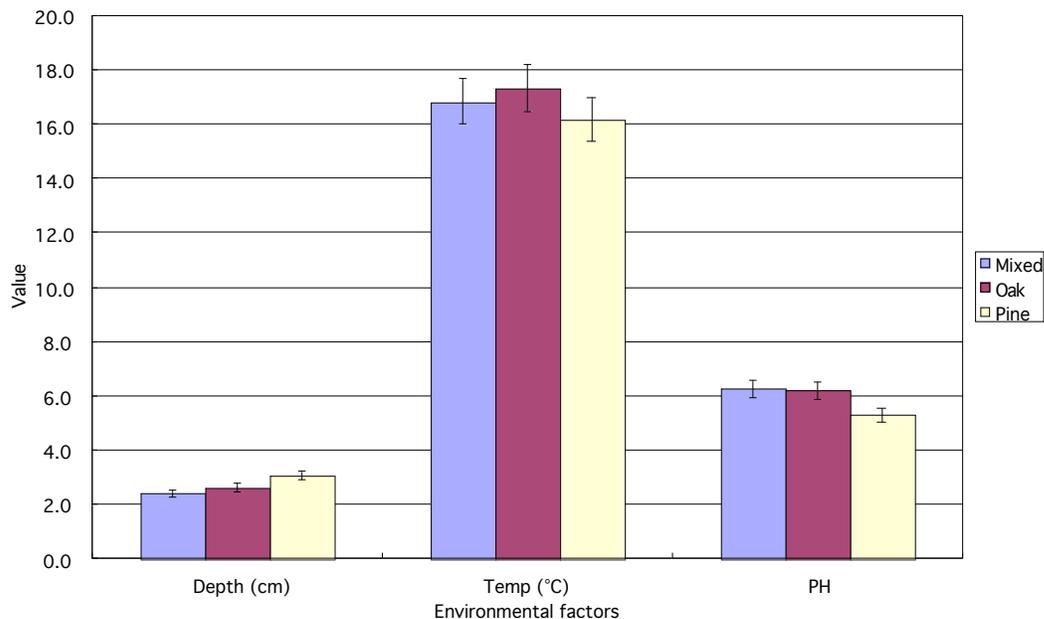
RESULTS

The average depth, temperature and PH of the three pine, oak and mixed forest are compared. The pine plantation has a relatively lower PH value. However, there are no significant differences between each forest type regarding of environmental factors.

Table 1. Site characters

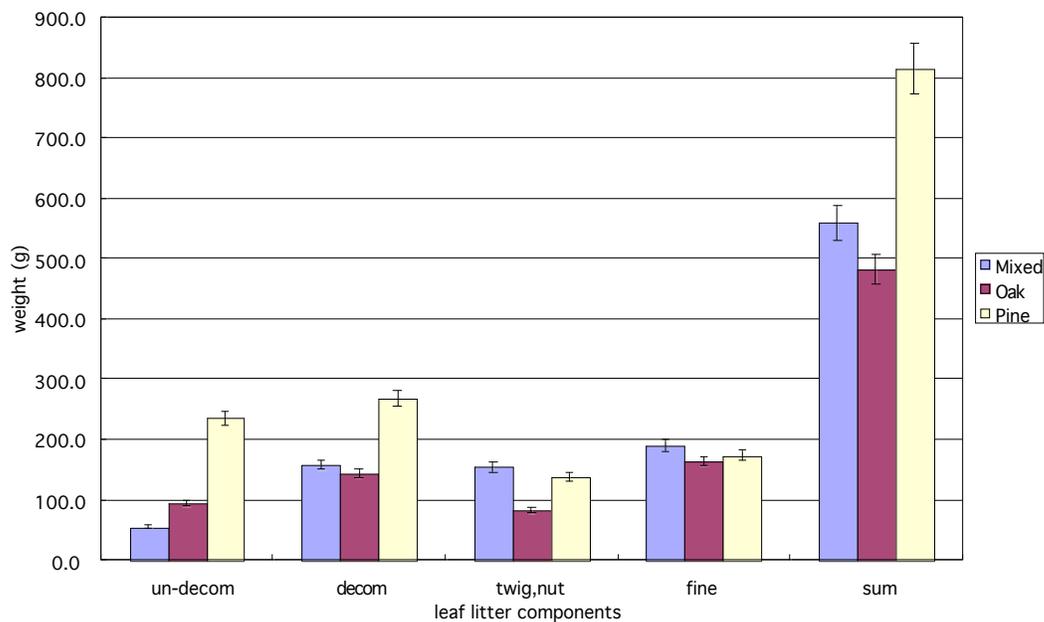
Forest type	Pine	Oak	Mixed
Depth (cm)	3	2.6	2.4
Temperature (°C)	16.2	17.3	16.8
PH	5.3	6.2	6.3
Total (g)	814.3	482.8	558.8
Decomposed (%)	30%	30%	30%
Undecomposed (%)	30%	20%	10%
Twig and unts (%)	20%	20%	30%
Fine (%)	20%	30%	30%

Figure 2. Environmental factors among the three forest types



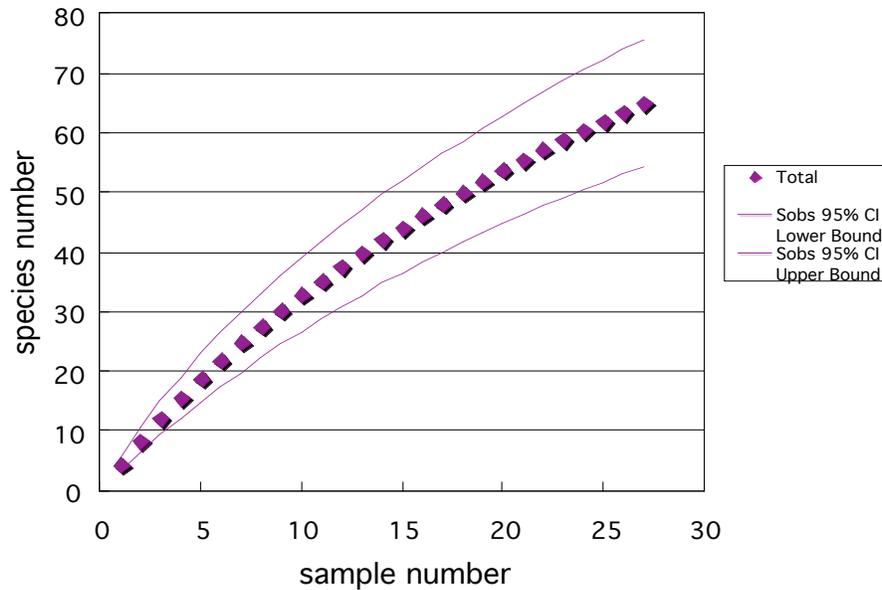
Weight of decomposed material, undecomposed material, twigs and nuts, fine material and total weight from the three leaf litter types are also compared. The leaf litter from pine plantation has a high proportion of undecomposed leaves. Its total weight is also relatively higher.

Figure 3. Leaf litter components among the three forest types



In the leaf litter from the 27 sampling quadrants, we obtained a total number of 140 specimens belonged to 65 morphospecies in 15 orders, including spiders (Arachnida), ants (Hymenoptera), mites (Acarida), springtails (Collembola), beetles (Coleoptera), flies (Diptera), wasps (Hymenoptera), moths (Lepidoptera), cockroaches (Orthoptera), false spiders (Opiliones), worms (Annelid, not arthropod), lice (Psocoptrea), pillbugs (Isopoda), centipedes (Chilopoda), and millipedes (Diplopoda), the most abundant groups among which are spiders, ants and beetles. A total species accumulation curve is showing as follows:

Figure 4. Species accumulation curve of total species



Arthropods diversity in pine, oak and mixed forest is calculated respectively, species abundance and richness are compared. The species accumulation curve for each forest is generated.

Figure 5. Number of individuals among the three forest types*

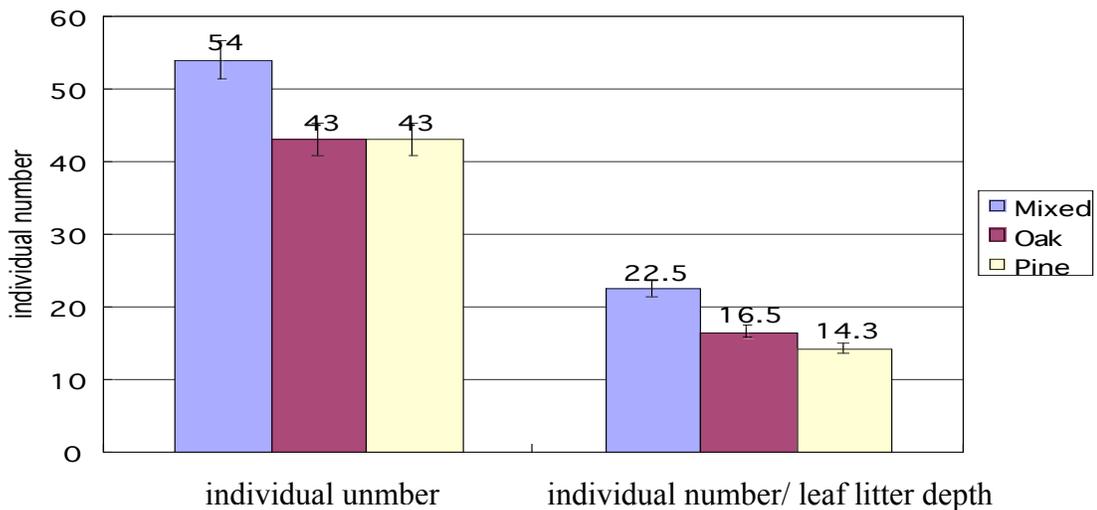


Figure 6. Species richness among the three forest types*

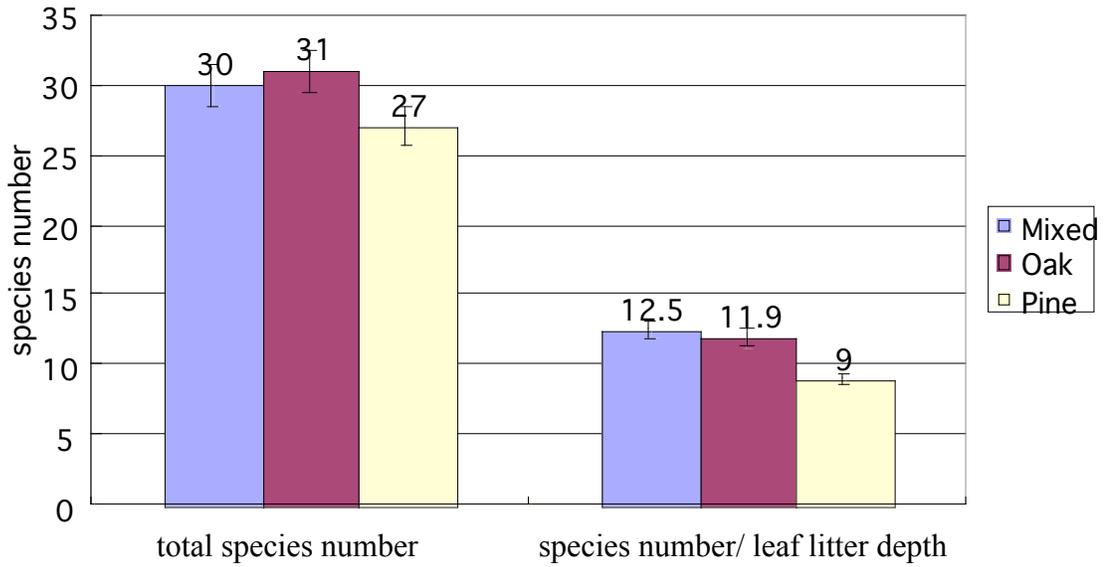
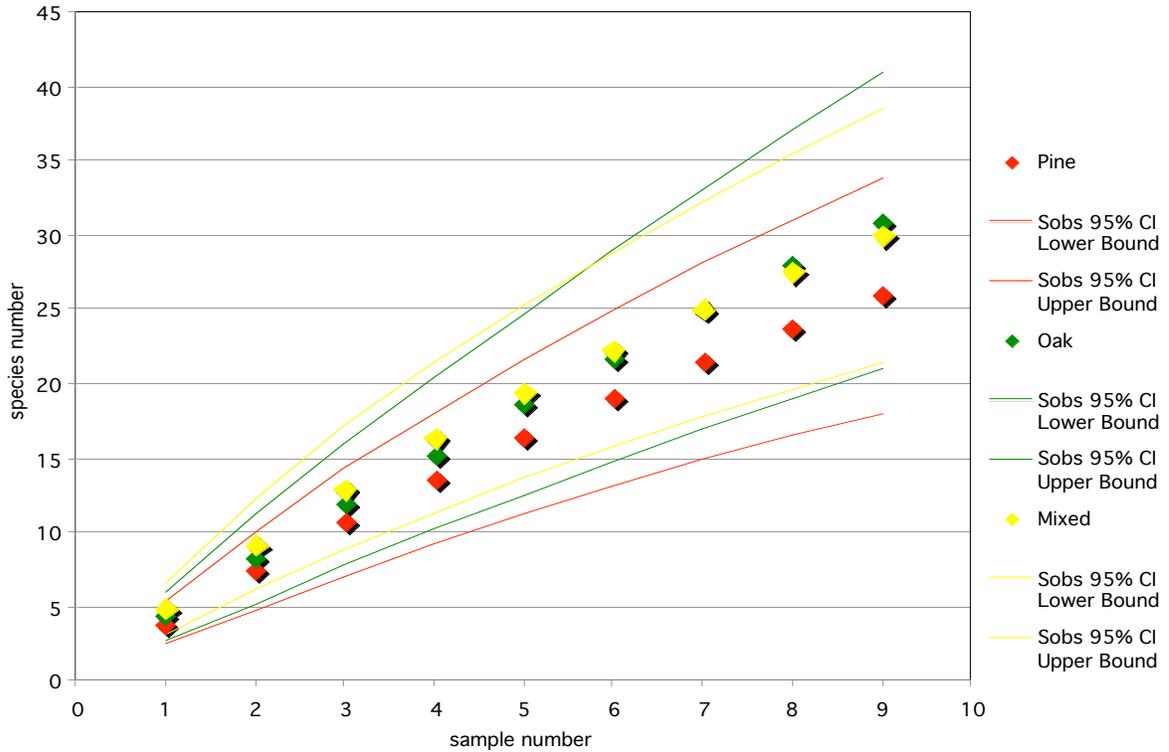


Figure 7. Species accumulation curve for the three forest types



Shared species between oak forest and pine plantation, oak and mixed, pine and mixed are calculated, result is showing as follows:

Table 2. Species composition similarity among the three forest types

Forest Type	Shared Species	Jaccard Classic
Pine and Oak	10	0.217
Pine and Mixed	9	0.188
Mixed and Oak	6	0.109

The species composition similarity between all 9 sites is compared. As described in the method section, the every sites pair is characterized by T (from same forest type), L (from same location group) and N (Others), also, sites share both forest type and location are indicated as ‘LT’. The average shared species and Jaccard Classic index was compared among those pair categories.

Table 3. Average shared species of different site pairs

Site Pair Type	Shared Species	Jaccard Classic
LT	2.3	0.125
T	2.3	0.113
L	2.1	0.106
N	1.7	0.079

The results shows that sites shared both forest type and close location have the most shared species and the most similar species composition. Sites belong to same forest type or same locations have similar numbers of shared species. Sites from different leaf litter type and far from each other have the least shared species number, as well as the lowest Jaccard Classic index value.

DISCUSSION

Our data show that there is no significant difference among the three leaf litter layer types in terms of habit characters. Although due to the nature character of pine leaves, the pine plantation sites have relatively lower PH and more decomposed leaves, it is not distinctively different from the other two forest types.

From the species accumulation curves, we are unable to get accurate estimate species numbers in each forest type (because the curves didn’t level off and reach a plateau), mainly because of insufficient sampling. However, we could still see a trend that species richness is similar among the different leaf litter types. We would have expected higher species richness in oak and mixed forests, since they have more decomposed material which may provide more suitable environment for arthropods species. But our result indicates that the pine plantations have similar species capacity.

From the shared species analyze, we are surprised to find that pine plantations shared most species with both oak and mixed forests. Against our expectations, oak and mixed leaf litter, which we thought could have shared more common environmental characters, have the least shared species, as well as the lowest Jaccard Classic index value. After examined our sample sites location, we found that the distance between oak forest sites and mixed forest sites are relatively longer compared to distance between pine and oak or pine and mixed. Thus, we reran the shared species analyze based on both leaf litter type and geographic location. The results confirmed that sites shared both forest type and

close location have the most shared species and the most similar species composition. Even sites from different forest type have relatively higher similarity of species composition if they are in the close range. This suggests a high connectivity of arthropods community between different forest types.

It is known that the forests in ESGR are undergoing a successional shift. Some of the oak forests are being colonized by red maple and certain invasive tree species. The leaf litter composition in some parts of the forests is affected by such shift. In the mixed forests, leaf litter layer tends to be more decomposed and form different microhabitats compare to oak dominate forests. Since leaf litter is a vital part of ecosystem function and leaf litter arthropods play an important role in forest nutrient dynamics, the changing of arthropod species might have great impact on the whole ecosystem in long term. However, our study shows that the arthropods species composition differs little across the three forest types. This indicates that, so far, it is possible that leaf litter arthropods communities have not been greatly affected by current forest transitions. In order to provide more accurate information and predictions in the future, large scale and long term sampling are needed.

In conclusion, our study find no major difference in species richness and abundance (α -diversity) of arthropod assemblages among the leaf litters from predominantly oak forest, old red pine plantation forest and mixed forest comprising cherry, maple, oak, and hickory. However, the result suggests that arthropods species composition (α -diversity) among different habitat in ESGR could be influenced by both vegetation type and geographic locations.

ACKNOWLEDGEMENTS

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DOES THE PRESENCE OF FALLEN TREES INCREASE LAND SNAIL ABUNDANCE AND DIVERSITY?

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ABSTRACT

There are over five hundred native species of land snails living in forests, fields, and wetlands in North America. This study provides additional information to the limited knowledge pool of the ecology of land snails. Because land snails feed on a common fungus abundant in decaying wood, we compared land snail abundance and diversity in food resource abundant communities to food resource limited communities. We also compared snail abundance and diversity along a moisture gradient. Our results indicate that areas with fallen trees have greater land snail abundance than areas without fallen trees. In addition, snail abundance increased at the drier hilltop sites. However, land snail diversity was similar at all study sites. Future research should investigate the role of land snails in the decomposition of fallen trees, as indicator species for forest transition, and in their importance as a food source for rodents.

INTRODUCTION

Although the mollusks have the second highest diversity in the animal kingdom, we know relatively little about their natural history and ecology. Land snails belong to the class Gastropod. The term “land snails” includes snails and slugs, which don’t have an obvious shell. They are common mollusks species found across Eastern North America with more than 500 native species. However, land snails remain a relatively neglected group in ecology research. Land snail species studied has been narrowly restricted as agricultural pests, disease carriers, and as an edible delicacy for human consumption.

Land snails live primarily in the upper leaf litter of forests, old fields, and wetlands. Their normal food consists of decayed remains of plants, fungi, lichens and algae. On the other hand, land snails are also consumed by many other vertebrates, e.g. rodents. Since land snail communities can consume less than 0.5% of annual litter input per year (Mason, 1970), it is speculated that few resources can limit their distribution. This concept is supported by high levels of microsympatry in land snail communities (Schmid, 1966; Cameron & Morgan-Huws, 1975; Nekola & Smith, 1999; Cameron, 2002). Co-existing taxa can be found in a very small habitat range. However, at large environmental and spatial scales, most land snail species possess pronounced ecological preferences. For example, land snails tend to be generalists in small scales, yet respond to specific environmental factors in large scales (Nekola, 2003).

There are many factors which could potentially affect land snail community composition such as geographical location, soil moisture, temperature, anthropogenic disturbance, food availability, and predation. This study examined land snail diversity along small scale environmental gradients. Specifically, we investigated the snail species abundance and richness in different habitats following the change of soil moisture. Since land snails require relatively high humidity in the habitats, we expected the snail community abundance has

positive relationship with soil moisture degree. We also cataloged the relationship between snail diversity and their food availability. We compared the snail species composition between dead trees and leaf litter habitats. Since the food resource is much more abundant on the dead trees, we hypothesized that habitats on and in close proximity to dead trees should have higher snail abundance and richness. In addition, we were able to examine the affect of rodent predation on local snail communities.

METHODS

In order to determine the distribution and diversity of snail species in the E.S. George Reserve, we chose three different topographical gradients: upland, sloped, and lowland. At each of these gradients, we created two 10 m² quadrats. One quadrat was created in an area that was devoid of dead trees and branches and another that had a great amount of dead wood. We searched for land snails within all six quadrats for about five minutes per quadrat. In the dead wood habitats, we pulled bark off rotting logs, overturned logs and branches, and searched piles of debris for snails of all sizes and species. In the habitats without dead wood, we looked for snails in the leaf litter. We collected all snails, placing them in Ziploc bags labeled with the site from which they were found. At the lab, we identified each snail to species whenever possible. We recorded whether or not the snail was alive, dead, or predated. Data was analyzed with the Jaccard Index for species diversity and chi-square contingency tables for quantitative statistics.

RESULTS

Analysis of collected snails yielded eleven distinct species of land snail of which ten were identified (table 1). The Jaccard species similarity index was found among the upland (0.333), sloped (0.200) and lowland habitat (0.0) to be 0.178 and for species found in the leaf litter (0) and decaying logs (0.280) was 0.140. The number snail species did not differ among the individual sites ($X^2 = 2.007$; $0.25 < p < 0.5$) (fig 1). However, snail abundance was significantly different among the six samples ($X^2 = 5.989$; $p = 0.05$) (fig 2). Snails were more abundant at the decaying woody vegetation habitats verses the leaf litter habitats ($X^2 = 25.363$; $p < 0.001$) and were in greater presence at the hilltop elevations ($X^2 = 26.411$; $p < 0.001$).

There was no evidence of increased predation between the decaying woody vegetation habitats and the leaf litter habitats ($X^2 = 1.00$; $0.3 < p < 0.4$), but predation was significantly greater on the hilltop locations ($X^2 = 6.25$; $p < 0.05$).

Table 1: Identified land snail species

Anguispira alternata
Euchemotrema fraternum
Mesodon thyroidus
Mesodon zaletus
Mesodon sp.
Gastrocopta similis
Zonitoidus arboreus
Euchonulus polygyratus
Punctum minutissimum
Striatura milium

Figure 1. Bar graphs for snail species number in wood debris (A) and leaf litter (B) sites at upland (1), slope (2), and lowland (3) habitats. The y-axis represents # of snail species and x-axis represents habitat locations.

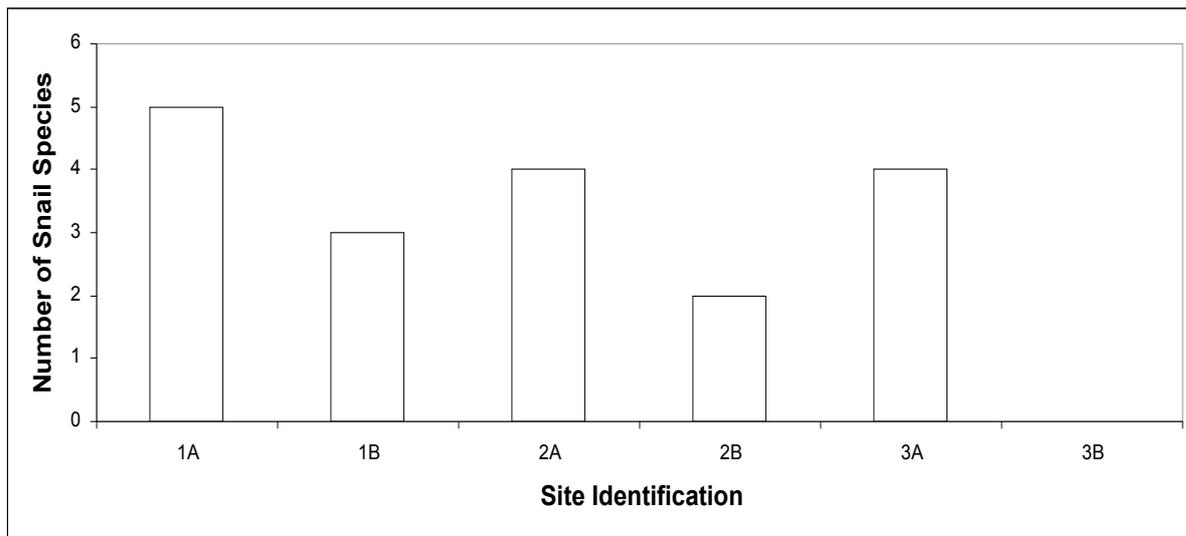
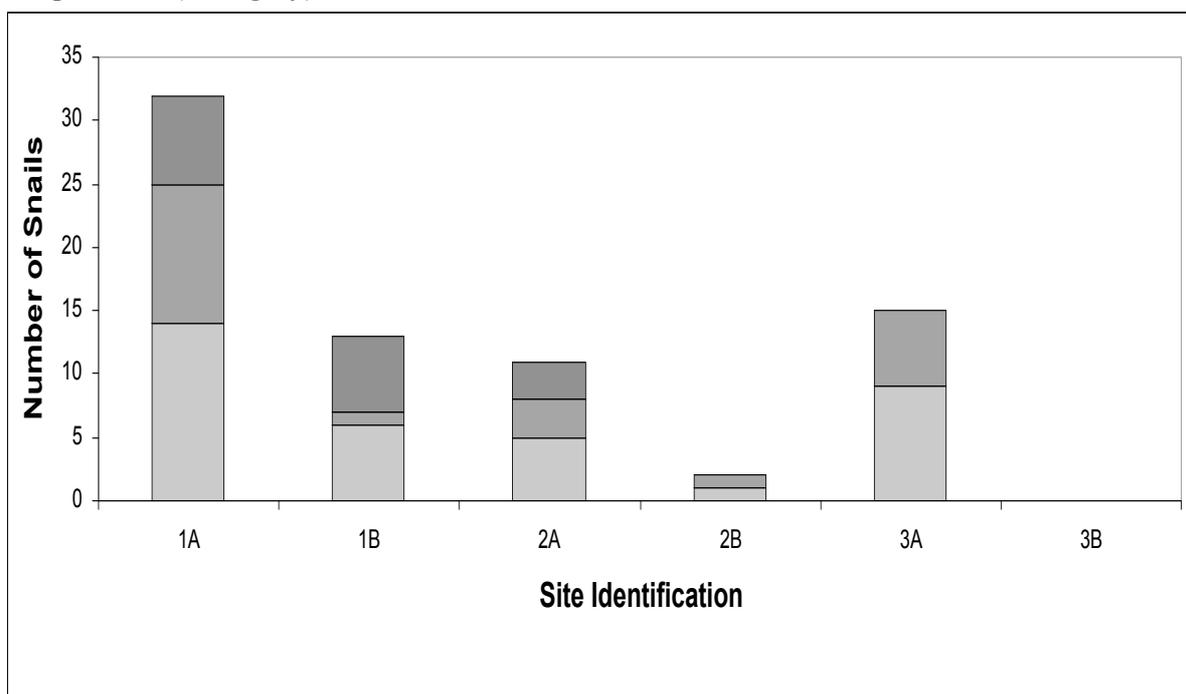


Figure 2. Bar graphs for snail abundances in wood debris (A) and leaf litter (B) sites at upland, slope, and low land habitats. The y-axis represents snail abundance and x-axis represent snail conditions in three different habitat—alive (light grey), dead (medium grey), and predated (dark grey).



DISCUSSION

This study demonstrated that snail species diversity remained relatively similar between habitat sites, whereas significant differences were found for snail abundances between dead wood and leaf litter habitats along moisture gradients. We observed greater shell predation, presumably by small mammals, in the upland site. However, no significant differences were found for shell predation between dead wood and leaf litter habitats.

These results explain that conditions at a local scale may vary substantially when placed within a larger geographical scale. For instance, we found no significant differences for snail species diversity despite our initial expectations for coexistence at smaller spatial scales. Meanwhile, we did find greater diversity of species in dead wood vegetation as compared to

leaf litter, which reveals the degree to which generalists land snails are sensitive to changing environmental conditions. Therefore, research efforts should focus on the underlying biological mechanisms that seek to explain habitat preferences for land snails.

Snail abundances were far more abundant in wood debris than leaf litter habitats. This can be explained by the fact that food sources are much more abundant in these habitats. For example, snails were primarily found inside barks and twigs of the fallen trees where fungus thrives. Furthermore, the rich organic material found in the wood debris sites are ideal habitats for snails since they provide an important calcium reservoir needed for shell construction. Meanwhile, leaf litter habitats exposed snails to greater predation risks. We found that shells were increasingly predated in the upland and slope leaf litter habitats. In particular, we observed that leaf litter habitats contained mammalian holes, which suggest that snails are at greater risk to be predated in these sites.

Soil moisture availability appears to be strongly correlated with snail abundance in wood debris sites. We found the majority of snails in regions of the trees where the moisture concentration appeared to be higher. For instance, in the wood debris habitat located in the slope and lowland sites, snail appeared to greater in abundance in areas of the trees that contained higher moisture concentrations, whereas regions that received greater sunlight contained lower snail abundances. The Jaccard index provides further support since it indicated that the location of the habitat was slightly more important than the content of the habitat. Thus, directional flow of water from the upland sites, transported through the slope site, and eventually reaching the lowland sites greatly increases snail abundances in wood debris receiving moisture.

This study was the first attempt to assess snail species composition and abundance at the E.S.G Reserve in Michigan. Future directions should aim to model decomposition rates of fallen trees and their respective contributions to forest transition, particularly in light of future climate change scenarios. Furthermore, field experiments can reveal predator-prey dynamics between mammals and snail on leaf litter habitats.

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RELATIONSHIP BETWEEN FALLEN TREE DIRECTION AND MUSHROOM
DISTRIBUTION, SPECIES RICHNESS AND ABUNDANCE IN E. S. GEORGE
RESERVE

LEILING TAO

ABSTRACT

Fallen tree are important habitats for mushrooms. The arrangement of fallen trees on the forest ground would affect the decomposition rate of the log and cause microenvironment differentiations. In this study, the relationship between fallen tree directions and mushroom distribution, species richness and abundance was studied in the E. S. George Reserve. It was found that mushroom had some preference in fallen wood directions, and there was notable relationship between mushroom species richness, abundance and log direction. These patterns might be the result of the combination of sunshine, wind and gravity. Compared to the direction, the rotten condition of fallen trees is a relatively weak predictor in deciding mushroom distribution and abundance.

INTRODUCTION

Fallen tree are very important in forest ecosystem processes. The opening of the forest gap will help the establishment of new trees, and the rich organic matter in fallen trees will facilitate the insects, mushrooms, worms, invertebrates and small vertebrates (Seidl 1985). When a tree decomposes, unique new habitats are created within its body as the outer and inner bark, sapwood and heartwood decompose at different rates. Fallen trees can also contribute to long-term accumulation of carbon and nutrients, create and maintain forest diversity, affect forest regeneration processes (Maser et al 1988).

Despite the universal phenomenon that fallen trees can hold high diversity of organisms, it is also predicted that the manner in which a fallen tree comes to rest on the forest floor greatly influences subsequent diversity of both external and internal plant and animal habitats (Pascoe 2003), because the different arrangement of fallen trees will cause microenvironment differentiation and affect the decomposition rate. For example, if a fallen tree lies up-and-down slope or falls across other downed trees, most of its volume is suspended above the ground, and such elevated relief adds complexity to the forest floor by creating cover and shade.

In this study, I took the direction of fallen trees into account in how they maintain arboreal mushroom diversity. The direction and length of the light gap consistently change with the height and direction of sunlight through the day. Because the sun goes from southeast to southwest everyday, the light gap covers more area in the west-east direction than the north-south direction. Under this circumstance, if a fallen tree lies more in the north-south direction, the probability for a larger proportion of it immersed in the sun would be lower. Since mushrooms prefer relatively shady environment, it would be reasonable to see more mushrooms distribute in the north-south logs, simply because it is more shady across the day.

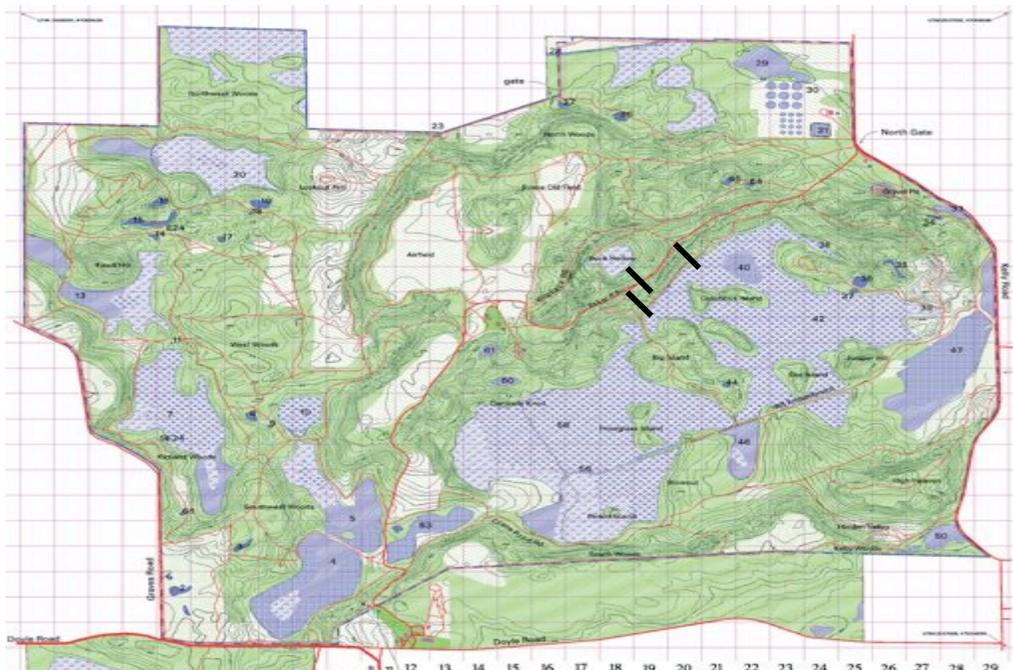
Once a mushroom establishes itself on a certain log, the abundance and species richness of mushrooms must depend on spore dispersal. Wind and gravity are two potential factors affecting the dispersal of the spores. In E. S. George Reserve, the prevailing wind direction in autumn and winter is from the west; for the Esker Road, which was the site of this study, the direction of the slope (also the direction of gravity) is about 135° from the north. If the two factors are considered simultaneously, then the combination of the two vectors is a new vector whose direction lies from 90° to 135° from the north. So a potential hypothesis is that a higher abundance and species richness of mushrooms would be found in logs from 90° to 135° .

In order to see whether the direction of fallen trees is an important factor in the distribution, species richness and abundance of mushrooms, I also studied the relationship between the rotten condition and mushroom abundance. Pascoe et al. 2003 found that the more decomposed the log is, the higher diversity and abundance of organisms it can maintain. In this study, the importance of rotten condition is compared with fallen tree direction to see which factor might be more dominant in deciding mushroom abundance and species richness.

METHOD

This study was conducted inside the E.S. George Reserve. Three transects (50m*1m) were set perpendicular to the Esker road and parallel to the slopes (yellow lines in Fig 1). Inside each transect, noted down the number of logs, the length, direction, mushroom species and abundance and rotten condition of each log. Only mushrooms on the outside of the log were counted. For the rotten condition of the logs, 1 represents no obvious decomposition (most of the barks still exist), 2 represents moderate decomposition when large proportion of the barks disappears, and 3 represents highly decomposition.

Fig 1 Study Site



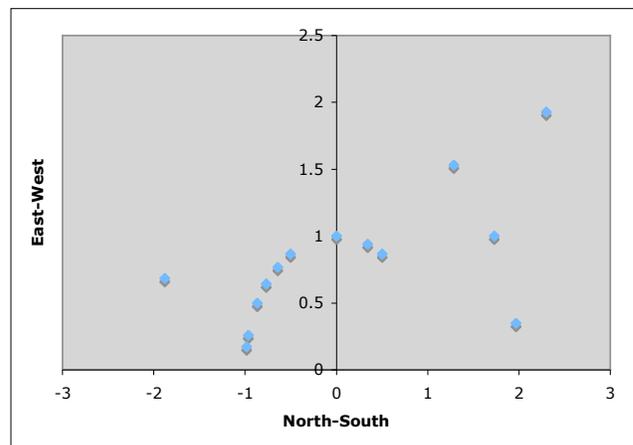
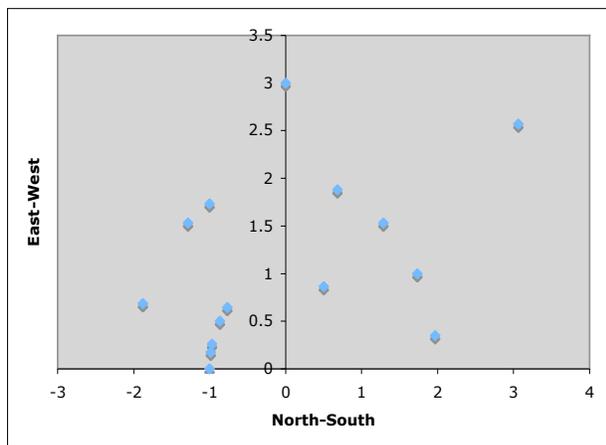
RESULT

Distribution of mushrooms on different direction of fallen trees

In the three transects, a total of 27 fallen trees were found and only 20 of them had mushrooms. For the logs, the maximum mushroom species is 3 and maximum abundance is 40. The direction distribution of all trees and trees with mushrooms is shown in Fig 2 and Fig 3 respectively. The x and y-axis represent for north-south and west-east direction respectively, the distance from the dot to the zero point is the number of trees and the angel between the x-axis and the connection line of the dot and zero point is the angel of the fallen tree. The direction of all fallen trees is almost evenly distributed for different angels and the average direction is 90.8° . For fallen trees with mushrooms, the direction distribution shifts a little from the west-east to the north-south direction, as many trees around 90° did not have any mushrooms. The average direction of fallen trees with mushrooms is 110.2° . Although the p-value of the T-test is 0.085 and not significant, considered the fact that the sample size is relatively small, there is still notable difference between the directions of the two groups.

Fig 2 Directional distribution of total fallen trees

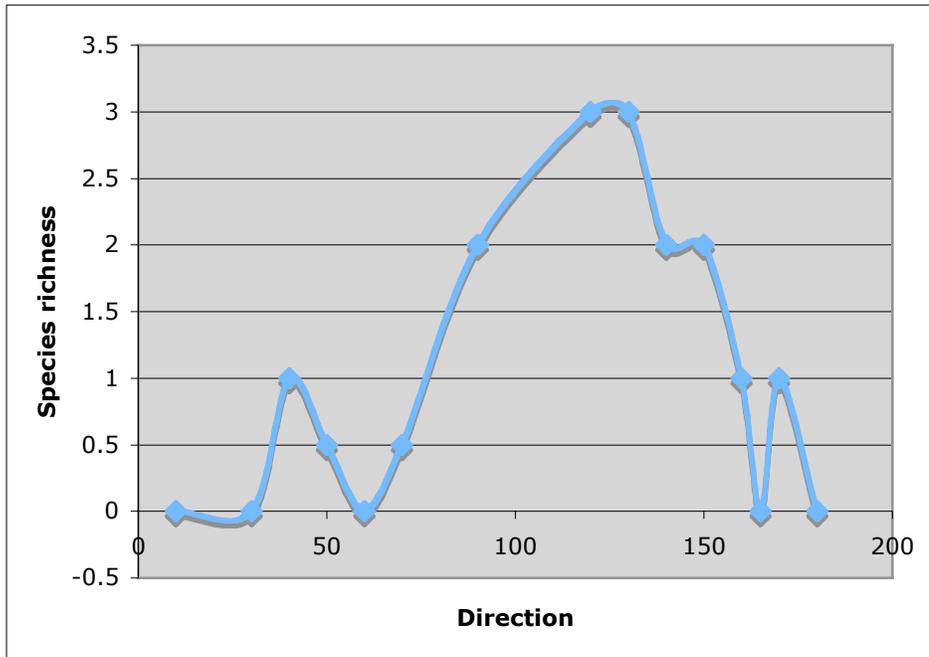
Fig 3 Directional distribution of fallen trees with mushrooms



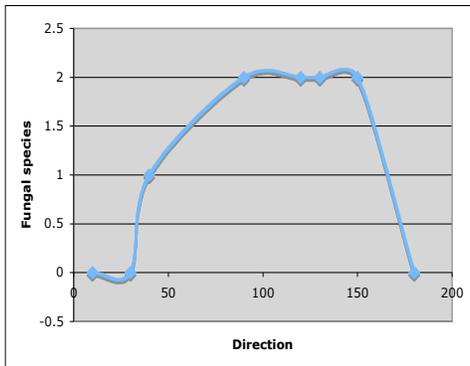
The species richness of mushrooms on different direction of fallen trees

The species richness of mushrooms is plotted against the direction of the fallen trees. As shown in Fig. 4, 4a is a total of 3 transects and 4b, 4c, 4d represent transect 1, 2, 3 respectively. As can be seen from the figure, the maximum of species richness for all transects is found at about 120° - 130° to the north.

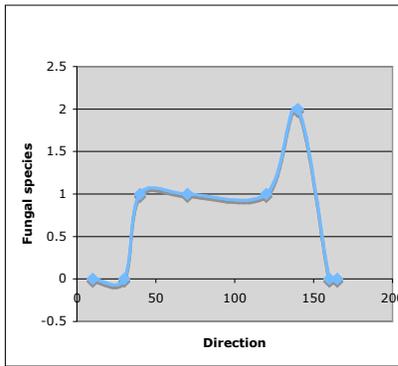
Fig 4a Species richness and direction of fallen trees



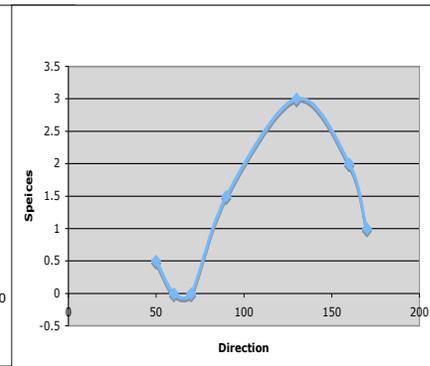
4b Transect 1



4c Transect 2



4d Transect 3



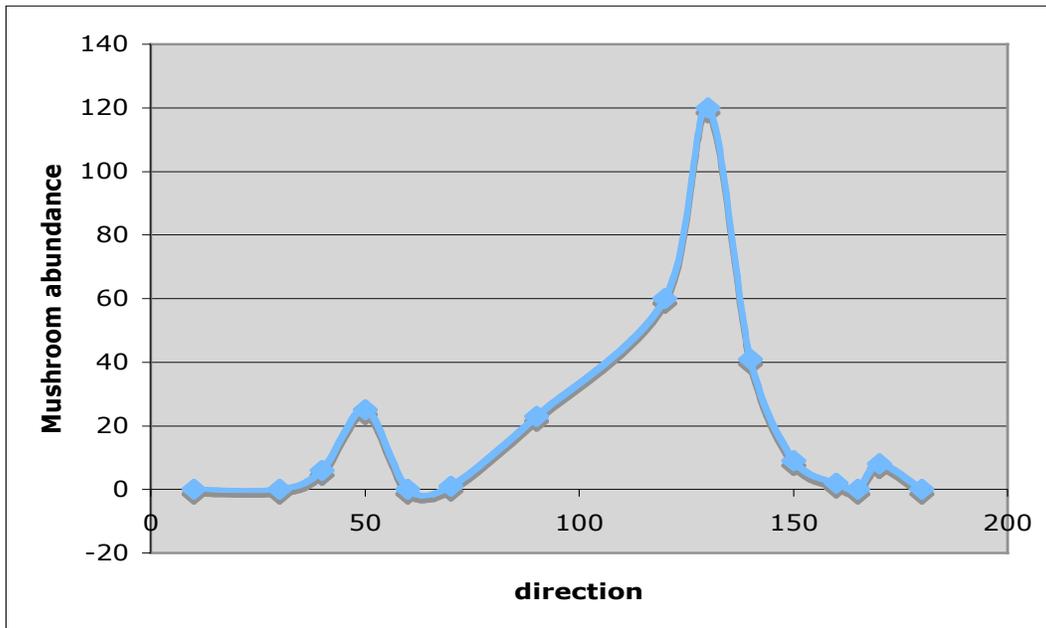
The mushroom abundance on different direction of fallen trees

Fig 5 shows the relationship between mushroom abundance and direction of fallen trees. 5a is a total of 3 transects and 5b, 5c, 5d represent transect 1, 2, 3 respectively. Like Fig.4, the maximum abundance is reached at about 120°-130° to the north for transect 2 and transect 3, but for transect 1, the maximum point is found at 90° instead.

Rotten condition of fallen trees and species richness and abundance of mushrooms

Although the average species richness and abundance increase as the fallen trees are more decomposed (shown in Fig 6 and Fig 7); however, there is no significant difference between the three rotten categories (ANOVA $p=0.097$, $p=0.495$ respectively).

Fig 5 a Mushroom abundance and direction of fallen trees



5b Transect 1

5c Transect 2

5d Transect 3

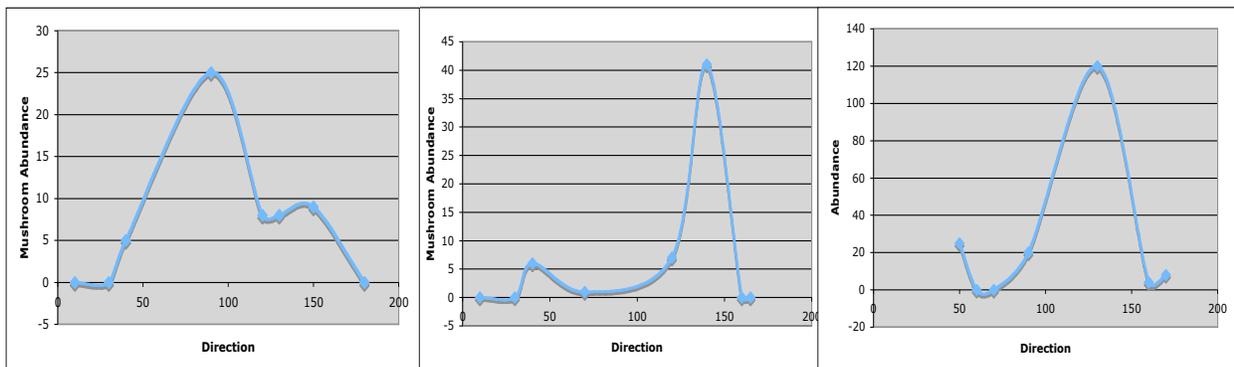


Fig 6 Rotten condition and abundance

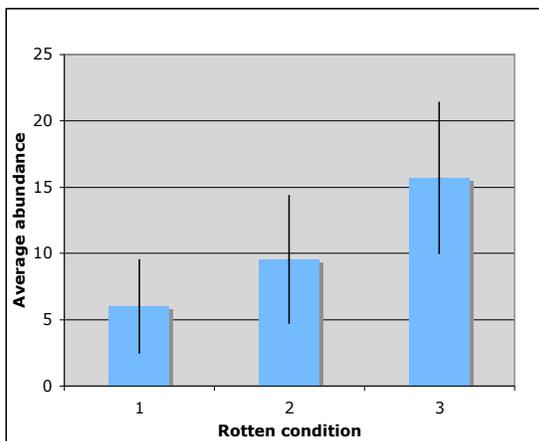
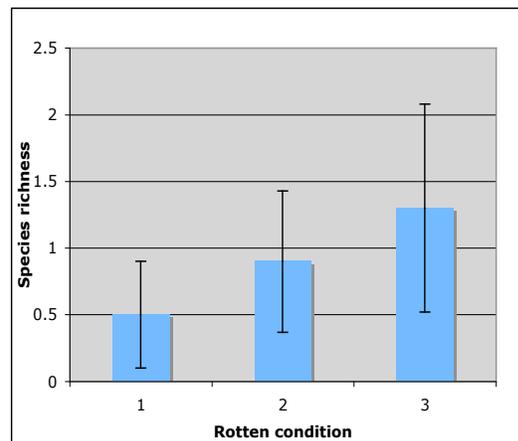


Fig 7 Rotten condition and species richness



Multivariate test between the rotten condition and direction of fallen trees

A multivariate test is taken to see which factor, the rotten condition or the direction of fallen trees is more dominant in deciding the species richness and abundance of the mushrooms. the relationship between direction and abundance is significant ($p=0.48$) while rotten condition is not ($p=0.13$); but for the species richness no significant relationship is found for either rotten condition or direction. But the p value for direction ($p=0.244$) is much smaller than p value for the rotten condition ($p=0.667$), which suggests that the direction might be more important in mushroom overall richness.

DISCUSSION

Considering the importance of the fallen tree in forest ecosystem processes, it is important to know how the patterns of the fallen trees, like the direction of the fallen trees in this particular study, affect the biodiversity of ecosystem functioning. There are two hypotheses here about the distribution, species richness and abundance of mushrooms and direction of the logs. Firstly, the existence of mushroom depends on the direction of the fallen trees. Because the north-south log will have less sunshine through the day, so it is proposed that there is a higher probability to find mushrooms on them rather than logs in the west-east direction. Secondly, once a mushroom establishes itself on a certain log, it will transport its spore by wind. Because the habitat of this study is on a slope, as the spores dispersed, they will also be limited by the gravity. If combining these two factors together, it is proposed that the highest mushroom abundance and species richness would be found at the range of 90° to 135° to the north.

About 2/3 of the logs have mushrooms. Logs in more west-east direction indeed have less mushroom existence, which is consistent with hypothesis 1. The p value is higher than 0.05, which might because other factors, like water also played a role in the distribution of the mushrooms, since different logs have different distance to the swamps. Increasing the sample size by doing more transects in other sites of George Reserve might help solve this problem.

As for the mushroom species richness and abundance, the highest species richness and abundance was reached at about 120° to 130° for most of the transects. This is consistent with the wind and gravity hypothesis. However, for transect 1, the largest abundance was found in degree 90, which was because that a single 90 tree in transect 1 held more than 40 mushrooms, while the average mushrooms for all the fallen trees was less than 10. Again, by enlarging the sample size will reduce such deviations.

Rotten condition is considered to be important in biodiversity in fallen trees, for the more decomposed the tree is, the more nutrient it can provide for different organisms. In this study, however, no significant difference is found in the rotten condition of the fallen trees and abundance of the mushrooms. In the multivariate test where I compared the significance of the rotten condition and the direction, a more significant role of direction is found than the rotten condition, which again suggests that the direction of the fallen trees might be very important in the distribution and abundance of the mushrooms.

For future study, a larger sample size across the George Reserve is needed. Also, it would be interesting to see if there is a species preference for the mushrooms to choose

fallen trees. And it would also interesting to see whether mushrooms living inside the logs have different preferences for fallen trees, since those who live inside will not be limited by sunshine, but other factors like moisture, other insects and worms, etc.

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CONSIDERING ROADS AND LICHEN ABUNDANCE

ELISSA CHASEN

ABSTRACT

In this study, presence of lichens was looked at as a factor of proximity to a road outside the E.S. George Reserve in Livingston County, MI. Other variables such as substrate tree species and diameter at breast height (dbh) of substrate and canopy transmissivity were taken in order to control for environmental heterogeneity. Lichen presence did vary with distance from the road as well as with dbh. Implications for lichen communities is discussed.

INTRODUCTION

Lichens are a symbiotic relationship between an algae and a fungus in which the fungus gives the support structure for the organism and the algae provides the food through photosynthesis. They live on many different substrates including rocks and soil and both living and dead trees and shrubs. Lichens are important components of an ecosystem providing both carbon storage through photosynthesis and aiding in the decomposition of rocks to soil by releasing chemicals that speed up the decomposition process. They are therefore very important as initial colonizers in primary succession.

Lichens are very sensitive to air pollution so there is a history of their use as bioindicators (Christofolini, 2008, Davies, 2007, Wolseley, 1991). Lichen diversity and abundance is often indicative of the health of the local environment with regards to air pollution. The effects on lichens due to different forms of air pollution range from a decline in health and even death in sensitive species and an increase in abundance of species that are tolerant of specific air pollutant, resulting overall in a decline in diversity and abundance (Wolseley, 1991). Christofolini et al (2008) found a negative response in lichen community to NO_x that was noticeable as a factor by proximity to the road. They also found that certain species of lichens could be considered nitrophytic as their presence increased with proximity to the road. In 2007, Davies et al noted that lichen is especially sensitive to SO₂ and when that is present it tends to outweigh the effects caused by other air pollutants.

With all of this in mind, I set out to determine if the lichen community in forest along the road just outside and to the south of the E.S. George Reserve showed signs of air pollution damage. I looked to see if lichen abundance was correlated with the distance from the road and I hypothesized that as I moved farther from the road I would see an increase in lichen abundance.

METHODS

Study Site

This survey was conducted just outside of the E.S. George Reserve in Livingston County, MI in the forest along Patterson Lake Road to the south and immediately outside of the south entrance to the reserve. The forest is part of University of Michigan's Fresh Air Camp property and was historically cut and farmed in the 1800s but has been regenerating since the early 1900s when the University bought the land (Vandermeer, 2008). Patterson Lake Road is a two-lane country road with somewhat limited use. In the time I was completing the survey (which was approximately four hours in the earlier part of a Sunday) I saw many motorcyclists and cars but little to no buses or trucks.

Survey Methods

I completed six transects perpendicular to the road that began at the forest edge and went 30 meters into the forest. On each transect I noted every possible vegetation substrate that a lichen could potentially live on within a meter on both sides of the transect line. For each of these substrates I noted distance from the road, lichen presence, substrate species as an indicator of bark texture, substrate diameter at breast height (dbh), canopy transmissivity as an indicator of light availability, and if lichens were present I noted relative surface area coverage of the lichens.

RESULTS

Figure 1 shows the results of lichen presence depending on the distance from the road. A binary logistic regression was run to determine if the results of the trend line were significant, which they were ($p=0.020$).

Figure 1: Lichen presence depending on proximity to road. On the y-axis, a value of 1 indicates lichen presence while a value of zero indicates lichen absence.

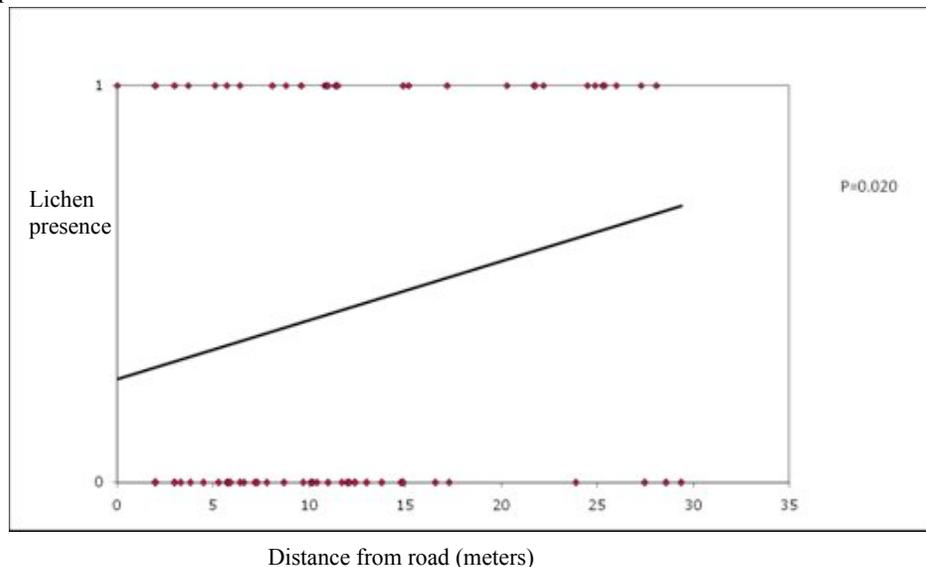
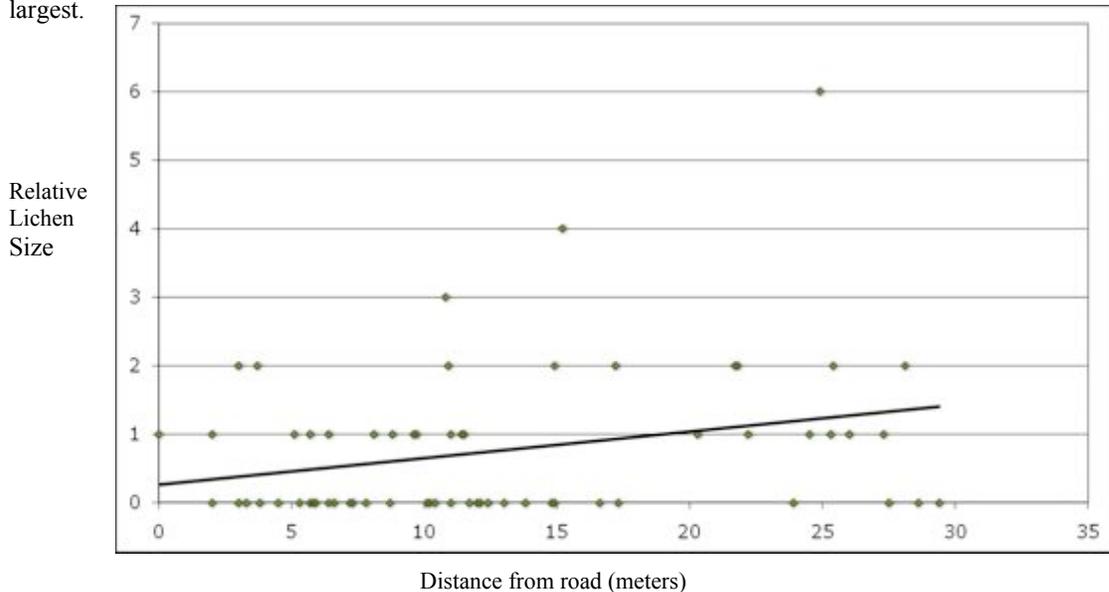


Figure 2 is similar to figure 1 but looks at relative lichen surface area as well in comparison to distance from the road. Because I had made no clear distinction between the size classes of lichen and they were determined only relatively, there were no statistics run on figure 2. It does show that the farther away from the road though, the more likely that lichen surface area gets larger which is to say that farther away from the road, lichen abundance grows.

Figure 2: Relative lichen sizes depending on proximity to the road. On the y-axis, a value of 0 indicates lichen absence and the numbers 1-6 indicate relative lichen surface area with 1 being the smallest and 6 the largest.



In order to control for various factors that may have also influenced lichen presence I ran tests for tree species as a proxy for bark texture, canopy transmissivity as a proxy for light availability, and dbh as a proxy for tree age.

When looking at tree species and lichen presence, the difference between the observed presence of lichen and the expected at random presence of lichen for all trees is not statistically significant ($p=0.46$) which means that lichen presence cannot be explained by a preference for particular bark texture. When looking at lichen presence and canopy transmissivity with a binary logistic regression there is no significant effect of canopy transmissivity ($p=0.69$).

However, when looking at dbh and lichen presence however, we do see a trend. Dbh is correlated with distance from road in my transects so in order to make sure that proximity to road is the factor determining lichen presence and not the age of the tree as indicated by dbh, a binary logistic regression was used with both dbh and distance from road as independent variables. We see that both variables show statistical significance, where $p=0.03$ for road distance and $p=0.02$ for dbh. This means that both variables are responsible for lichen presence.

DISCUSSION

At this study site, lichen presence was affected by the distance from road while canopy transmissivity and tree species did not show an effect on lichen presence. Dbh was also correlated with distance from road, the smaller trees located closer to the edge of the forest and the larger trees farther into the forest. Dbh, the indicator value for tree age, also had an effect on lichen presence but it is not possible to determine in this study whether lichen presence was determined more strongly by road presence or dbh.

Even though dbh did have an effect on lichen presence, distance from the road was still a strong determining factor. Davies et al (2007) found that NO₂ disperses rapidly as one moves away from the road, to the effect of 70% dispersal at just 20-30 meters. Because the transects in this study were 30 meters long, they were just long enough to catch a pattern such as this and I hypothesize that NO₂ is the pollutant affecting lichen presence in this forest as we move away from the road. If that is the case there are several possible outcomes as Davies et al (2007) wrote: rare species of lichen are confined to areas of low NO_x, and diversity is inversely related to NO_x concentrations and nitrophytic lichen species will increase in abundance. If NO₂ is the reason that lichen presence varied with distance from the road, we can expect in time that we will see an increase in nitrophytic lichens and a decrease in all other lichen species within 20-30 meters from the road.

The road outside of the E.S. George Reserve is moderately well traveled and yet the traffic from this road still emits enough NO₂ to impact the lichen community. In another experiment it would be beneficial to complete similar transects in forests on the side of roads with different use patterns (country roads and freeways) in order to determine a maximum amount of NO_x emissions that permits for healthy lichen communities.

One problem I noted with this experiment was the use of a densiometer reading as an indicator for amount of light available for lichen photosynthesis. Densiometer readings only take light into account that comes from directly above and does not account for light that comes in from the side. In the future, to more accurately determine whether light was a determining factor in lichen abundance, a better method of measurement needs to be used.

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A BRIEF SURVEY OF ZEBRA MUSSELS IN PATTERSON LAKE, E.S.
GEORGE RESERVE

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HANNAH FOSTER, DOUG JACKSON, GERALD SMITH

ABSTRACT

Dreissena Polymorpha, commonly referred to as the Zebra Mussel, is an invasive bivalve mollusk which has spread rapidly and widely through the Great Lakes and surrounding watersheds since mid-1980s. Patterson Lake, which is on top of a chain of lakes in the Huron River Watershed in Southeastern Michigan, was first reported to have zebra mussels in 2005, but the population is still difficult to detect. Our brief survey of the lake confirmed that the density of zebra mussel in the lake is very low ($6.5/m^2$), and most of the mussels are quite small. However, the ridges of the largest mussel found in the lake indicate that the population may have been present as many as eight years ago. Body size did not differ significantly among sites along the lake, which suggests that there is not one single, continuous source of zebra mussels to the Patterson Lake. Further study and continued monitoring are needed to clarify whether the population has reached its peak and is being controlled by other factors, or if it will explode in the coming years.

INTRODUCTION

Dreissena Polymorpha, commonly referred to as the Zebra Mussel, is a bivalve Mollusk native to Eurasia. It was first detected in St. Clair Lake in North America in the mid 1980s, likely introduced via ballast water in commercial freighters arriving from Russia and other parts of Eurasia (Herbert et al. 1989). Because of their high fecundity, early maturity, and rapid growth rate, zebra mussels have spread widely and rapidly in the great lakes and associated watersheds (Mackie 1991). They live on any submerged hard substrates, including rock surface, macrophytes, native mollusks, canals and docks, boats, motor outdrives and even water intake pipes, causing great economic cost in fisheries and water utilities (Maclsaac, 1996). They also out-compete many native mollusks species and alter the nutrient cycling and the structure and function of local aquatic ecosystems (Arnott and Vanni 1996; Schloesser et al.1996).

Because of their great economic and ecological impact, the invasion patterns and corridors have attracted the attention of many land managers and ecologists (Zanden and Olden, 2008). After the rapid spread of zebra mussels through navigable waterways in the Great Lakes area during the late 1980s to early 1990s, their spread to isolated inland lakes was expected. It was suggested that any given inland lake can be invaded through primary invasion from a Great Lakes source population, secondary overland invasion from a population established by a primary invasion, or downstream or hydrologic connection dispersal (Jonathan et al. 2007). Understanding the mechanism and pathway of inland invasion will provide profound insight to how to control and prevent the invasion.

Patterson Lake in the E.S George Reserve is part of a chain of lakes located just north of the Waterloo State Recreation area in Livingston County, MI. Although there have been reports of zebra mussel in Patterson lake in 2005 (Michigan Sea Grant), people in the George Reserve and residents around the lake hardly noticed

the existence of zebra mussel and thought there were no zebra mussel in the lake until it was accidentally found in Sep. 13, 2008 by Professor Smith. Due to the amount of time the zebra mussels had been in the lake and their low population size, we became interested in how many zebra mussels are in the lake and their population structure. Since Patterson lake is on the top on the lake chain and we already know that two lakes downstream (Halfmoon lake and Bruin lake) have been heavily colonized by zebra mussel, we were interested in whether the zebra mussels spread from Halfmoon lake (first report of Zebra mussel in 2002, Michigan Sea Grant) or Bruin lake (first report of Zebra Mussel in 2005, Michigan Sea Grant); or if they were introduced through trailered boating traffic, which is thought to be one of the most important vector for the transport of zebra mussels among unconnected bodies of water (Padilla et al., 1996). If Halfmoon Lake or Bruin Lake provides continuous sources of zebra mussels in Patterson Lake, we expect that there will be higher percentage of older zebra mussel around the outlet of the lake compared to other sites round the lake.

METHODS

Study Sites and Sampling Methods

Patterson Lake is part of a chain of lakes located just north of the Waterloo State Recreation area in Livingston County, MI. Patterson Lake, and the chain of lakes with which it is associated, is part of the Huron River Watershed in Southeastern Michigan.

The lake itself is slightly eutrophic with a sandy bottom and flows into (feeds) Watson and Halfmoon Lake downstream. The eastern and southern shores of the lake are densely populated contributing to boat traffic between the various lakes in the chain as well as around Patterson Lake itself.

Three sites around Patterson Lake were surveyed and sampled for zebra mussel abundance: one site located on the western edge of the lake near the UM “Fresh Air Camp” where there is little development (site 1); one site on the eastern edge of the lake where it is densely populated and disturbed (site 2); and one site at the southern tip of the lake where a culvert connects Patterson to Watson and Halfmoon Lake (site 3).

Fig 1. Patterson Lake in Southeastern Michigan



The choice of these three sites was meant to provide a representative sample of the lake and produce data indicative of the potential Zebra Mussel habitat of the lake as a whole. It was also meant to test for potential point of initial colonization of the lake and the direction of spread as well as the age and population structure of the population of the lake as a whole.

Site 1 (Fresh Air Camp) was extensively surveyed between the shoreline and approximately five meters out into the lake (roughly 1 meter in depth) along a 125 m transect. This area was combed for solid substrate (sticks, rocks, cans etc.) onto which Zebra Mussels are capable of attaching themselves. Sticks, rocks, etc. that were encountered were removed and catalogued (dimensions to estimate surface area and location in the study site). Any Zebra Mussels encountered were catalogued (substrate type, dimensions and location were noted as well as number of attached Zebra Mussels) and collected for measurement and analysis back at the Reserve. Site 2 was surveyed in the same way though the lack of Zebra Mussels resulted in very different data accumulation (including the survey of rocks holding up the shore – the only suitable substrate at the site). Site 3, due to time constraints, was briefly surveyed in order to gauge the density and age structure of the culvert as well as the potential direction and source of colonization of Patterson Lake (both sides of the culvert, Watson and Patterson Lake, were investigated).

The Zebra Mussels collected were returned to the lab, they were all weighed and measured (length of each specimen was measured as well as the weight in grams using an electronic scale). The “growth rings” (a possible indicator of age) were measured using a microscope for a representative sample of Mussels.

Fig 2. Our three sampling sites in Patterson Lake.



Statistical Analysis

We performed a one-way ANOVA to analyze the difference of length distribution of zebra mussels (SPSS version 16.)

RESULTS

Altogether, we encountered a total number of 279 zebra mussels. Based on the 191 zebra mussel in the sampling surface area (125 m * 5 m = 625 m²) on site 1, we can scale up to the entire lake with potential habitat area (5 m away from the shore * perimeter 5333), we get a rough estimate of zebra mussel in the whole lake, that is about 8149. The density of zebra mussels is about 6.5 individuals per substrate area, with similar magnitude of density among different sites) the sites (table1).

Table 1. Density of zebra mussels per substrate area in Patterson Lake. We don't have a estimate of substrate area in site 3 (the culvert), but according to our observations, the density at the culvert is almost the same as those in other two sizes.

site	Substrate Area(m ²)	Number	Density(m ⁻²)
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camp	27.4	191	6.9
house	14.6	76	5.2
culvert	*	12	*
total	42.8	279	6.5

The average weight of zebra mussels we have collected is 0.16 g with a maximum at 2g, and most of them are about 0.1 g (Fig 3). We did not distinguish those individuals less than 0.1 g because the poor sensitivity of the scale we used. The distribution of body length is ranging from 3.7-26 mm, with an average at 10.7 mm (Fig 3). We picked out the largest one and carefully examined the ridges on its shell under microscope. We find that there are about 8 ridges (Fig 4), that means the largest one is about 8 years old if we are correct about its ridges.

Fig 3. The body weight and length distribution of all the zebra mussels we collected.

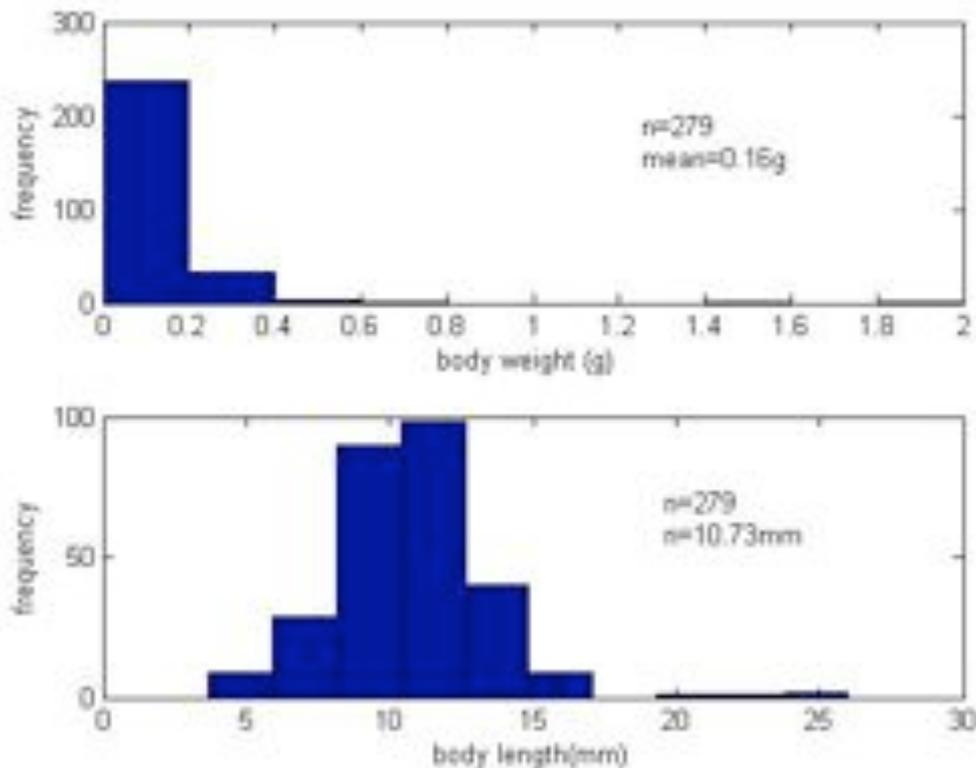
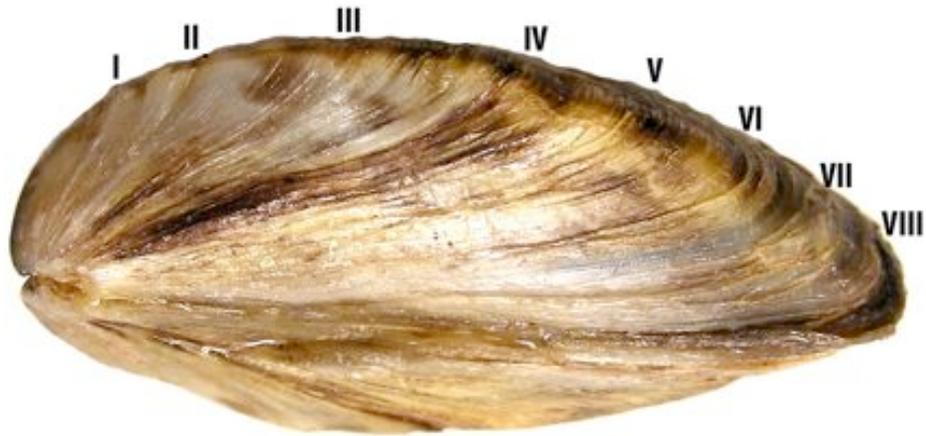


Fig 4. The ridges on the shell of the biggest zebra mussel: Every ridge shows the discontinuities of growth between winter and the next spring, allowing one to estimate the age of the mussel.

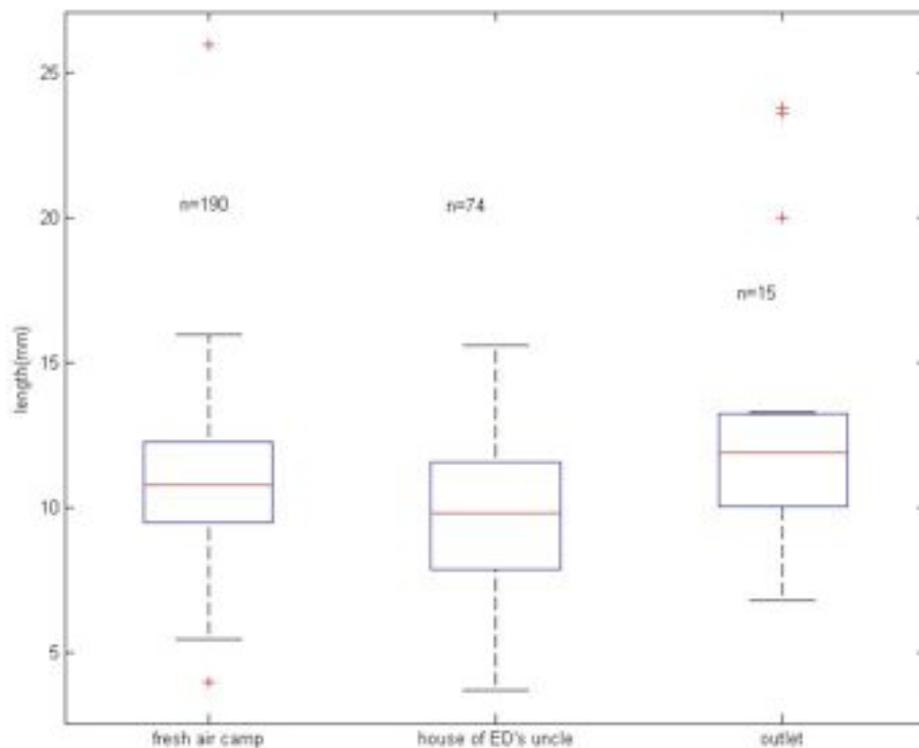


We used the body lengths of the mussels as an indicator of population structure for comparison among different sites. A one-way ANOVA shows that there is a significant difference among the length distribution among different sites (table2), and following multiple comparisons, indicates that the lengths of zebra mussel in the Fresh Air Camp shore is higher than those in the corner of the resident house (Dunnett T3 test, $p=0.07$, Fig 5). Zebra mussels in the outlet of the lake (site 3) had slightly, but not significantly, longer body length compared to those in the other two sites.

Table 2. One-way ANOVA of body lengths of zebra mussels in different sites along Patterson Lake.

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	169.968	2	84.984	11.490	.000
Within Groups	2041.411	276	7.396		
Total	2211.379	278			

Fig 5. Comparison of body lengths of zebra mussel in different sites. Multiple comparisons (Dunnett T3 test) show that average length of zebra mussels at the Fresh Air Camp shore is higher than the average length of the zebra mussels in the corner of the resident house ($p=0.07$). Zebra mussels in the outlet of the lake (site 3) are slightly, but not significantly longer, compared to those in the other two sites.



Discussion

Compared to lakes heavily colonized by zebra mussels with substrate densities as high as 5000-6000/m² (Schloesser 1996), the density of zebra mussel in Patterson Lake is quite low, averaging only about 6.5/m², and most of the individuals are small in body size. This suggests that the zebra mussel population in the Patterson Lake is a young and small one. However, based on our interpretation of the eight ridges on the shell of the largest zebra mussel we found, the zebra mussels may have been in Patterson Lake for up to eight years, which would place their invasion even earlier than the time of the first report of zebra mussels in Halfmoon Lake. Therefore, it is unlikely that zebra mussel first spread from Halfmoon Lake. Our observations at the outflow of the culvert from Patterson Lake also indicate that it is unlikely that the zebra mussels spread from downstream to Patterson Lake because it is difficult for them to go against the water flow. The lack of significant difference of density and body size distribution between the outlet and other sites along the lake would also indicate that Halfmoon Lake is not the continuous source of the zebra mussel in Patterson Lake. The more large zebra mussels we found in the fresh air camp mainly due to the more sampling effort we made in that site.

It has been reported that zebra mussels usually reach maximum population density 7–12 years after initial introduction, or about 2–3 years after populations are large enough to be detected (Burlakova et al, 2006). In the case of Patterson Lake, zebra mussels have been there possibly up to eight years, but at least since 2005. The population has not yet exploded, but it is possible that we may see this explosion in the next 2-3 years. However, due to the fact that surrounding lakes were infested around the same time, but have suffered greatly due to the invasion, it also might be

true that there are some factors that suppress the growth of zebra mussels in Patterson Lake. Possible future studies include comparisons between Patterson Lake and the surrounding lakes. The presence of a potential predator in Patterson Lake, differences in substrate quality between lakes, or differences in nutrient chemical composition could explain the slow growth rate of Zebra Mussels that we have witnessed in Patterson Lake. Continued monitoring of population growth over the course of the next few years will be of great importance for understanding the progression of zebra mussel invasions, and our research provides baseline information for further study.

Acknowledgements

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CATTAIL HYBRIDIZATION AND DISTRIBUTION AROUND TWO LAKES OUTSIDE THE GEORGE RESERVE

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ABSTRACT

Typha latifolia, the native cattail in Northern America is being replaced by *Typha angustifolia*, an introduced species from Europe. *T. latifolia* is able to hybridize with *T. angustifolia*, and the hybrid *T x glauca* is found to be dominant in disturbed areas. In this study we surveyed marshy areas around Patterson Lake and Woodburn Lake outside the George Reserve, found that *T. x glauca* was much more prevalent than the two other species which supports the concept that hybrid vigor can be important to biological invasions. Although the hybrid can be distinguished from *T. latifolia* and *T. angustifolia* by morphological features, in terms of habitat ranges and preferences, however, the hybrid did not show any significant differences with the other two types.

INTRODUCTION

Non-indigenous aquatic plant can alter the local biodiversity and ecosystem functioning, which might have huge impact on community structure and ecosystem processes (Ruiz et al, 1997). An urgent current question is what factors contribute to the distribution and spread of invasive species. An additional layer to this question evolves when invasives can hybridize with natives to form what may possibly be a “superspecies”, because the hybrids are often more competitive and have broader range of habitat. What’s more, natural selection favors invader displacement via genetic assimilation but not overwhelming immigration, which means hybridization might be important in the process of invasion (Huxel, 1998).

In the wetlands of the northern United States, *Typha latifolia* is a commonly found native plant. Many in fact consider this native plant a pest-like weed as it colonizes shallow water reproducing vegetatively to form huge stands and chokes out other plant species. *Typha angustifolia* is a non-native cattail often found in disturbed areas. Since the early 20th century, the range of *T. angustifolia* has been spreading rapidly (Shih and Finkelstein 2008). These two species can be identified by morphological features: *T. latifolia* always has broader leaves and a bare area on the stem between male and female inflorescence, and the ratio of spike length to width is always smaller than *T. angustifolia*. They can hybridize to create *Typha x glauca* (Selbo and Snow 2004), a form which has been suggested to be most successful in areas where human activity has stabilized water tables and increased the availability of phosphorus (Boers and Zelder 2008).

Previous Field Ecology studies found *T. angustifolia* only in the experimental ponds on the ES George Reserve, and found the native *T. latifolia* in all other surveyed locations within the reserve (Barrow et al. 2008, unpublished). Our objective was to survey areas outside the reserve to see whether distinct patterns of *Typha* species distribution were observed in relation

to relative levels of disturbance. Based on the theory of hybrid vigor, we would expect that *T. x glauca* would show stronger competitive ability than either of the two parent species. Thus we would expect to find a greater abundance of *T. x glauca* in a wider range of habitats.

MATERIALS AND METHOD

Study site

This study was conducted to the south of the E.S. George Reserve, Michigan. We took 13 2m by 2m plots in the marshes along the east side of Patterson Lake and west side of Woodburn Lake. We surveyed 5, 4, 4 plots for *T. X glauca*, *T. angustifolia*, *T. latifolia* respectively.

Method

For each of the plot, we noted down the type of cattails and cattail numbers. We measured average water depth, litter depth, the number and coverage of other species and the canopy cover condition of each plot. Then we randomly selected 3 individual plants and measure the length of the longest leaf, leaf width, stem diameter, gap length, spike length and width of each plant. We used the principle component analysis (PCA) for speciation identification, and multivariate analysis to see whether significant difference existed between three types. All the data analysis was taken by SPSS 16.0.

RESULT

Species composition and distribution of cattails

We had 5, 4, 4 out of 13 plots for *T. X glauca*, *T. angustifolia*, *T. latifolia* respectively. The positions of plots of different types of cattails were shown in Fig. 1. In areas we have surveyed, the *T. X glauca* is the dominant species, comprising more than 90% of the total cattail abundance; we found more *T. angustifolia* on the west side of Woodburn Lake and more *T. latifolia* on the east side of Patterson Lake.

Speciation identification based on PCA factor analysis

We used principal component analysis to see how different morphological features (plant height, leaf width, stem diameter, gap length, spike shape) contribute to differences between three types of cattails. The result is shown in Table 1. The height and leaf width were most significantly different of all features. And as shown in Fig.2, the three types can be clustered into three distinct groups, which means they have relatively significant differences in morphological features. In comparison between groups, we found that the hybrid tend to resemble the *T. latifolia* more by having more overlapping features (data not shown).

Fig.1 Study site and plot distribution

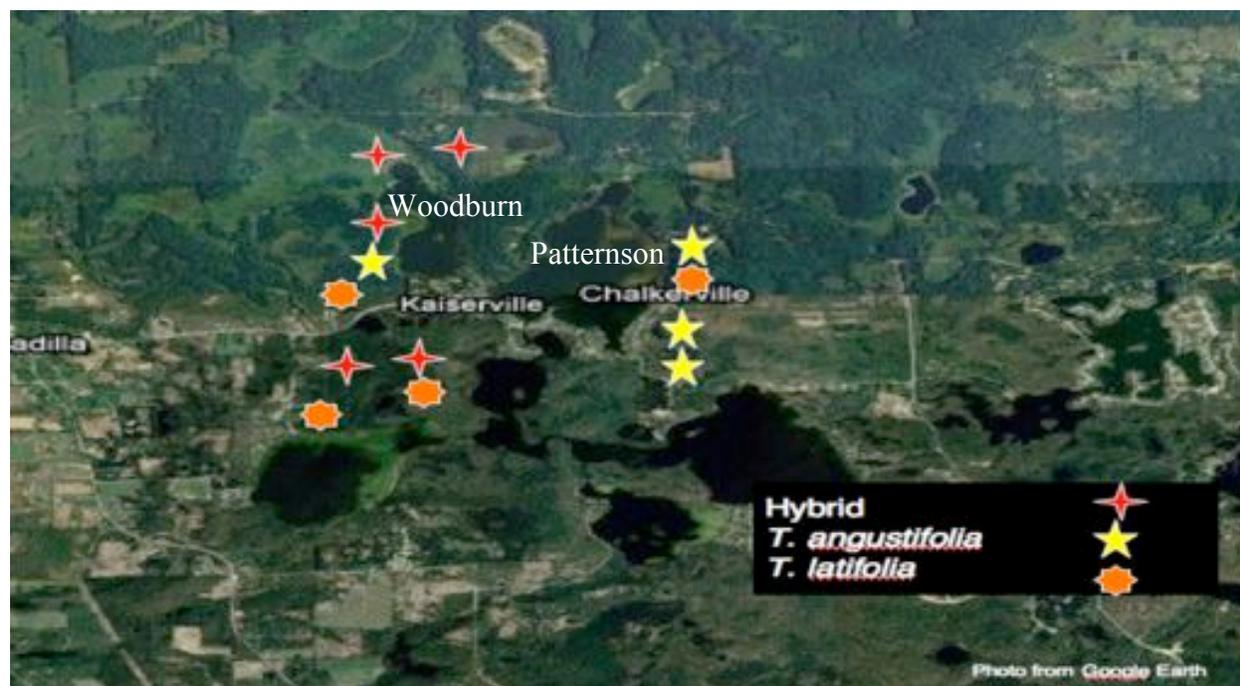


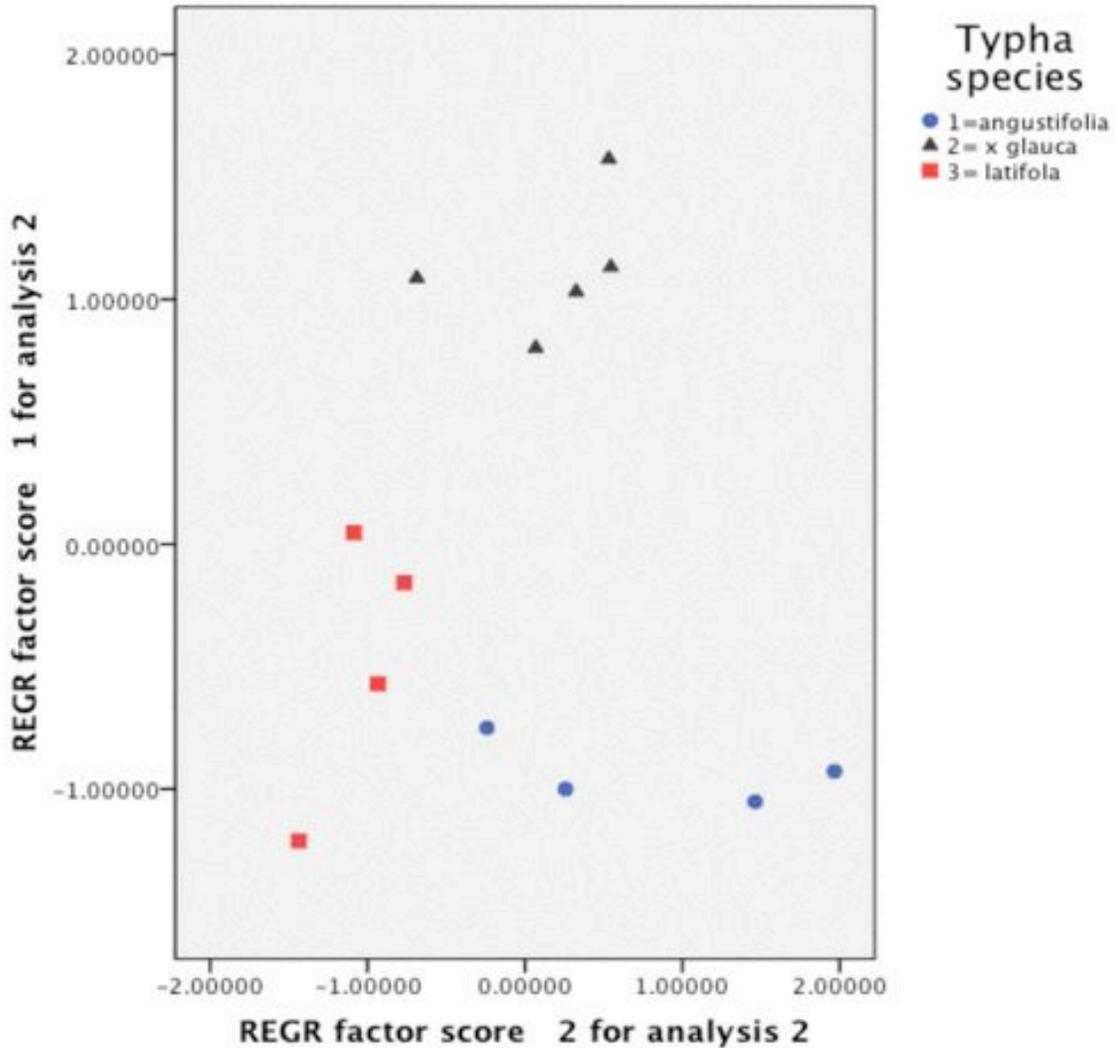
Table 1 Principal component analysis based on morphological features

	Component	
	1	2
height (m)	.888	.280
Length longest leaf (m)	.931	.133
Stem diameter (mm)	.738	-.533
Spike length (cm)	.768	.243
Spike width(mm)	-.859	-.150
gap length (mm)	-.327	.901

Extraction Method: Principal Component Analysis.

a. 2 components extracted.

Fig. 2 Species identification based on PCA



Environmental differences between three types of cattail

By using multivariate analysis (MANOVA), we tested whether the three types have environmental preferences. As shown in Table 2, after the Bonferroin's correction ($p=0.007$), none of the 7 environmental factors are significantly different between the three types. For the density of the plot, however, the three types did show some differences ($p=0.011$), and the respective density of the three plots is shown in Fig. 3. *T. angustifolia* has higher density than *T. latifolia* and the hybrid, which means that it might be able to bear higher density plots, and it might be one of the reasons for *T. angustifolia* to spread and successfully invade.

Table 2. Multivariate analysis of environmental preferences between three types

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	# live	1227.277 ^a	2	613.638	7.324	.011
	# dead	666.623 ^b	2	333.312	5.516	.024
	H2O (cm)	41.885 ^c	2	20.942	.332	.725
	litter (cm)	20.820 ^d	2	10.410	.989	.405
	species	34.742 ^e	2	17.371	2.257	.155
	% cover 1=0-5,2=5-20,3=20-50,4=50-100	3.108 ^f	2	1.554	2.158	.166
	canopy 1=open, 2=semi-shade	.681 ^g	2	.340	1.335	.306

Fig 3 Cattail density for different types

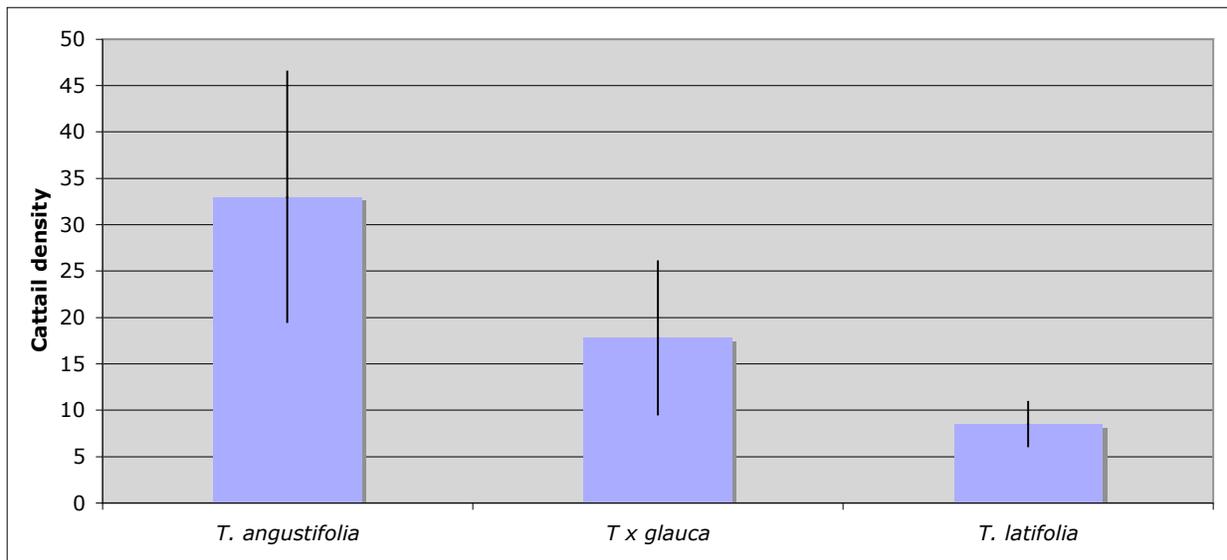


Fig 4-6 shows the water depth, litter depth, number of different species for the three types. Again, they don't have any difference in these three environmental measurements, and the hybrid does not seem to have broader range of habitat compared with the other two types.

Fig 4 Habitat water depth of different types of cattails

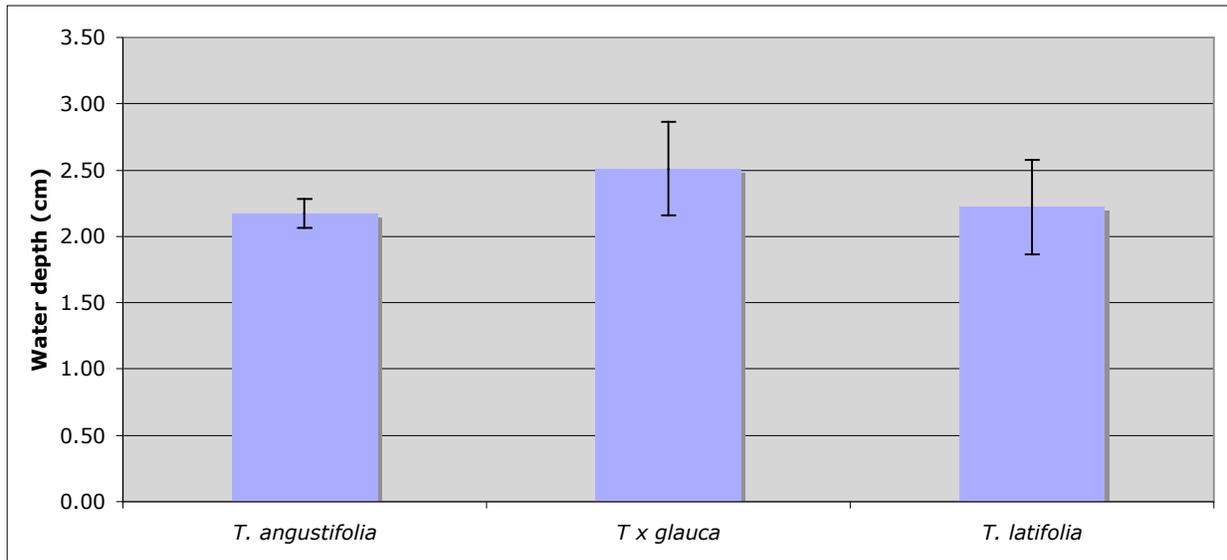


Fig 5 Habitat litter depth of different types of cattails

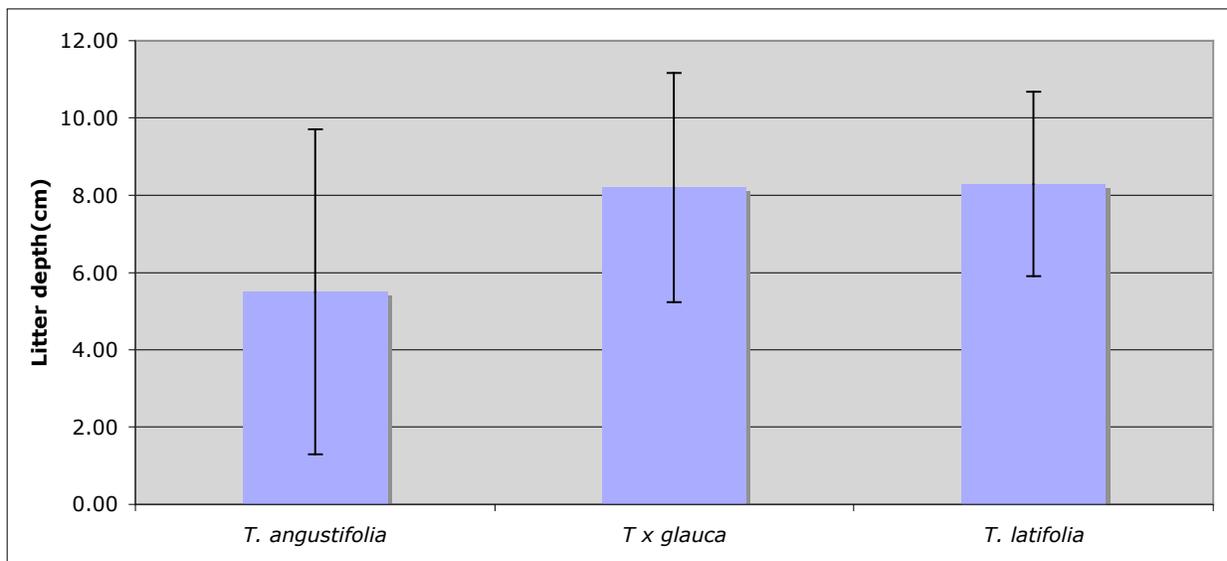
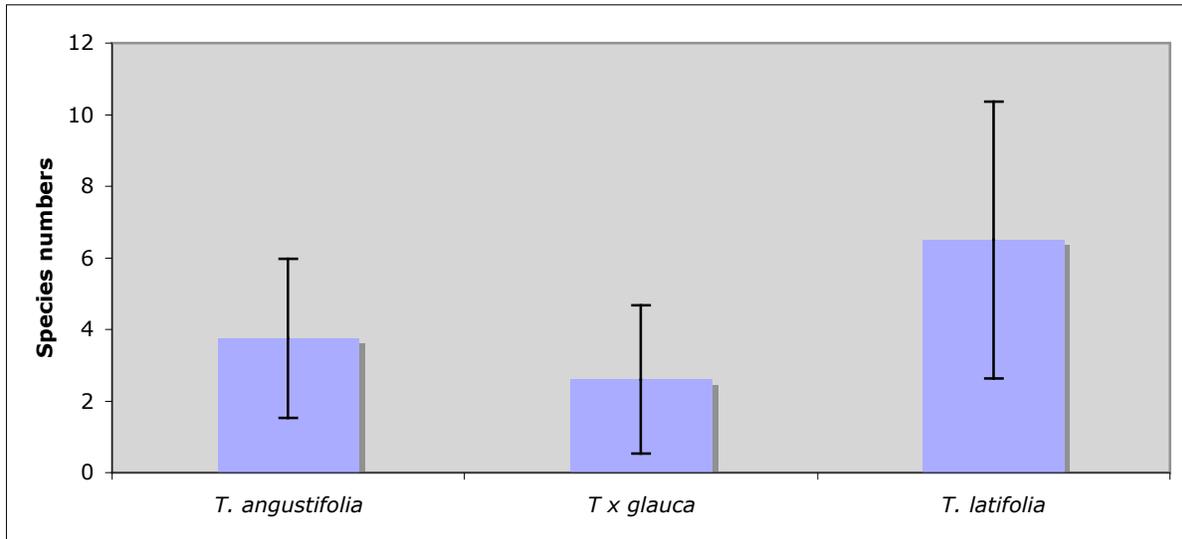


Fig 6 Number of other species in habitats of different types of cattails



DISCUSSION

Our results indicate that *T. x glauca* is dominant in marshes around Patterson Lake and Woodburn Lake outside the E.S. George Reserve. Plots of *T. x glauca*, *T. latifolia*, and *T. angustifolia* did not vary significantly by habitat characteristics such as water depth, leaf litter, canopy cover, and species composition. All three species were commonly found interspersed in the same area. Our a priori hypothesis that *T.x glauca* has a broader range of habitat was unfounded. However, this does not necessarily mean that *T. x glauca* does not have greater tolerance; on the contrary, at the beginning of invasion, it might indeed be more tolerant in environment and have a broader range of habitat; later it is able to outcompete its parent species and dominate in regions where the *T. latifolia* and *T. angustifolia* originally lived, which will reduce the habitat differences between the hybrid and the parent species.

In the study done in George Reserve last year (Barrow et al. 2008), *T. latifolia* existed only in natural pond while *T. angustifolia* existed in experimental ponds. In our study, the density of *T. angustifolia* seems to be higher than *T. latifolia* in the marshes outside George Reserve, which might be because all of the plot sites were in disturbed areas adjacent to a road outside the George Reserve, which favors the *T. angustifolia*.

The most striking difference of the two studies, however, is that no *T. x glauca* was found in the George Reserve but it dominates in marshes outside the reserve. There might be strong spatial separation between ponds in George Reserve so the two types cannot hybridize. Also, George Reserve has much less total disturbance than outside, so in established parent communities, the hybrid is not as successful perhaps because the germination opportunity is limited. At the same time, a majority of cattails reproduce vegetatively through root, thus *T. x glauca* outside might not be able to disperse into the Reserve due to fences.

In terms of invasion strategy, this might be an example of an invasion characteristic that improves the genetic success of the invasive species (*T. angustifolia*) by accepting the pollen of a closely related native species (*T. latifolia*) that has coevolved with native environmental conditions. Perhaps *T. angustifolia* uses a form of parasitic introgression to dominate the landscape by taking successful genes from the native species and incorporating them into a superior variation of Typhus. From the perspective of a genetic invasion, a genome that can sequester successful genes from a competing genome will at minimum match beneficial traits. If the invading genome has pre-existing beneficial genes in addition to the introgressed beneficial genes, then it is likely the invading genome will out-compete the native genome.

Future research could investigate the detail mechanisms of how *T. x glauca* outcompetes the parent species by genetic analysis. Also, it is interesting to find how the dominance of *T. x glauca* and *T. angustifolia* affect the ecosystem processes and structures of the local community.

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SPECIES RICHNESS, COMPOSITION, AND ZONAL CHARACTERISTICS IN A TRANSITIONAL BOG AND MINEROTROPHIC FEN

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ABSTRACT

Wetlands are diverse and dynamic communities that have characteristics critical to ecosystem health. There are several types of wetlands each defined by unique abiotic and biotic conditions, and each supporting different biological communities. In this study we focused on the similarities and differences in plant community composition between a temperate bog and fen. We predicted diversity would be higher in the fen reflecting higher relative nutrient availability, and that richness would decrease closer to the open water for both habitat types due to an assumed pH gradient. Due to the extreme difference in abiotic conditions, we predicted that evenness and shared species would be low in both sites. We found diversity, richness and evenness to be similar for both the bog and the fen. We observed a strong trend of decreasing richness relative to proximity to open water for both sites. As expected, the number of shared species was very low.

INTRODUCTION

Wetlands play several critical roles within the landscape, yet their importance is often overlooked, or more likely avoided. As the interface and ecotone between terrestrial and aquatic systems, wetlands are characteristically soggy, generally difficult to travel through, and are often filled with undesirable blood-sucking macroinvertebrates (mosquitoes, ticks, leeches, and more). Yet these characteristics reveal wetlands' great importance in the landscape and the ecosystem health. Wetlands are some of the most diverse and productive ecosystems on earth, provide water purification functions, stabilize water supplies by abating floodwaters and by slowly releasing water back into the groundwater table during droughts, stabilize inland and coastal shorelines, produce commercial products (from peat to rice to cranberries), and have more recently become realized as large carbon sinks of global climate importance (Mitsch and Gosselink, 2000).

Numerous wetland types exist, with names as numerous as the hydrologic, vegetative, and chemical processes that characterize them. This study focuses on two specific types – fens and bogs. These systems share great similarities and are marked by as many dissimilarities. While both are peatlands, plant communities differ primarily as a function of differing hydrologic and nutrient regimes. Peatland vegetation is particularly sensitive to variations in water chemistry, with certain taxa only able to survive in specific ranges of pH and Ca concentrations (Heinselman, 1970). Vascular and bryophyte species richness tend to be lower in bogs compared to fens and tends to follow a gradient from low (bogs) to high (fens) pH and Ca concentrations (Glaser et al. 1990). The presence of rare and threatened species is significantly correlated with high species richness in wetland habitats (Johnson and Leopold 1994; Locky and Bayley 2006). Thus, fens may be an important target for conservation.

In the case of the study areas Tiplady Fen and Hidden Lake Bog, the differences in hydrology and nutrient regimes are one and the same—essentially the abundance or lack of

mineral laden groundwater. Both Tiplady Fen and Hidden Lake Bog appear to be kettle hole lakes which have undergone terrestrialization, or the infilling of shallow lakes (Mitsch and Gosselink, 2000). Both peatlands have portions of floating or quaking mats of vegetation unsupported by mineral soils. Despite these similarities, the major difference derives from mineral rich groundwater. Tiplady Fen would be characterized as a minerotrophic peatland which receives water that has passed through mineral soil (Gorham, 1967). The most evident example of rich groundwater is the presence of marl, or precipitated calcium carbonate deposits within portions of the fen. As a result of higher nutrient levels, plant communities in fens are characterized by high species diversity and a high proportion of graminoids, woody plants, and brown mosses (Locky and Bayley 2006). In contrast, Hidden Lake Bog appears to be a mesotrophic (Mitsch and Gosselink, 2000), or transitional, mineral poor fen, with the most evident example being the dominance of *Sphagnum* mosses characteristic of low nutrient and low pH conditions. Other species well suited to these harsh abiotic conditions are ericaceous (acidophilic) shrubs and a high proportion of mosses and liverworts compared to fens (Wheeler 1993). Hidden Lake Bog would not be considered a technical bog as it is not ombrotrophic, or a true raised bog higher than the surrounding landform and therefore receiving nutrients only from precipitation (Mitsch and Gosselink, 2000). For the purpose of this discourse, Hidden Lake Bog will be referred to as a bog considering the notable dissimilarity in plant community composition and, though extrapolation, nutrient and mineral levels.

This study investigates and documents the hypothesized differences between the wetland characteristics of Tiplady Fen and Hidden Lake Bog and the resultant differences in plant species diversity and community composition. The investigators predicted that diversity values would be higher in the fen than in the bog because of the higher nutrient availability, that evenness would be low for both (i.e. graminoids would be the dominant vegetation habit of the fen and *Sphagnum* mosses would be the dominant vegetation habit of the bog), that species shared between the two distinct wetlands would be low, and that species richness would decrease within the plant communities along the gradient from the forest edge to the open water.

METHODS

Field measurements were taken from two wetland sites in Southeast Michigan. The first site, Hidden Lake Bog, is located within the E.S. George Reserve. The second site, the Tiplady Fen, is situated adjacent to Hell, Michigan approximately five miles outside of the Reserve to the southeast.

Within each of the two wetland habitats, we established three transect lines extending from the forest edge to the open water edge. The length of the transect lines ranged from 11 to 65 meters, varying in accordance with the distance in between the forest edge and the open water. The three transects were spread out to different sides of the habitats in order to get a good representation of plant species composition across microclimate gradients.

In each transect, we laid out three evenly spaced 1 m quadrats representative of forest edge, transitional, and open water zones. Within each quadrat, each observed vascular plant and *Sphagnum* species was identified.

We calculated species diversity using the Shannon Diversity Index and community evenness using Shannon's Equitability. Community similarity was calculated using the Classic Jaccard Index. Rarefaction curves were calculated for each habitat using EstimateS (Colwell

2005). A two-way ANOVA was used to determine any differences among the sampling zones within and between each habitat. Pearson's R correlation coefficients were calculated for species richness and distance from forest edge for data pooled from both habitats and within each habitat.

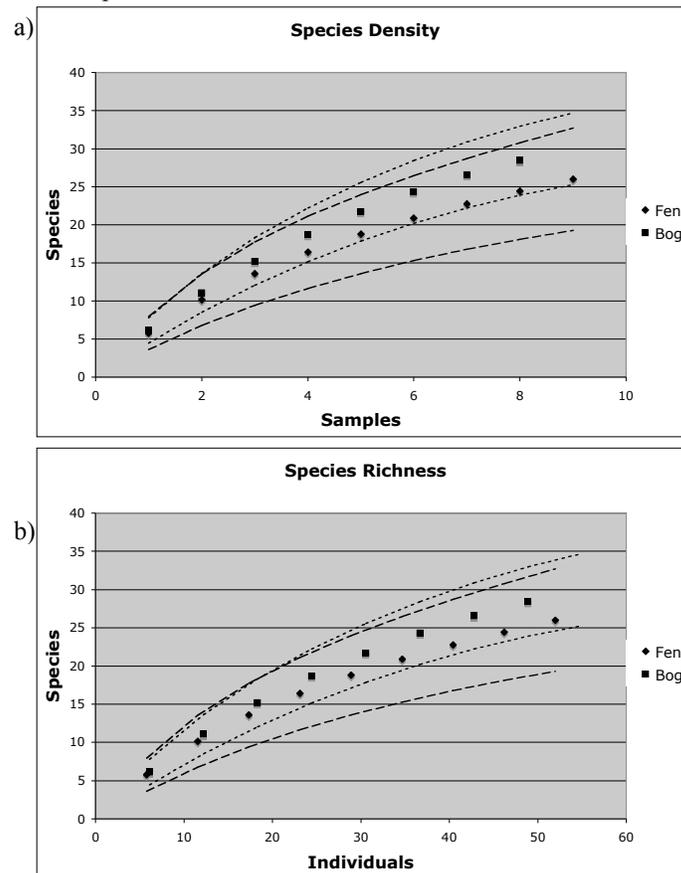
RESULTS

We identified 25 species unique to the bog and 25 unique to the fen from our transect sampling. The two habitats shared a total of only 4 species (Appendix A). An additional 10 species were found outside of the bog transects while 9 were found outside the fen transects, with only one species shared by both (not shown).

Species diversity was calculated using the Shannon Diversity Index. A Shannon index value of 1.38 was obtained for the bog and a value of 1.33 was obtained for the fen. Both habitats showed very high evenness values (0.93 for the bog, 0.94 for the fen), indicating that no single or group of species dominates either community.

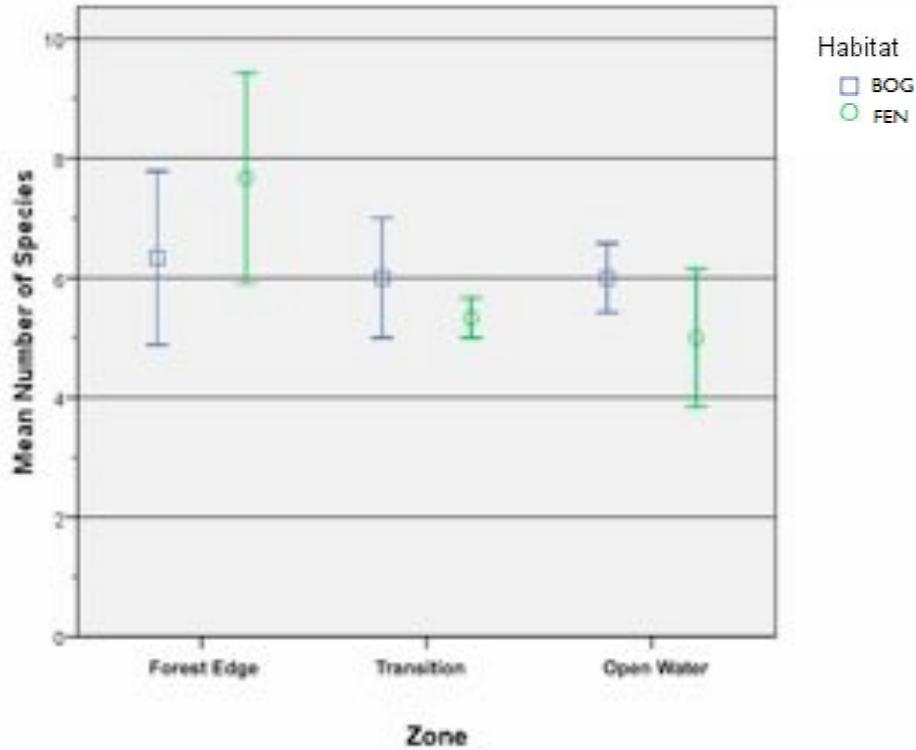
Rarefaction curves are shown in Figure 1. Both species richness and density in the bog are accumulated at a similar rate, with the bog slightly higher than the fen. It appears the curves are beginning to plateau, but do not do so until after the majority of samples or individuals are included. This suggests each habitat is relatively heterogeneous in their species distribution.

Figure 1: Sample based rarefaction curves for a) species density and b) species richness for all species found during transect sampling. Dashed lines represent 95% confidence intervals.



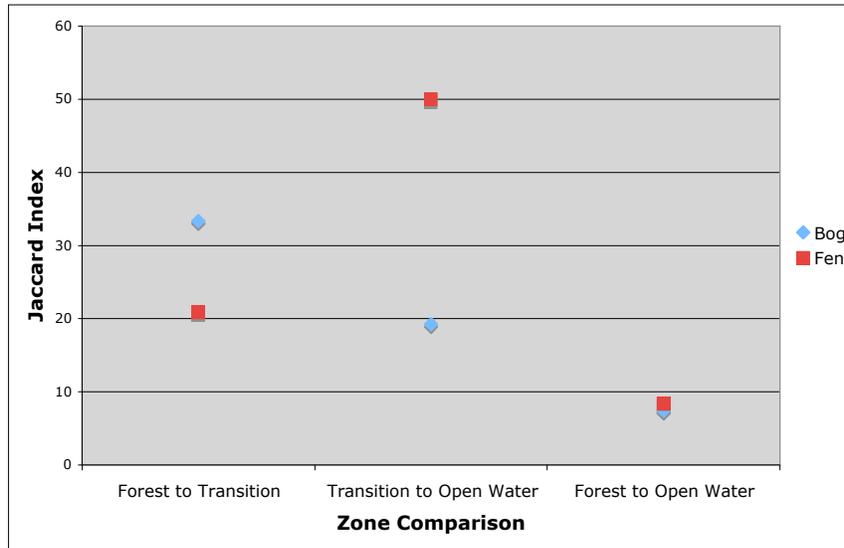
For each sampling zone (forest edge, transition, open water), the mean number of species was calculated across samples. There was no significant difference found among sampling zones either within each habitat or across the habitats using a two-way ANOVA, $F(5,17) = 0.674$, $p = 0.669$ (Figure 2).

Figure 2: Comparison of the mean number of species within specific sampling zones for the bog and fen.



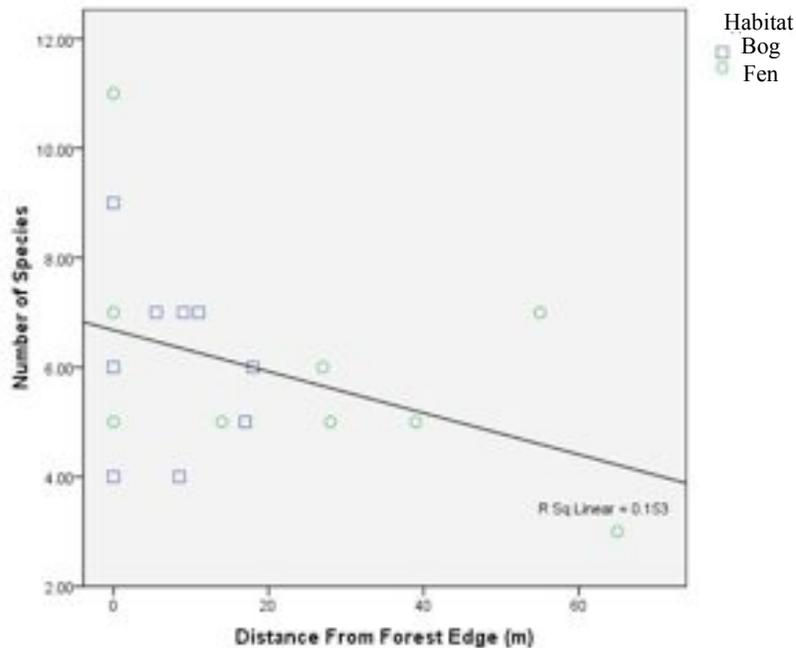
Within each habitat, we compared the similarity (Classic Jaccard Index) among the sampling zones (Figure 3). When comparing the forest edge zone to the transition zone the bog had a higher similarity than the fen. The opposite result is found when comparing the transition to the open water, while the bog and fen have a similar community similarity when comparing the forest to the open water. Overall, within each habitat forest and transition zones are less similar to the open water zone.

Figure 3: Community similarity (Classic Jaccard Index) among sampling zones within each habitat.



Species richness along the transect varied as a function of distance from the forest edge. We found that as the distance from the forest edge zone increased, the number of species found per quadrat decreased when the data was aggregated for the bog and fen, $R = -0.391$, $p = 0.054$ (Figure 4). The correlation is stronger in the fen than in the bog; however, it fails to reach significance, $R = -0.509$, $p = 0.081$. This is likely due to the greater average transect length used in the fen (mean transect fen = 49.3m; mean transect bog = 15.3m).

Figure 4: Species richness as a function of distance from forest edge.



DISCUSSION

Measures of diversity for the bog and fen indicate a high level of diversity exists in both but with no difference between the habitats. This result is unexpected given our prediction that the bog would have a lower overall diversity because we would expect the abiotic environment to be more extreme than the fen (i.e. the bog would have lower nutrient levels and lower pH). The very high evenness index for both habitats indicates that no one species dominates either habitat and the abundance of individuals is evenly distributed across all species. This defies our prediction and the general literature that mosses would dominate in the bog and graminoid species would dominate the fen (Bedford and Goodwin 2003); however, this may be due to the limited area sampled in both habitats.

Only 7% (n=4) of the total species identified were shared by the bog and fen. Thus the species composition of the habitats is very different. Looking at sampling zones, we see that the likelihood of sharing species is reduced when open water is compared to the forest and transition zones. The trend indicates the open water zone is dissimilar compared to the other zones, partially supporting our prediction that shared species among zones would be low. This trend may be due to the more extreme pH levels (low in bog, high in fen) being located within the open water zone (Bragazza et al 2005), requiring species living in that zone to be more specialized. Anaerobic conditions are also likely to persist throughout the year in the open water zone (Bridgham and Richardson 1993), further decreasing the number and types of species able to inhabit the zone.

We find further evidence for the zone dissimilarity in the decreasing species richness as distance from forest edge increases (Figure 4). Both increasingly extreme pH levels and the possible decrease in nutrients due to decreased litter fall (Bedford et al 1999) may contribute to this result. Additionally, while statistical significance was not reached, there was a decreasing trend in the mean number of species by zone moving from the forest to the open water zone (Figure 3). Based on the sample rarefaction curves we estimate both habitats to be relatively heterogeneous in species distribution, adding further support to our conclusion that species composition varies within each habitat.

Our finding that species composition greatly differs between a bog and fen is supported by the literature (Locky and Bayley 2006); however, the similarity in species diversity contrasts with previous studies (Schwintzer 1981; Anderson and Davis 1997; Locky and Bayley 2006). The differing species richness and low similarity among sampling zones for both habitats found in this study seems likely given that abiotic conditions tend to be more extreme with increasing proximity to open water (Bridgham and Richardson 1993; Bedford et al 1999; Bragazza et al 2005).

In light of these preliminary conclusions, we believe a larger and more robust sampling is needed before our findings can be confirmed. This includes a larger number of transects, a higher number of quadrats per transect to achieve a finer sampling zone gradient, and the inclusion of multiple fen and true bog habitats. Finally, measurements of pH and nutrient levels along each transect would greatly help to determine the drivers of the differences we found.

The critical importance of wetlands across landscapes in terms of species diversity and ecosystems services emphasizes the need for investigating the plant communities they support.

Many wetlands are threatened by development, nutrient deposition, and climate change (Kettles and Tarnocai 1999; Bragazza et al 2006). Gathering baseline knowledge of wetland plant communities allows researchers to measure future change of these systems. Wetlands, especially fens, tend to harbor a high proportion of rare and endangered species (Vitt 1994; Bedford and Goodwin 2003; Locky and Bayley 2006). Therefore understanding the plant communities of bogs and fens is important from a conservation standpoint.

Acknowledgements

We would like to thank Ben Davids from Moorehouse College for his assistance with this study.

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APPENDIX A

Table 1: Species identified for both habitats. * denotes shared species.

Bog		Fen	
Species Name	Common Name	Species Name	Common Name
<i>Acer rubrum</i>	Red Maple	<i>Elymus trachycaulus</i>	Slender Wheat Grass
<i>Bidens cernua</i>	Nodding Bur Marigold	<i>Aster borealis</i>	Rush Aster
<i>Carex lasiocarpa</i> *	Narrow-Leaved Woolly Sedge	<i>Aster species</i>	Aster
<i>Chamaedaphne calyculata</i>	Leatherleaf	<i>Bromus ciliatus</i>	Fringed Brome
<i>Eleocharis acicularis</i> *	Needle Spike Rush	<i>Calamagrostis canadensis</i>	Blue Joint Grass
<i>Eleocharis smallii</i> *	Marsh Spike Rush	<i>Campanula aparinoides</i>	Marsh Bellflower
<i>Eupatorium perfoliatum</i>	Common Boneset	<i>Carex lasiocarpa</i> *	Narrow-Leaved Woolly Sedge
<i>Glyceria striata</i> *	Fowl Manna Grass	<i>Carex stricta</i>	Common Tussock Sedge
<i>Ilex verticillata</i>	Winterberry	<i>Cornus stolonifera</i>	Red-Osier Dogwood
<i>Juncus nodosus</i>	Joint Rush	<i>Thelypteris palustris</i>	Marsh Shield Fern
<i>Larix laricina</i>	Tamarack	<i>Eleocharis acicularis</i> *	Needle Spike Rush
<i>Leersia oryzoides</i>	Rice Cut Grass	<i>Eleocharis species</i>	Spike Rush
<i>Lycopus uniflorus</i>	Northern Bugle Weed	<i>Eleocharis smallii</i> *	Marsh Spike Rush
<i>Onoclea sensibilis</i>	Sensitive Fern	<i>Eupatorium maculatum</i>	Spotted Joe Pye Weed
<i>Osmunda cinnamomea</i>	Cinnamon Fern	<i>Glyceria striata</i> *	Fowl Manna Grass
<i>Poa species</i>	Blue Grass	<i>Impatiens capensis</i>	Orange Jewelweed
<i>Polygonum sagittatum</i>	Arrow-Leaved Tear-Thumb	<i>Juncus balticus</i>	Lake Shore Rush
<i>Potentilla palustris</i>	Marsh Cinquefoil	<i>Juniperus virginiana</i>	Red Cedar
<i>Rosa palustris</i>	Swamp Rose	<i>LACTUCA species</i>	Lettuce
<i>Sphagnum recurvatum</i>	Peat Moss	<i>Lycopus americanus</i>	Common Water Horehound
<i>Sphagnum squarrosum</i>	Peat Moss	<i>Mentha arvensis</i>	Wild Mint
<i>Sphagnum magellanicum</i>	Peat Moss	<i>Muhlenbergia glomerata</i>	Marsh Wild Timothy
<i>Symplocarpus foetidus</i>	Skunk Cabbage	<i>Potentilla fruticosa</i>	Shrubby Cinquefoil
<i>Toxicodendron vernix</i>	Poison Sumac	<i>Schoenoplectus acutus</i>	Hard-Stemmed Bulrush
<i>Triadenum virginicum</i>	Marsh St. John's Wort	<i>Schoenoplectus americanus</i>	Common Three-Square
<i>Typha latifolia</i>	Broad-Leaved Cattail	<i>Schoenoplectus tabernaemontani</i>	Softstem Bulrush
<i>Ulmus americana</i>	American Elm	<i>Solidago gigantea</i>	Late Goldenrod
<i>Vaccinium corymbosum</i>	Highbush Blueberry	<i>Solidago species</i>	Goldenrod
<i>Vaccinium oxycoccos</i>	Small Cranberry	<i>Solidago riddellii</i>	Riddell's Goldenrod

SIMILARITY OR DISPARITY BETWEEN SPHAGNUM HUMMOCK AND SPHAGNUM LAWN PLANT COMMUNITY COMPOSITION WITHIN A MESOTROPHIC POOR FEN

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ABSTRACT

The plant communities and water chemistry were studied within a peatland in southeast Michigan locally known as Hidden Lake Bog. The abundance of *Sphagnum* moss suggested that the pH of both the hummock and *Sphagnum* lawn would be lower than the open water portion of Hidden Lake, which was observed. Because of the anticipated disparity of pH gradients from the *Sphagnum* lawn to the top of the hummock, notable variation in the plant community between these two extremes was expected. The plant communities were overall very similar, though poor methodology likely blurred the distinction between the two communities. Using the water chemistry data, the overall plant community diversity within the peatland, and modern peatland nomenclature classification, Hidden Lake Bog was technically classified as a mesotrophic poor fen.

INTRODUCTION

Wetland nomenclature has provided fodder for long debates, as international, colloquial, and scientific terms intermingle and defy one another. Marshes, swamps, carrs, fens, and bogs, are all wetland terms often used interchangeably in colloquial use, though scientifically these names are much better defined. A marsh is an open, graminoid dominated wetland with at least seasonal shallow standing water. A swamp is a wetland dominated by trees. A carr is a wetland dominated by shrubs (Crum, 2000). A fen is ... not so easily defined. In fact, quantitatively defining the difference between fens and bogs has defied consensus for the better part of a century.

Researchers have commonly based classification of peatlands on hydrologic source (Gorham, 1967; Moore & Bellamy, 1974; Sjors, 1961), nutrient levels (Weber, 1907), pH level (Wheeler and Proctor, 2000), and pH/ calcium ion levels (Sjors, 2002), among numerous other classification paradigms. Perhaps the most commonly used classification system (Mitsch and Gosselink, 2000) is that based on hydrologic source, or more specifically the proportion of hydrology provided by groundwater inflow versus precipitation. This peatland classification includes three types: minerotrophic which is heavily influenced by mineral rich groundwater; mesotrophic which is weakly influenced by mineral rich groundwater; and ombrotrophic which is solely fed by mineral poor precipitation. Generally the terms minerotrophic and mesotrophic are applied to fens (rich fens and poor fens respectively) and ombrotrophic is applied to bog.

Water chemistry gradients exhibit significant overlap between peatlands, from ombrotrophic bogs to poor fens to rich fens (Sjors, 2002), supporting the concept of transitional mesotrophic fens supplying a continuous gradient from bog to rich fen. In response to hydrologic source and the related amount of minerals, plant communities vary among bogs and

fens. Ombrotrophic fens are generally vegetated by *Sphagnum* mosses. *Sphagnum* is acidophilic and actually acidifies its surroundings by trading hydrogen ions for mineral ions in the environment (Crum, 2000). *Sphagnum* can be found as a “lawn” or forming hummocks, often with the most acidophilic species dominating the top of hummocks (Crum, 2000). As a result, ombrotrophic bogs are highly acidic, often having pH ranging from 3.7 to 4.2 (Sjors, 2002). Rich fens are vegetated by graminoid species including various species of grasses and sedges. Influx of mineral rich groundwater into rich fens tends to provide for a circumneutral pH. Mesotrophic poor fens are somewhere in between bogs and rich fens with a mixture of *Sphagnum* and graminoids. All landforms can contain trees and shrubs, with species dependent on tolerance to pH and mineral and nutrient availability.

Hidden Lake Bog is a peatland surrounding a small kettle hole lake at the E.S. George Reserve in southeast Michigan. Despite its name, Hidden Lake Bog appears to exhibit the qualities associated with a mesotrophic poor fen. The wetland is characterized by a small floating mat of vegetation surrounding the lake, extending toward a swamp. The transition from bog (or more appropriately, mesotrophic fen) to swamp is known as a lagg, which is the mineral rich zone surrounding a mineral poor peatland (Crum, 2000). Approximately one half of Hidden Lake displayed a developed peat mat, the majority of which was less than 20 m in length.

This study investigates the plant community and basic water chemistry (pH and specific conductivity) of Hidden Lake Bog. Areas dominated by *Sphagnum* are predicted to have lower pH than the open water (assumed to have properties similar to the groundwater). Further, it is anticipated that pH will be lower at the top of the *Sphagnum* hummocks than at the base because of the acidifying nature of the moss. It is predicted that specific conductivity, a relative measure of mineral ions, will be highest in the open water and lowest at the hummock tops. The plant communities are expected to differ based on location at the hummock top and *Sphagnum* lawn (referred to as hummock bottom). Because vegetation and water chemistry can be used as a proxy for hydrology (Glaser et al., 1990), synthesis of this information will provide parameters in which Hidden Lake Bog can be classified as a mesotrophic poor fen.

METHODS

The study was conducted within Hidden Lake Bog at the E.S. George Reserve, a 464 ha tract of forests, wetlands, and old fields, located within Livingston County, MI.

The northern and eastern portions of Hidden Lake Bog were included within this study as these areas encompassed the majority of poor fen/ bog vegetation. Six transect lines were established from the shrubby lagg to the edge of the floating mat (where it would support a person’s weight) perpendicular to the open water, ranging from 5 to 20 m in length. Each transect was spaced approximately 20 m apart; shrubs and gaps in the floating mat prevented precise distance measurements. Within each transect, a 1 m^2 quadrat was placed at the transect origin at the lagg edge and every subsequent 5 m.

This study focused on the differences between the top portions of the hummock, or highest point within the quadrat, and the bottom of the hummock, the *Sphagnum* lawn or lowest point within the quadrat. The height of the hummock top from the lowest point in the quadrat

was recorded. For the sake of this study, the midway elevation was used to divide the hummock top and hummock bottom plant communities. Within each quadrat, all observed vascular plant species and *Sphagnum* species were identified and recorded with respect to their location. The pH and specific conductivity were measured at the top and bottom of the hummock and the open water at the end of the transect. A meander search survey was conducted to record all observed species within the peatland from lagg to open water and create a comprehensive species inventory.

Hummock top and hummock bottom plant community similarity was calculated using the Jaccard index. The Jaccard index was conducted for species communities within quadrats and compared to species communities among the quadrats.

RESULTS

A total of 46 species were identified within the quadrats. 48% of the species (22) were shared among the top and bottom of the hummocks. The hummock top contained 13 unique species, and the hummock bottom contained 11 unique species (Appendix A, Table 2.). A total of 64 species were observed through the peatland (Appendix A, Table 2.).

The pH measurements among the hummock tops, hummock bottoms, and open water were totaled and averaged (Figure 1.). The hummock top pH average was relatively low at 5.1, which was raised above the water table (assumed to be at the level of the open water). The pH increased at the hummock bottom to 5.7. The composite pH average of all quadrats, top and bottom of hummocks, equaled 5.3. The open water pH was close to neutral at 6.5. Locations of the hummocks were compared to note any pattern of a pH gradient around the lake. A trend was noted that the northwest side of the lake was more alkaline than the southeast side, though this trend was more significantly demonstrated by the hummock tops (Figure 2.) than by hummock bottoms (Figure 3.). No significant trend was noted when the difference of pH between the hummock tops and bottoms was compared with respect to height of the hummock (Figure 4.).

To compare the similarity of plant communities of the hummock top and hummock bottoms, a Jaccard index was utilized (Figure 5.). The Jaccard index expresses the probability that two randomly chosen vascular plant or *Sphagnum* individuals, one from each of two samples (top and bottom of hummocks in this study) both belong to species shared by both samples (but not necessarily the same species) (Colwell, 2005). The plant communities of hummock tops and hummock bottoms were overall very similar within quadrats with a Jaccard index value of 0.14 (or 14% of species not overlapping). When the plant communities were compared among quadrats, they were still very similar with a Jaccard index of nearly 0.17. By comparing the plant communities among quadrats, it is apparent that there is not a significant difference in the plant communities of hummock tops or hummock bottoms at different locations within the fen.

The specific conductivity measurements among the hummock tops, hummock bottoms, and open water were totaled and averaged (Figure 6.). Specific conductivity measures the ability of water to conduct electricity; therefore, it is a convenient way to estimate the total dissolved ions in solution (Hem, 1992). Ionic content of water represents presence of minerals. Conductivity here is used as a surrogate for mineral richness, and therefore a rough surrogate for

alkalinity. The hummock top conductivity average is low at 23 $\mu\text{S}/\text{cm}$; the hummock bottom conductivity average was a bit higher at 54 $\mu\text{S}/\text{cm}$; and the open was highest at 83 $\mu\text{S}/\text{cm}$.

Figure 1. Average pH values of hummock tops, hummock bottoms, and open water.

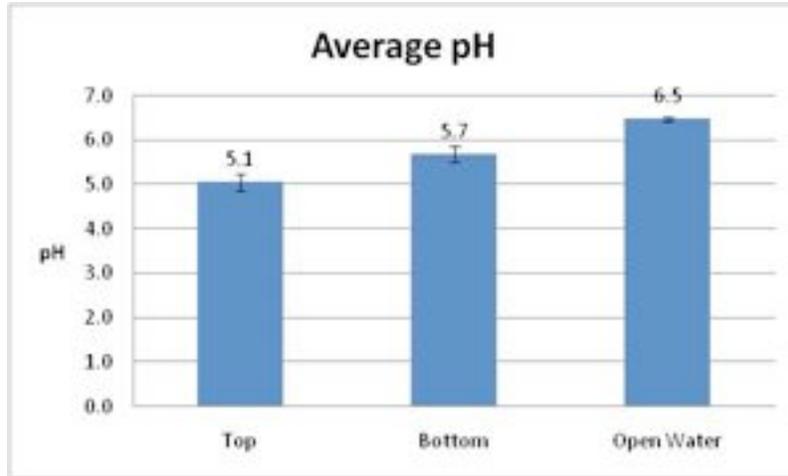


Figure 2. Average pH of hummock tops within each transect. A trend of decreasing pH is apparent from Transect 1 to Transect 6.

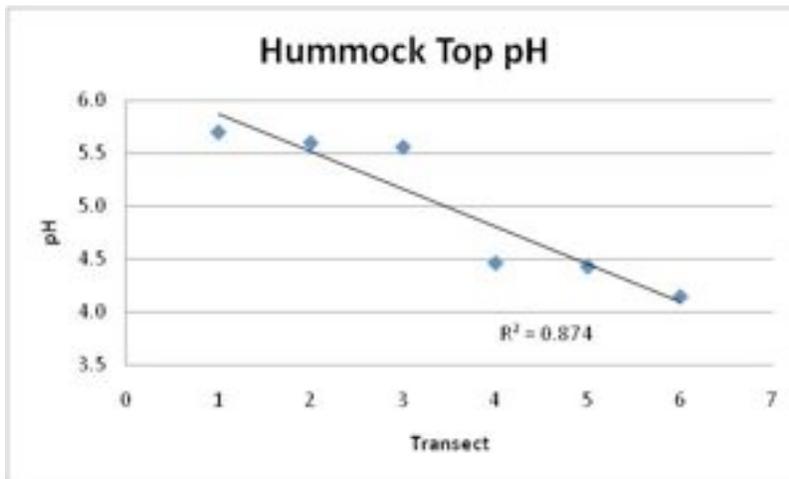


Figure 3. Average pH of hummock bottoms within each transect. A trend of decreasing pH is apparent from Transect 1 to Transect 6.

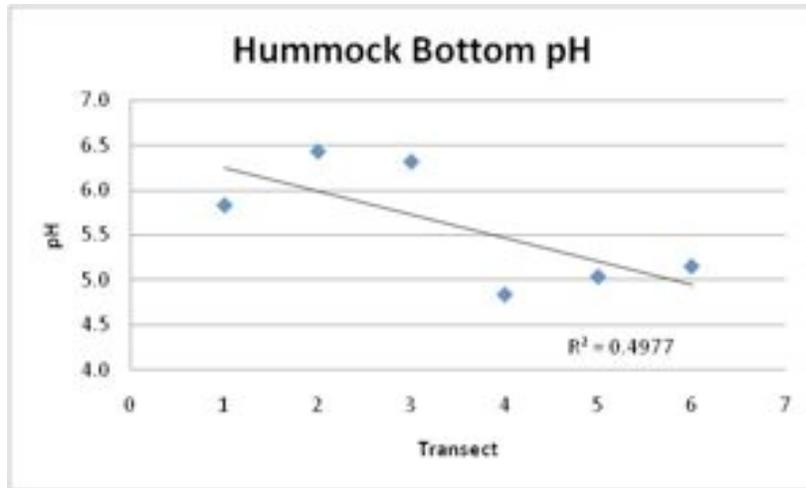


Figure 4. pH value difference between the hummock tops and hummock bottoms with respect to hummock height. The pH of the hummock top was subtracted from the hummock bottom (typically a higher pH than the top). Hummock height was measured by taking the lowest point (no lower than standing water) in the quadrat and the highest point within the quadrat.

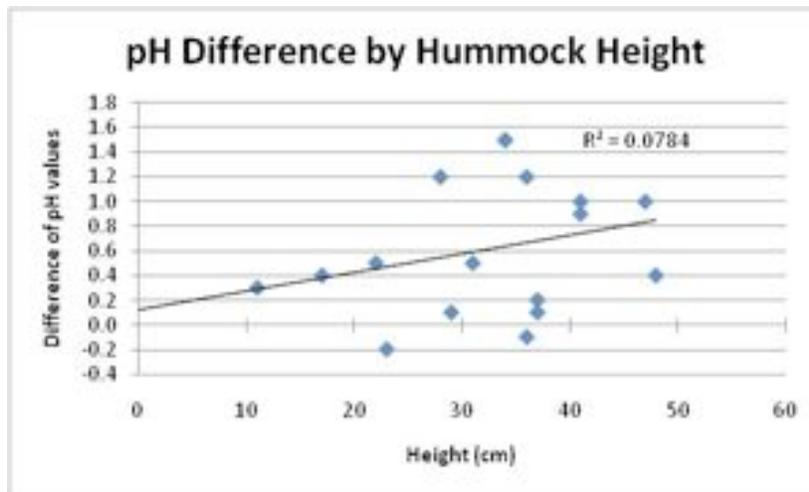


Figure 5. Plant community similarity between hummock top and hummock bottoms. “1” below signifies the plant community similarity of hummock tops and bottoms within quadrats; “2” below signifies the plant community similarity between hummock tops and bottoms among quadrats. 0.00 on the y-axis would demonstrate identical plant communities with complete species overlap; 1.00 on the y-axis would demonstrate no overlap of species.

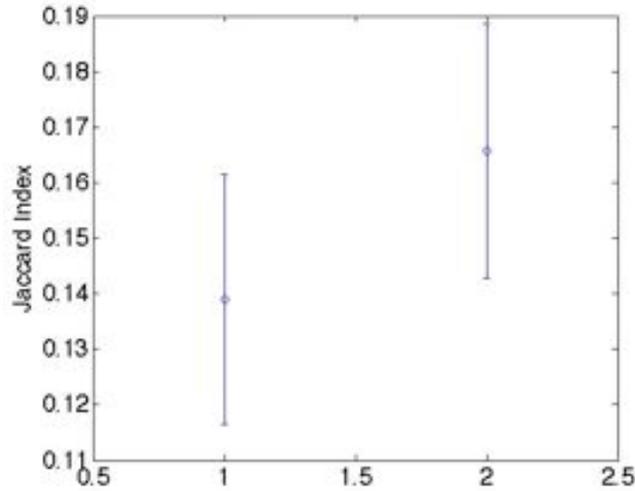
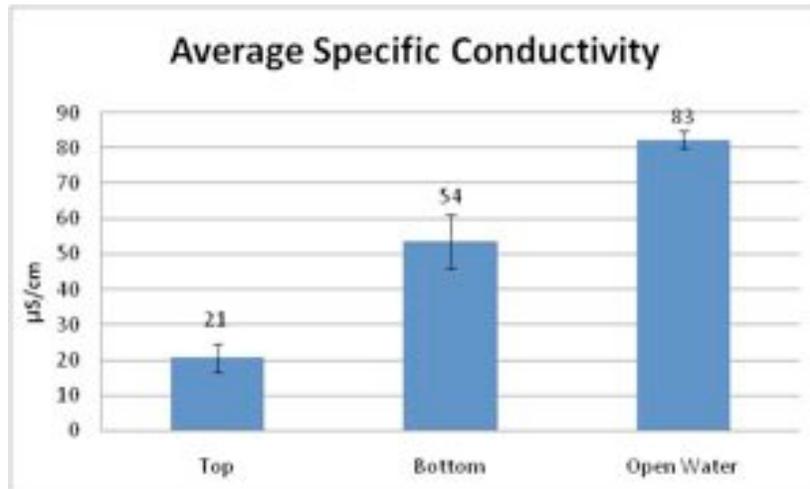


Figure 6. Average specific conductivity values of hummock tops, hummock bottoms, and open water. Only 4 of the transects were measured as the batteries on the conductivity meter failed before Transects 1 and 2 could be measured.



DISCUSSION

Measures of pH indicate that areas dominated by *Sphagnum* exhibit a lower pH compared to open water, and the pH at the hummock tops is lower than at the *Sphagnum* lawn. These findings correspond to the well documented capacity of *Sphagnum* to acidify its environment. The disparity between the hummock tops and hummock bottom, or *Sphagnum* lawn, was not as great as anticipated. Raised ombrotrophic bogs are separated from groundwater by dense layers of impermeable peat (Weber, 1902; Von Post and Granlund, 1926; Sjørs, 1948). Depth to any minerotrophic (mineral rich) peat in a raised bog comes no closer than 50 cm from the surface and usually deeper (Siegel and Glaser, 1987). As the hummocks at Hidden Lake Bog were

raised as much as 48 cm above the *Sphagnum* lawn (and likely deeper to groundwater), it was anticipated that the tops of these hummocks would exhibit a pH closer to a raised bog, approximately 3.8-4.2.

Only a few hummock tops exhibited pH between 3.8 and 4.2. Hidden Lake Bog is not a raised ombrotrophic bog, and the average hummock height was only 30 cm. Because *Sphagnum* moss does not have vascular tissue, hummocks can only grow as tall as capillary action of water will allow, which is 50 cm (Crum 2000). The pH of the lower hummocks could have been influenced by groundwater. Influx of as little as 10% of mineral rich groundwater can have drastic effects, raising even acidic bog water with a pH of 3.6 to circumneutral values as high as 6.8 (Glaser et al., 1990).

It must be noted that several factors may have resulted in flawed pH readings. The pH meter was calibrated only once with a pH buffer of 7.0, and the readings were taken in the field on the same day. Measurements from the *Sphagnum* were taken by pressing the moss into the probe to release water. Several factors can influence pH readings, notably degrees of aeration, the time of day, the temperature of water (Crum, 2000; Tahvanainen and Tuomaala, 2003). Standardization of sampling technique would be necessary to ensure more precise results, including placing water samples (including squeezings from *Sphagnum*) into containers for later testing (equalizing amount of aeration), taking all samples around the same time of day, calibrate the pH meter with both 4.0 and 7.0 standards, recalibrate routinely, and make sure that the buffer standard is at the same temperature as the samples (Crum, 2000; Tahvanainen and Tuomaala, 2003).

Measures of specific conductivity indicate fewer mineral ions in areas dominated by *Sphagnum* compared to open water, and the amount of mineral ions in the hummock tops is lower than the *Sphagnum* lawn. Large numbers of mineral ions are present in mineral rich groundwater; otherwise the only mineral sources are from decomposition and trace amounts in precipitation. The hummock tops are furthest from groundwater and exhibited predictably low conductivity. The open water, presumably similar to groundwater, exhibited conductivity nearly four times that of the hummock tops. A sample of open water with the lagg was taken for reference, and this measurement exhibited the highest specific conductivity of 130 μ S/cm. The highest measurement in the open was 90 μ S/cm.

Similar to measuring pH, certain factors may have reduced the accuracy of the specific conductivity. Sjors (2002) noted that at pH lower than 4.7, significant errors may occur in specific conductivity measurements. Most noteworthy is the fact that the batteries of the specific conductivity meter used in this study died during the study. Only four of six transects and four of six open water samples were sampled. It is possible that the values measured were flawed altogether because of low battery strength; however, readings were consistent among the samples measured. For future testing, it is also important to note that seasonality affects the availability of mineral ions in solution (Proctor, 1994; Hajek, 2004).

Despite the disparity of water chemistry between the hummock tops and the *Sphagnum* lawn, the plant community composition was not significantly different. The species compositions were not very different between the hummock top and bottom within a quadrat,

and the hummock tops and bottoms were also not very different when compared to other quadrats. Although observations in the field did in fact indicate more similarity between hummock and lawn communities than expected, greater differences between these communities existed than portrayed by the Jaccard index. The methodology utilized in this experiment turned out to be fairly flawed for this analysis. In order to maintain consistency, plant communities were determined by using the midpoint of the hummock as the division between hummock top and hummock bottom. Unfortunately, this method significantly increased the potential for shared species. Furthermore, a 1 m^2 quadrat was too small to effectively measure hummocks and *Sphagnum* lawn together—some quadrats were actually all hummock or all *Sphagnum* lawn. Future investigations need to account for these experimental design failures. An additional measure of species abundance, likely through percent cover, may be useful for establishing comparisons between plant communities.

From the findings of this investigation, it is the opinion of the author that sufficient evidence was gathered to successfully classify Hidden Lake Bog as a mesotrophic poor fen. Plant species representative of raised bogs were present, although the strongest acidophiles only found in such landforms were not present. Conversely, species associated with rich fens and other minerotrophic wetlands were also represented, although they were not as abundant. The most compelling evidence for classification is the water chemistry. The specific conductivity is low, indicating a relative lack of mineral ions consistent with ombrotrophic bogs; however, portions of the peatland have a high enough conductivity to suggest influence from groundwater, suggesting mesotrophy. The composite pH average of all quadrats, top and bottom of hummocks, equals 5.3, which by some researchers (Wheeler and Proctor, 2000) would qualify Hidden Lake Bog as a bog as it is under 5.5. The variation in plant species consisting of both acidophiles and more mineral tolerant species, as well as the range of pH from 3.9 to 6.8, classification as a mesotrophic transitional or poor fen appears more appropriate. In the peatland parlance of our time, Hidden Lake Bog should be renamed to be Hidden Lake Poor Fen.

ACKNOWLEDGEMENTS

The author would like to thank Michael J. Wiley, PhD. of the University of Michigan School of Natural Resources and Environment for the use of a pH meter and specific conductivity meter to carry out this study. Special thanks to David Allen, PhD candidate of the University of Michigan Department of Ecology and Evolutionary Biology for his statistical assistance, particularly with respect to the Jaccard index. The author wishes to pay respects to the late Barbara J. Madsen, PhD. of the University of Michigan for inspiring the author's interest and fervor for peatlands and wetlands of all types.

Table 1: Hidden Lake Bog Comprehensive Species Inventory

SCIENTIFIC NAME	COMMON NAME
<i>Acer rubrum</i>	RED MAPLE
<i>Aronia prunifolia</i>	CHOKEBERRY
<i>Aster puniceus</i>	BRISTLY ASTER
<i>Aster sp.</i>	ASTER
<i>Betula pumila</i>	BOG BIRCH
<i>Bidens aristosa</i>	SWAMP MARIGOLD
<i>Bidens cernua</i>	NODDING BUR MARIGOLD
<i>Bidens frondosa</i>	COMMON BEGGAR'S TICKS
<i>Calla palustris</i>	WATER ARUM
<i>Carex comosa</i>	BRISTLY SEDGE
<i>Carex lasiocarpa americana</i>	NARROW-LEAVED WOOLLY SEDGE
<i>Carex sp.</i>	SEDGE
<i>Chamaedaphne calyculata angustifolia</i>	LEATHERLEAF
<i>Decodon verticillatus</i>	WATER WILLOW
<i>Dulichium arundinaceum</i>	THREE-WAY SEDGE
<i>Eleocharis acicularis</i>	NEEDLE SPIKE RUSH
<i>Eleocharis compressa</i>	FLAT-STEMMED SPIKE RUSH
<i>Eleocharis smallii</i>	MARSH SPIKE RUSH
<i>Epilobium leptophyllum</i>	FEN WILLOW HERB
<i>Eriophorum virginicum</i>	RUSTY COTTON GRASS
<i>Eupatorium maculatum</i>	SPOTTED JOE PYE WEED
<i>Eupatorium perfoliatum</i>	COMMON BONESET
<i>Galium boreale</i>	NORTHERN BEDSTRAW
<i>Glyceria striata</i>	FOWL MANNA GRASS
<i>Ilex verticillata</i>	WINTERBERRY
<i>Juncus balticus littoralis</i>	LAKE SHORE RUSH
<i>Juncus brachycarpus</i>	SHORT-FRUITED RUSH
<i>Juncus nodosus</i>	JOINT RUSH
<i>Larix laricina</i>	TAMARACK
<i>Leersia oryzoides</i>	RICE CUT GRASS
<i>Lemna minor</i>	SMALL DUCKWEED
<i>Lycopus uniflorus</i>	NORTHERN BUGLE WEED
<i>Menyanthes trifoliata</i>	BUCKBEAN
<i>Muhlenbergia glomerata</i>	MARSH WILD TIMOTHY
<i>Onoclea sensibilis</i>	SENSITIVE FERN
<i>Osmunda cinnamomea</i>	CINNAMON FERN
<i>Osmunda regalis spectabilis</i>	ROYAL FERN
<i>Polygonum sagittatum</i>	ARROW-LEAVED TEAR-THUMB

<i>Polygonum sp.</i>	WATER KNOTWEED
<i>Potentilla palustris</i>	MARSH CINQUEFOIL
<i>Rosa palustris</i>	SWAMP ROSE
<i>Rubus pubescens</i>	DWARF RASPBERRY
<i>Rumex orbiculatus</i>	GREAT WATER DOCK
<i>Salix serissima</i>	AUTUMN WILLOW
<i>Sarracenia purpurea</i>	PITCHER PLANT
<i>Solidago patula</i>	SWAMP GOLDENROD
<i>Solidago uliginosa</i>	BOG GOLDENROD
<i>Sphagnum angustifolium</i>	PEAT MOSS
<i>Sphagnum girgensohnii</i>	PEAT MOSS
<i>Sphagnum magellanicum</i>	PEAT MOSS
<i>Sphagnum papillosum</i>	PEAT MOSS
<i>Sphagnum squarrosum</i>	PEAT MOSS
<i>Sphagnum wulfianum</i>	PEAT MOSS
<i>Symplocarpus foetidus</i>	SKUNK CABBAGE
<i>Thelypteris palustris</i>	MARSH SHIELD FERN
<i>Toxicodendron vernix</i>	POISON SUMAC
<i>Triadenum virginicum</i>	MARSH ST. JOHN'S WORT
<i>Typha latifolia</i>	BROAD-LEAVED CATTAIL
<i>Ulmus americana</i>	AMERICAN ELM
<i>Vaccinium angustifolium</i>	EARLY LOW BLUEBERRY
<i>Vaccinium corymbosum</i>	HIGHBUSH BLUEBERRY
<i>Vaccinium macrocarpon</i>	LARGE CRANBERRY
<i>Vaccinium oxycoccos</i>	SMALL CRANBERRY
<i>Viola nephrophylla</i>	NORTHERN BOG VIOLET

Table 2. Species unique to hummock top and hummock bottom from the transect survey.

TOP	BOTTOM
<i>Aronia prunifolia</i>	<i>Bidens frondosa</i>
<i>Aster borealis</i>	<i>Eupatorium maculatum</i>
<i>Aster puniceus</i>	<i>Eupatorium perfoliatum</i>
<i>Aster sp.</i>	<i>Juncus brachycarpus</i>
<i>Eriophorum virginicum</i>	<i>Leersia oryzoides</i>
<i>Galium boreale</i>	<i>Lemna minor</i>
<i>Osmunda cinnamomea</i>	<i>Polygonum sagittatum</i>
<i>Osmunda regalis</i>	<i>Salix serissima</i>
<i>Rubus pubescens</i>	<i>Sphagnum papillosum</i>
<i>Toxicodendron vernix</i>	<i>Sphagnum squarrosum</i>
<i>Vaccinium angustifolium</i>	<i>Typha latifolia</i>
<i>Vaccinium corymbosum</i>	
<i>Vaccinium macrocarpon</i>	

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UNDERSTORY LIANA DIVERSITY IN A MESIC TEMPERATE FOREST

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ABSTRACT

While woody vines (or lianas) have historically been ignored in many studies of forest function and diversity, a surge of studies has been published in the past two decades. The biomass of lianas only comprise a small proportion of tropical forests, however they account for up to one-quarter of tropical plant species richness. Additionally, lianas play an important role in forest dynamics by increasing tree mortality, reducing tree growth and fecundity, and dominating the colonization of canopy gaps. In turn, canopy gaps promote the density and species richness of lianas when compared to closed forest understorey. We tested the hypothesis that canopy gaps help maintain the diversity of small vines in mesic temperate forests by surveying a half-hectare plot for vine diversity, canopy gaps, and coarse downed woody debris. No significant effects or correlations were found between canopy gaps and vine diversity. However, the abundance of large vines was found to be significantly higher in areas with a canopy gap. Before applying these results more broadly, multiple study plots should be surveyed incorporating improvements in gap identification and categorization.

INTRODUCTION

Woody vines (or lianas), a significant component of forest structure and function, have attracted interest over the past two decades leading to a surge of studies (Gerwing et al. 2006). Historically, lianas were excluded from forest censuses (Schnitzer and Bongers 2002) but now a standardized protocol exists (Gerwing et al. 2006) and liana assessments are increasing in major forest surveys across the tropics (e.g. Schnitzer et al. 2008). As a result, there is a growing body of research demonstrating the importance of lianas to forest dynamics (Schnitzer et al. 2000; Laurance et al. 2001; Perez-Salicrup 2001; Phillips et al. 2002, 2005; Kainer et al. 2006).

Lianas comprise about 5-10% of plant biomass in tropical forests (Putz 1984). However, the density of lianas can range between 10-45% of total woody stems (Schnitzer 2005) and they account for approximately 25% of total tropical forest species richness (Gentry 1991). Additionally, up to 30% of seedlings colonizing tropical forest floors are lianas (Comita et al. 2007), many of which are suppressed due to the low light availability of the understory (Putz and Chai 1987; Cai et al 2008). Similar studies for temperate zone lianas are lacking.

Trees infested with lianas have higher mortality rates (Putz 1984; Phillips et al. 2002, 2005), exhibit decreased growth and biomass (Laurance et al. 2001; Perez-Salicrup 2001), and reduced fecundity (Kainer et al. 2006). Given these characteristics, it is of little surprise that lianas play an important role in forest function, especially gap dynamics. Lianas are

disproportionately associated with non-pioneer tree taxa in canopy gaps (Schnitzer et al. 2000). As a result, when a canopy gap forms, lianas quickly colonize the high light environment and gap-phase regeneration of the forest is arrested. Schnitzer et al. (2000) found that lianas dominated 22% of gaps where regeneration had been stalled for at least 13 years. Lianas reduce the success of slow growing, shade tolerant tree species while promoting the growth of pioneer species (Laurance et al. 2000). Canopy gaps stay open as pioneers species comprise the majority of gap habitat tree species. These mechanisms can create a feedback cycle where forest gaps invite liana infestation which in turn leads to an increased likelihood of forest disturbance (Laurance et al. 2000, Phillips et al. 2002).

The same forest gaps that lianas help to create and maintain may also play an integral role in the maintenance of liana species diversity. Density and species richness of lianas can be higher in gap than in non-gap sites (Schnitzer and Carson 2001). Their results suggest that gaps support liana diversity independent of the increased probability of having high liana density in a gap site. Malizia and Grau (2008) found that absolute liana richness increased with increasing canopy openness. Recruitment and density of liana seedlings is also higher in large gaps than in smaller gaps or closed canopy (Dupuy and Chazdon 2006).

A result of the increasing study of lianas has been the discovery that their dominance and growth are intensifying. In the tropics, the dominance (stem density and basal area) of large lianas has increased by up to 4.6% per year over the last two decades of the 20th century (Phillips et al. 2002) In tropical Panamanian forests leaf litter production and the proportion of liana leaf litter increased as well (Wright et al. 2004). These trends have been implicated in the recent increase of Neotropical tree mortality (Phillips et al. 2002; Wright et al. 2004). The trends are not isolated to the tropics. Allen et al. (2007) found that liana importance (as measured by density, stem proportion, and basal area) has increased across a southeastern U.S. temperate forest (but see Londre and Schnitzer 2006). Rising atmospheric CO₂ has been implicated as a driver of these trends (Phillips et al. 2002) and studies of both tropical and temperate lianas grown under enhanced CO₂ conditions add substance to this claim (Granados and Korner 2002; Zotz et al. 2006).

We tested the hypothesis that canopy gaps help to maintain the diversity of small lianas – vines that have either not begun to climb or are considered low-climbing vines – in mesic temperate forests. We measured both current light gaps in the forest canopy and the presence of downed trees as a proxy for historical light gaps. Liana diversity was predicted to be higher in areas with current light gaps and areas with a larger number of downed trees.

METHODOLOGY

The location of the study was the Newcomb Tract, a 206-acre former farm now used as a research preserve. The forest was dominated by oaks (*Q. alba*, *Q. rubra*, and *Q. velutina*) and with lower abundance of *Prunus serotina*, *Ulmus americana*, and *Carya glabra*. *Carpinus caroliniana* was an abundant understorey tree. The survey was conducted in September, 2008.

The plot was located approximately 50m from an unused dirt access road. Our survey methods follow a modified protocol for surveying lianas (Gerwing et al. 2006). A 50m x 100m

plot was established with the 100m baseline on 20° azimuth and 50m baseline on 290° azimuth. The half-hectare plot was subdivided into fifty 10m² cells. Each cell was surveyed for large measurable lianas (≥0.5cm diameter at 20cm above the ground and at least 1.3m tall), small vine diversity (all other climbing plant species), dominant small vine species, downed trees, and presence of large canopy gaps. Lianas included all woody climbing plants, including climbing monocots that produce woody tissue (i.e. not true xylem tissue). Exact position of each large liana stem was recorded (measurable lianas). *Rubus allegheniensis* and *Rubus pensilvanicus* were aggregated because of the difficulty differentiating the two species in the field. The two most dominant small liana species were documented within each cell. Dominance was determined by overall vegetative coverage through a visual estimate. The length, size, and location of coarse woody debris – fallen trunks or limbs with a diameter ≥ 10cm determined by visual estimation – was recorded. Within each cell, we visually estimated the size and location of all canopy gaps greater than 5m in diameter. Canopy gap size and location were gathered only for the first 40 cells in the plot. Consequently, all analyses of canopy gaps do not include last 10 cells of the Newcomb Tract plot.

RESULTS

Fourteen species of climbers, including all measurable lianas and small vines, were identified at the Newcomb Tract plot. The abundance of measurable lianas was high (n=116) compared to other plots of the same size and methodology in southeastern Michigan (Sedio et al. 2007; R. Burnham, personal communication). However, these individuals were distributed among only five species. The distribution of all measurable lianas surveyed is shown in Figure 1.

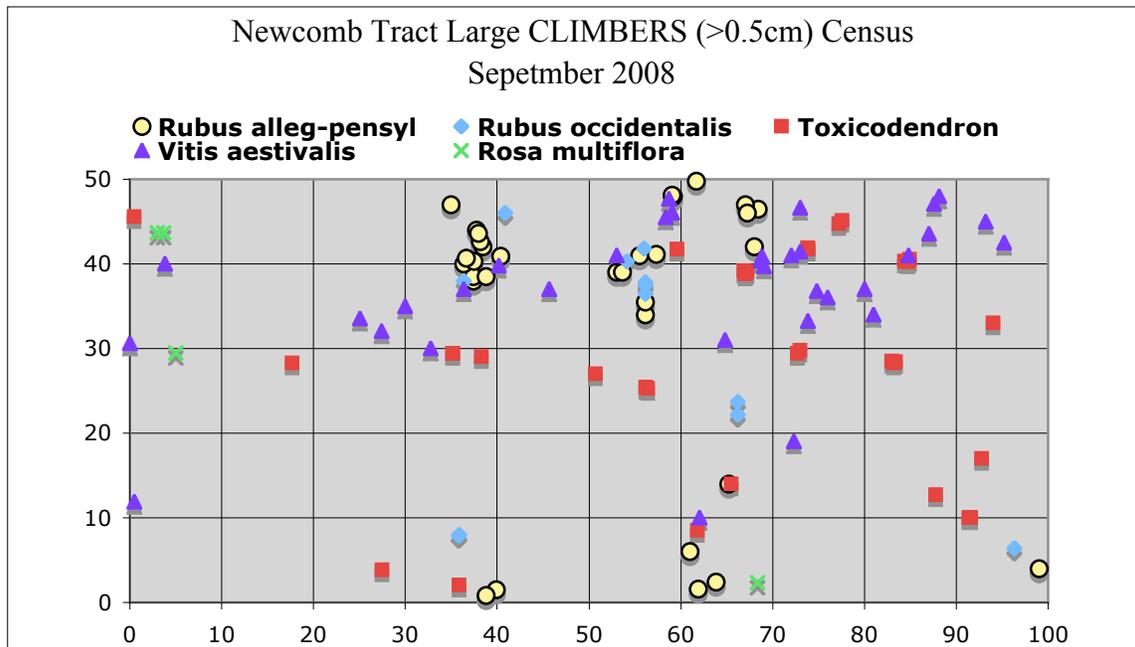


Figure 1: The distribution of measurable lianas (≥ 0.5cm at 20cm or 1.37m DBH) by species in the Newcomb Tract plot.

Species accumulation curves were calculated using EstimateS (Colwell 2005). For comparison, data from the 2007 climber survey at Shanahan Hill are included here (Figure 2). In both graphs, species accumulated by sample plateau after about 12 to 15 cells. The rates at which new species are accumulated are similar in both density and richness graphs. The quick accumulation of species suggest both sites are relatively homogenous in their species distribution.

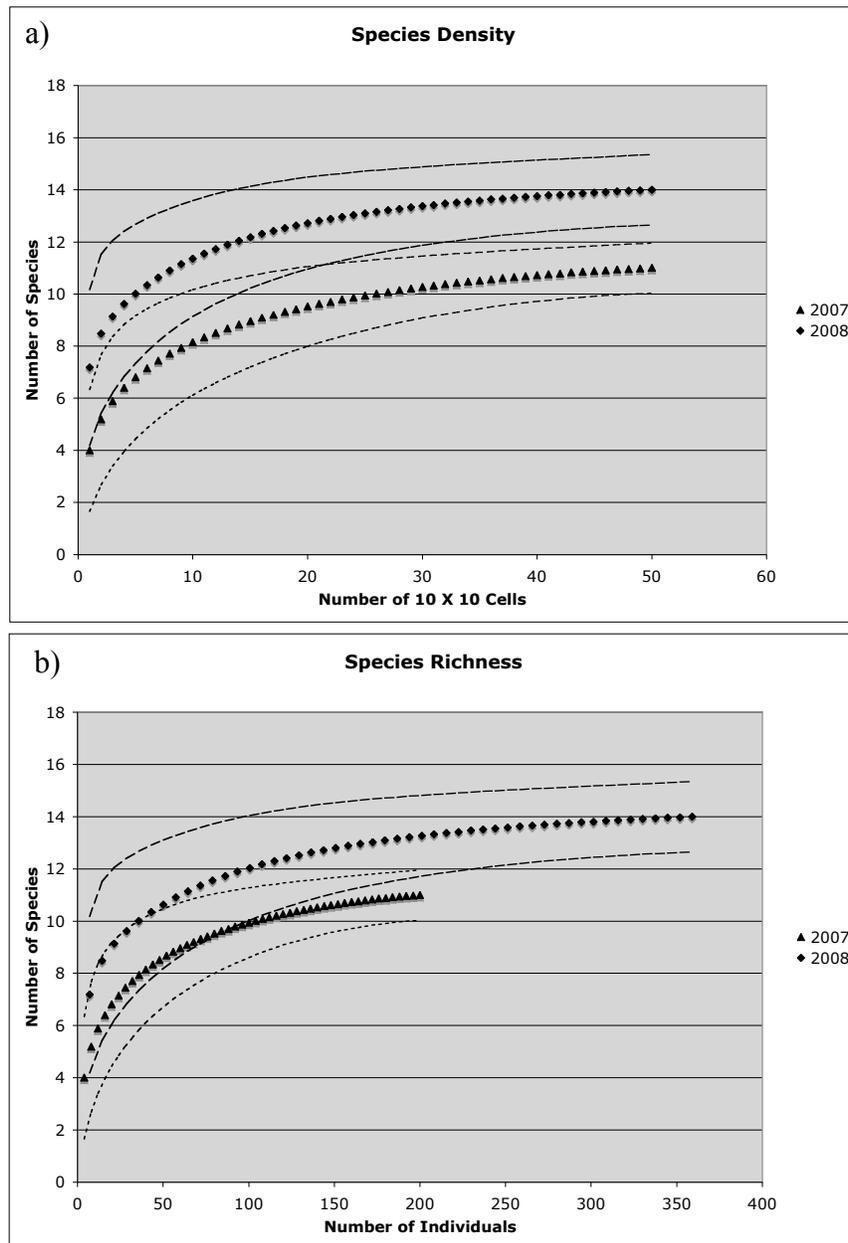


Figure 2: Sample based rarefaction curves for a) species density and b) species richness for all vine species found in the plot. Dashed lines represent 95% confidence intervals.

No significant correlation was found between coarse downed woody debris and either measurable climber diversity ($R = -0.044$, $p = 0.394$) or small climber diversity ($R = -0.173$, $p = 0.143$), using Pearson's R correlation coefficients. Depictions of both relationships are shown in Figure 3.

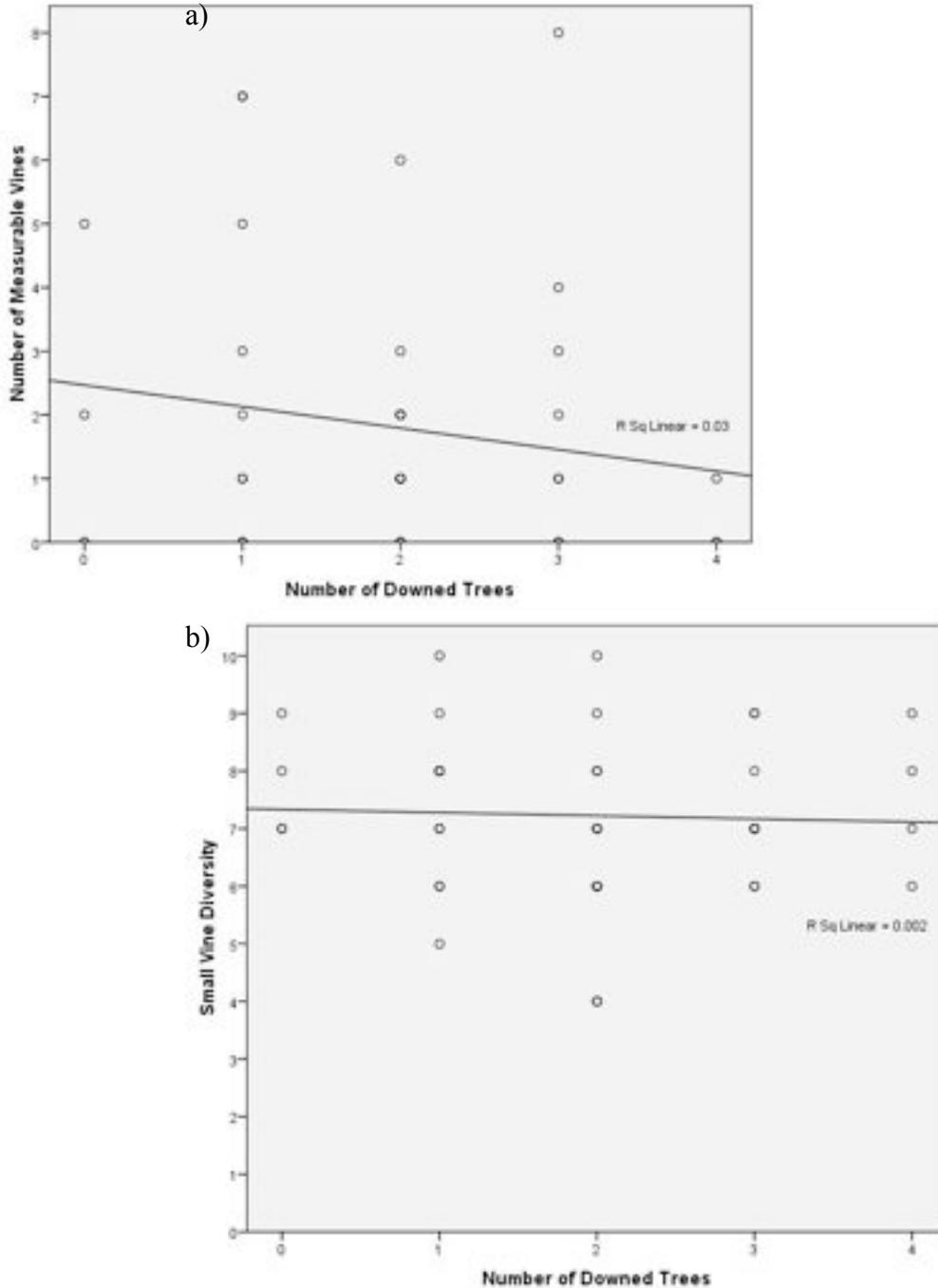


Figure 3: Linear regressions for coarse downed woody debris and a) measurable lianas and b) small vine diversity

No difference between the presence of a canopy gap and small climber diversity was revealed by a one-tailed independent sample t-test ($t= 0.405$, $d.f.= 23.1$, $p= 0.345$). However, a significant difference was detected between the presence of light gaps and the mean number of measurable lianas per cell ($t= 1.794$, $d.f.= 20.7$, $p= 0.044$; Figure 4).

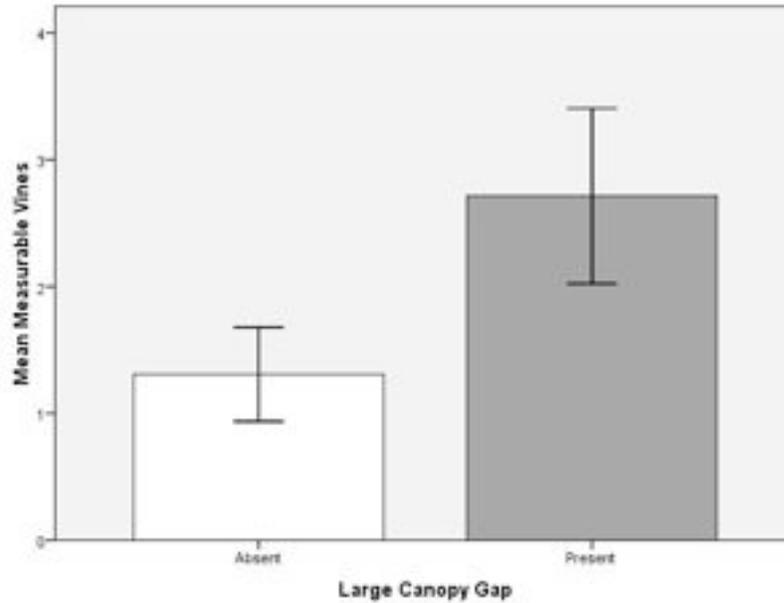


Figure 4: Mean measurable vines in cells with and without canopy gaps. Error bars represent ± 1 SE.

The dominant small vine species had no significant effect on the small vine diversity as measured by a one-way ANOVA ($F= 1.349$, $d.f.=5$, $p= 0.262$; Figure 5).

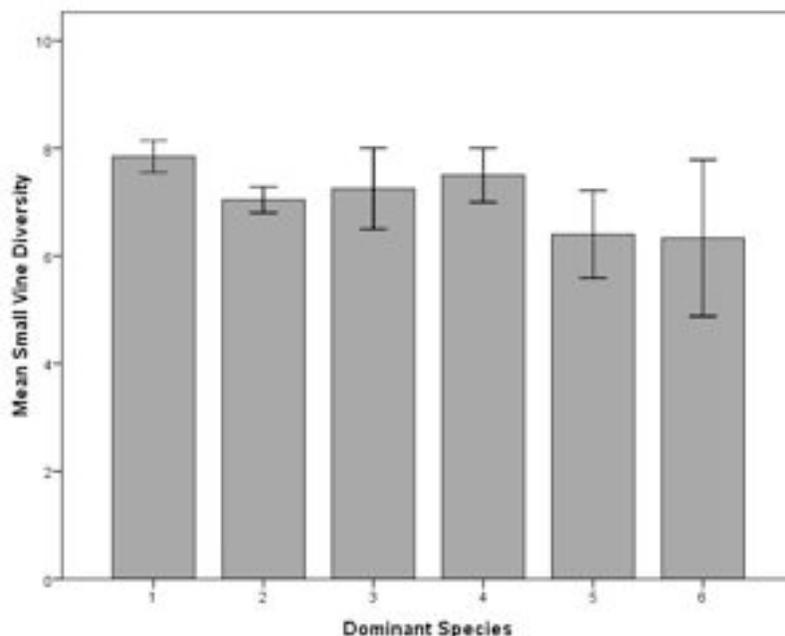


Figure 5: Mean small vine diversity by the dominant species of small vine present in the cell; 1: *Rubus allegheniensis/pensilvanicus*, 2: *Rubus flagellaris*, 3: *Amphricarpaea bracteata*, 4: *Rubus occidentalis*, 5: *Parthenocissus quinquefolia*, 6: *Toxicodendron radicans*. Error bars represent +/- 1 SE

DISCUSSION

No relationship was detected between the presence of light gaps and small climber diversity in the Newcomb Tract, defying the hypothesis that liana diversity is maintained by forest canopy light gaps. Although light gaps have been observed to increase liana species diversity richness and abundance of individuals in tropical forests (Schnitzer and Caron 2001; Dupuy and Chazdon 2006), our study in a temperate forest did not find the same result.

However, the number of large measurable lianas was significantly higher in cells containing a light gap. This result is consistent with previous studies in which light gaps promoted liana abundance (Schnitzer et al. 2000; Dupuy and Chazdon 2006). Liana seedlings previously suppressed in undisturbed forests proliferate upon gap formation (Malizia and Grau 2008). In addition, the presence of downed trees and limbs may act as a climbing substrate, allowing smaller vines to increase to measurable size (Malizia and Grau 2008). It is thus probable that the increase in measurable vines in the presence of gaps is a reflection of the ability of lianas to proliferate in gap microclimates.

No relationship between the dominant small vine species and small vine diversity was observed. Analysis of data not presented here reflects a possible negative relationship between the dominant small vine species and small vine diversity in the presence of light gaps. This suggests that the presence of specific dominant small vine species might influence overall small vine diversity in light gaps. A much larger sample size would be needed to evaluate such a hypothesis and generate meaningful results. Data collected in nearby liana survey plots did not

record the presence of light gaps, down coarse woody debris, or dominant small liana species for comparison.

The scope of this analysis was limited by the short duration of the project. This study looked at only the presence and absence of gaps within each cell influencing liana diversity. In forest ecosystems, gaps can vary significantly in characteristics such as light levels, temperature, evaporation, and soil chemistry. In addition, the variation of forest gaps in space and time within a particular region may influence liana community dynamics (Malizia and Grau 2008). For instance, recently formed gaps should provide greater resource availability than well-established gaps (Malizia and Grau 2008). Gap age has also been found to influence the liana community within a gap (Schnitzer et al. 2000). None of these factors were measured in the current study.

A thorough evaluation of forest gaps within the study site may lead to useful predictions regarding liana-gap dynamics. Standardization of gap measurements and recording of small liana dominance is recommended. For example, a densitometer can be used to estimate forest canopy coverage, establish limits for downed coarse woody debris length as well as diameter, record the precise location of gaps and woody debris, and identify dominant species through a method of 50% or greater cover and subdominant species with coverage of 20% or more. It is recommended that future study plots include data on presence of light gaps, downed coarse woody debris, and dominant small liana species for comparison and establishment of a more significant sample size.

Acknowledgements

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LEAF COLORS CHANGE IN AUTUMN: IS THERE ANY ADAPTIVE SIGNIFICANCE OF
BEING YELLOW OR RED?

HUIJIE GAN JINGCHUN LI LEILING TAO

ABSTRACT

Recently two hypotheses were proposed to explain the possible adaptive significance of leaf colors change in autumn. Photoprotection hypothesis states that the yellow and red pigments (carotenoids and anthocyanins) can serve as antioxidants and protect leaf organelles from light damage in autumn; coevolution hypothesis suggests the bright color may serve as a 'signal' revealing the level of defensive commitment of the plant to insects that migrate to the tree in autumn and exploit it as a host for the winter. We study autumn leaf colors of maples (*Acer spp.*) in George Reserve to test the above hypotheses and find that consistent with photoprotection hypothesis, red maples (*Acer rubrum*) in more open area have a higher red index (redness of the leaf). We also find that silver maples (*Acer saccharinum*) have a higher red index and tend to have heavier gall infection compared to red maple. On the interspecific level the coevolution hypothesis would suggest that silver maple is more vulnerable to gall infection thus invests more to signaling and show brighter color. On intraspecific level of red maple, there is a negative relationship between gall density and red index; however, we didn't find any color difference between leaves with and without aphid load. Without the understanding of the life cycle of this kind of gall species and extra information of aphid loading of the whole tree, it is hard to say whether our finding support the coevolution hypothesis or not.

INTRODUCTION

Leaf color change from green to yellow or red is one of the most striking phenomena in many deciduous forests. In autumn, when temperature decreases, chlorophylls in the leaves begin to degrade and other pigments (e.g. carotenoids and anthocyanins) are unmasked and begin to show the yellow or red colors (Matile 2000). This is the usual explanation of leaf coloration and it is believed that leaf color change in autumn is simply the byproduct of the process of leaf senescence. It is not until recently that ecologists began to consider the phenomena in ecology and evolutionary perspectives and a few hypotheses have been proposed to explain the adaptive significance of colorful autumn leaves (Ougham et al. 2008). From the perspective of possible physiological function of being yellow or red, the photoprotection hypothesis states that senescence-related processes lead to increased vulnerability to damage from visible light; and carotenoids and anthocyanins can serve as antioxidants and protect leaf organelles and ensure foliar nutrients recovery (Lee and Gould 2002). The coevolutionary hypothesis suggests the bright color may serve as a 'signal' revealing the level of defensive commitment of the plant to insects that migrate to the tree in autumn and exploit it as a host for the winter. Coevolution of color preference would allow well-defended plants to reduce parasite load and the parasites to locate the most profitable hosts for the winter (Hamilton and Brown 2001). Hamilton and Brown made two predictions that (i) on an interspecific level, species of trees suffering greater insect attack invest more in defence and consequently more in defensive signaling than less troubled species; and (ii) on an intraspecific level, individuals of signaling species vary in expression of this signal, the ones with bright leaves

will suffer a lower level of insect attack than will those that are dull colored.

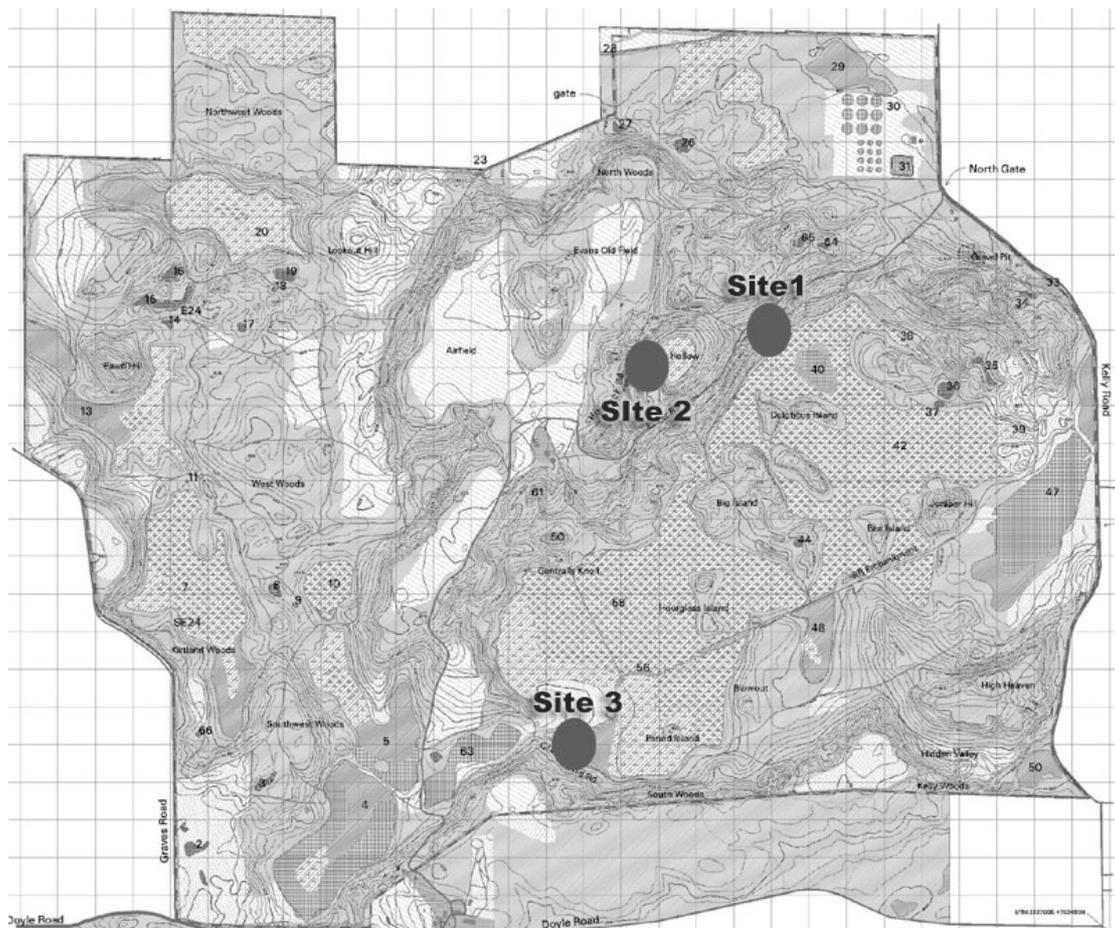
Based on our understanding of the above hypotheses, we want to know whether they are applied to the maples here in George Reserve or not. According to the photo-protection hypothesis, we predict that maples in the open area will have brighter colors. And if the co-evolution hypothesis is correct, we expect that between species, the brighter one will have heavier insect infection and within the same species, the brighter individual suffer less insect infection.

METHODS

Study Site

The E. S. George Reserve is about 25 km northwest of Ann Arbor (approximately 42° 28' N, -84° 00' W). The climate is a humid type characterized by low thermal efficiency and by rainfall throughout the year. We collected our leaf samples mainly from three randomly selected sampling sites. Site one is located on the north shore of the swamp; site two is along the southwest of Buck Hollow; site three is on the southwest shore of the swamp (fig.1). All three sites are near wooded wetland.

Figure 1. Sampling sites in E. S. George Reserve



Sampling

Samples were collected on October 5, 2008, from the three sites described above. Eight maple trees (leaf colors have changed completely) were randomly selected from site one, five from site two and ten from site three (uneven sampling due to the limit numbers of trees with fully changed leaves). Ten leaves were collected from each tree (except for site three, only 9 leaves were collected from the second tree), a total number of 229 leaves were obtained. To ensure that the leaves are from the same developmental stage, we shook each tree and only collected the fresh leaves falling after shaking.

For each leaf, the number of galls, aphids, and aphid eggs on leaf surface were counted respectively and recorded. Physical damage degree of leaves was determined by percentage.

Leaf color analysis

Every individual leaf was photographed from same distance under same lighting condition by using Canon PowerShot SD1100IS 8MP digital camera, a white background was provided, image size was set to 640*800. Photos were input into Adobe Photoshop 7.0, the leaf area was selected and total pixels of the area were recoded to reflect the size of the leaf. The red degree (red index) and luminosity of each leaf were determined by the median number obtained from the color histogram (read from red channel for red degree and luminosity channel for luminosity).

Data analysis

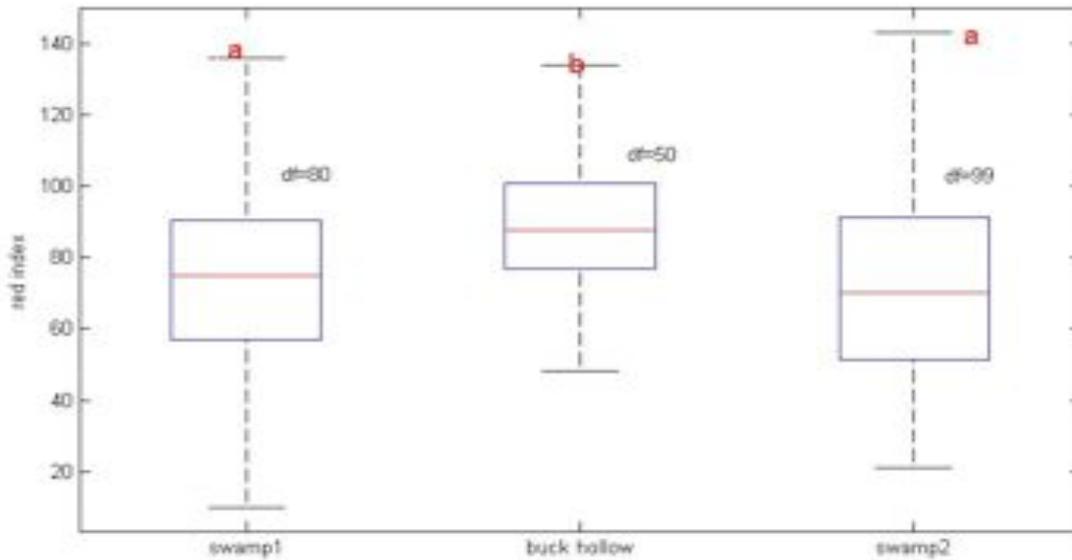
We used individual leaf characters for statistical analysis. Gall density, average red index and luminosity per tree were calculated using Microsoft Excel 2003. The relationship between leaf red degree and insect damage degree were analyzed by SPSS (version 16.0).

RESULTS

Red color index in different habitats

As shown in Fig. 2, the red color index in Buck hallow is higher than that of the two swamps. And compared to the swamps, the Buck hallow is a relatively open region, so it is consistent with our hypothesis that trees in open areas tend to turn their color first.

Fig 2 Average leaf index in three different habitats



Interspecific differences in red color index

We collected leaves from two maples: red maple and silver maple. Red maple tended to have higher gall infection and red index than that of silver maple (Fig. 3, 4). This proved our hypothesis that in terms of interspecific comparison, the more vulnerable species would spend more energy in synthesizing defensive compounds, thus have a more intensified signal.

Fig 3 Red color index in different maple species

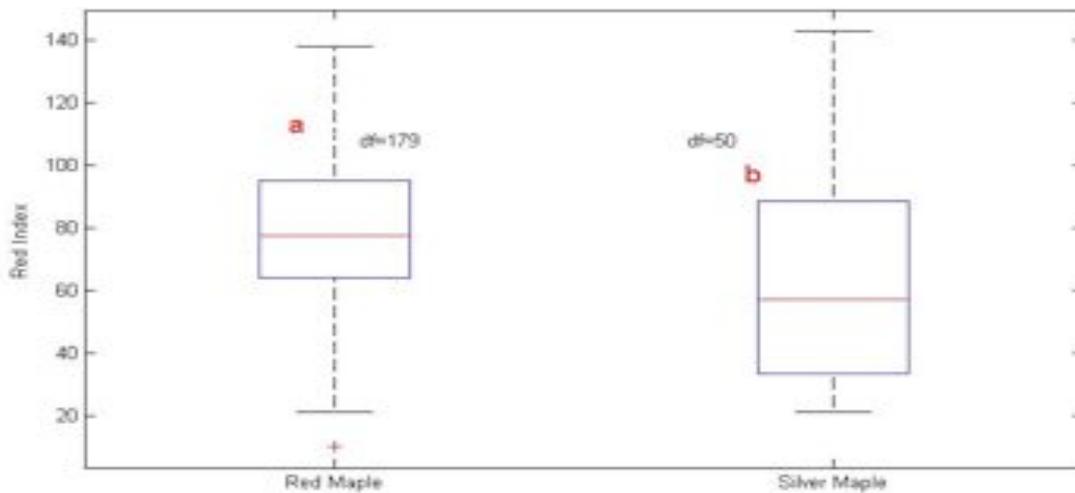
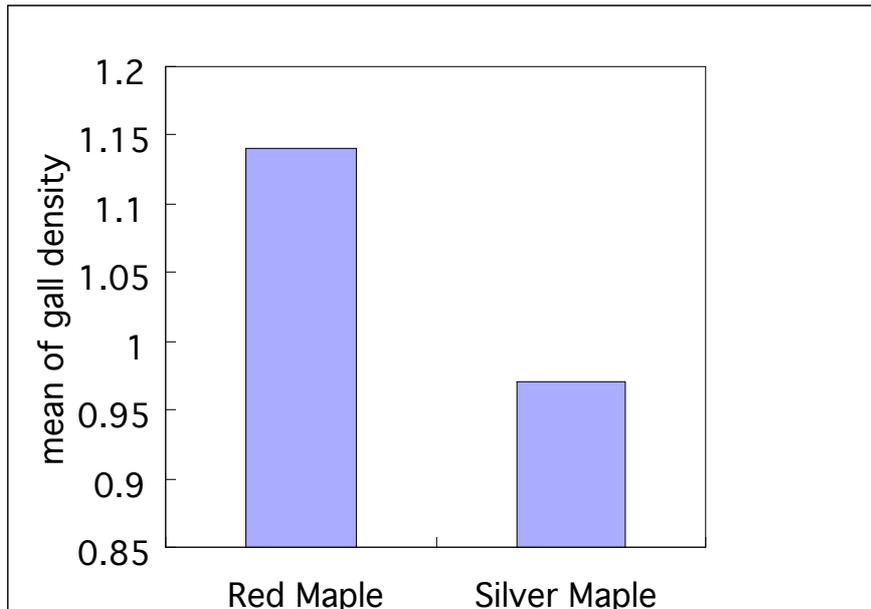


Fig 4 Gall density in red maple and silver maple. The mean of gall density in red maple is a little higher than silver maple, but the difference is not significant (t-test, $p=0.089$).



Intraspecific differences in red color index

There is no significant relationship between the red color index and gall density of all the leaves (Fig 5). However, the strength of red color is a feature more of a whole tree than individual leaves; so for different plot, the average red index was calculated for different trees. Although silver maple trees did not show any relationship between red index and gall infections (Fig 6), red maples in swamps showed a negative relationship (Fig 7), which signified that within species, the red color tended to be an effective signal of defensive compounds. However, it is hard to see any pattern of red index and gall infection of the red maples in Buck Hollow (Fig 8), which might be simply because we just have 4 trees collected there.

Fig 5 Red color index and gall density relationship of individual leaves

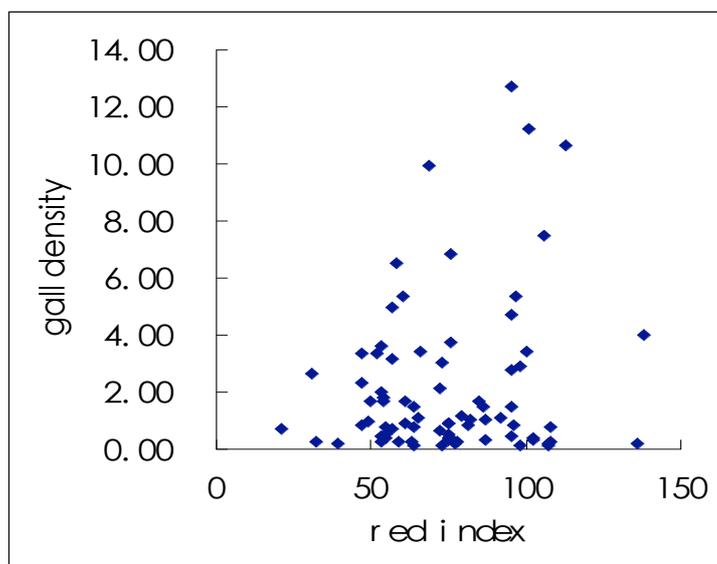


Fig 6 Red and gall

color index density

relationship of individual trees of Silver Maple

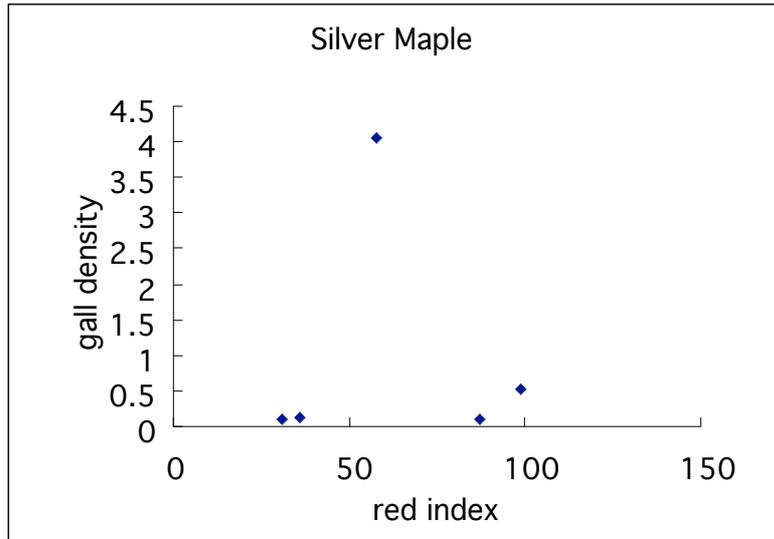


Fig 7 Red color index and gall density relationship of individual trees of Red Maple in swamp 1

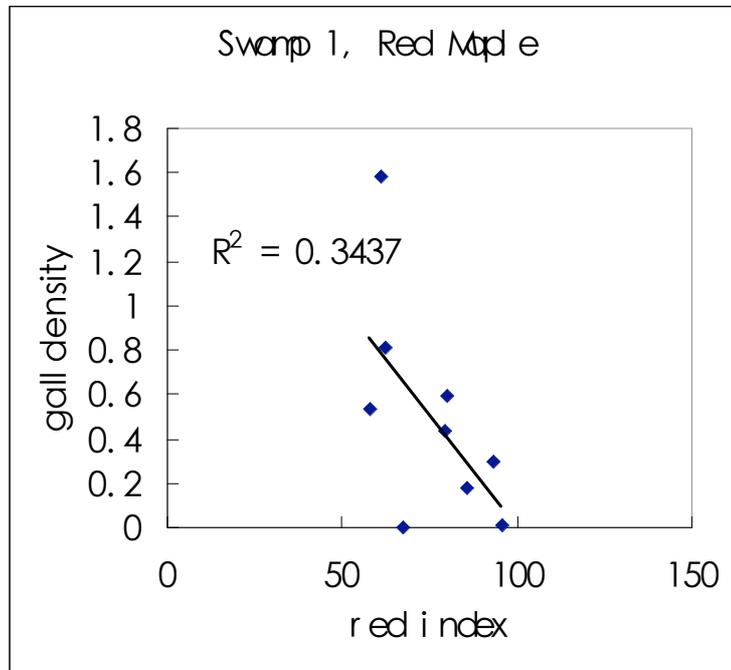
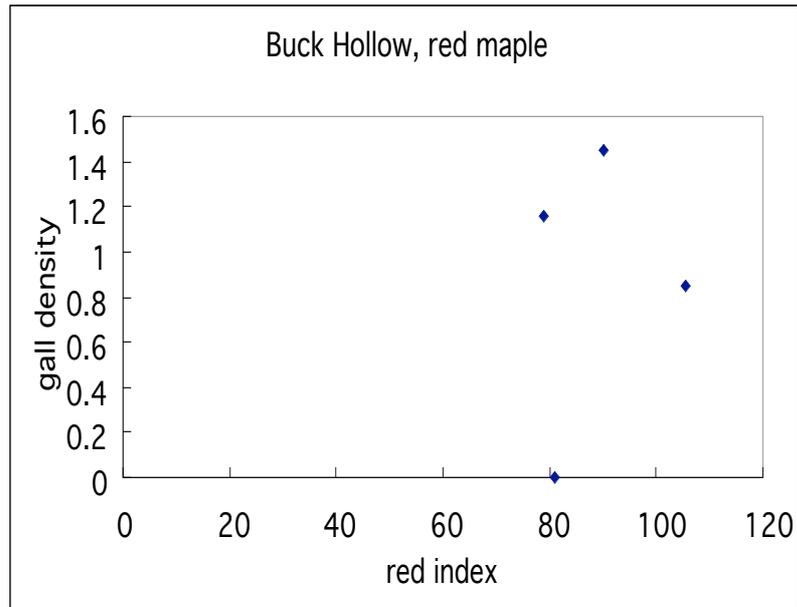


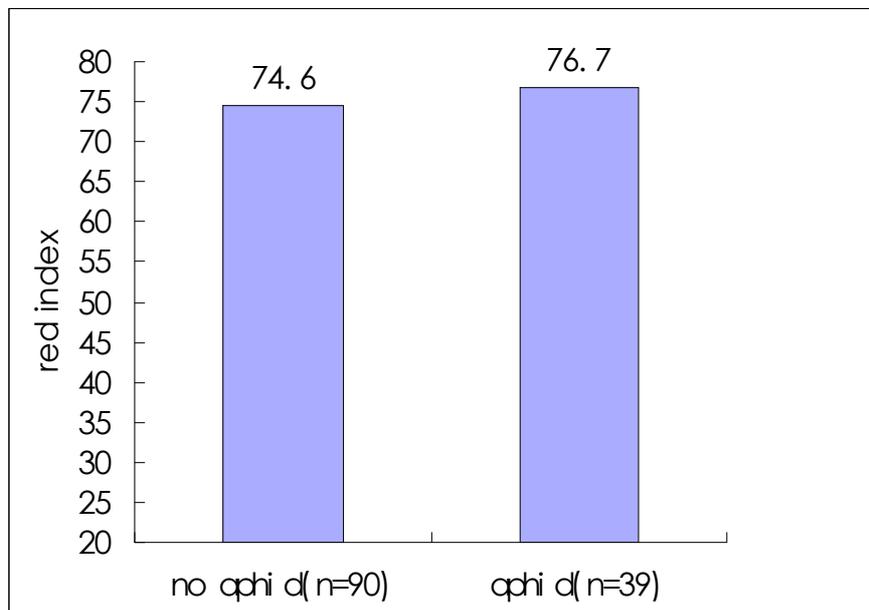
Fig 8 Red color index and gall density relationship of individual trees of Red Maple in Buck Hollow.



Red color index and aphid existence

Unlike gall density, the leaves with and without aphids have no obvious differences in red color index ($p=0.62$, Fig 9).

Fig 9 Red color index and aphid existence



DISCUSSION

Our finding that leaves of red maple in Buck Hollow have a higher index supports the photoprotection hypothesis that colorful pigments help to protect the leaf from excess light damage. Compared to other two swamp sites, Buck Hollow is a more open area and exposed to a higher light level in autumn; so the brighter color there may play the role of antioxidant and help to absorb excess light.

While silver maples tend to have a heavier but not significant gall infection, they do show a higher red index compared to red maple. According to co evolution hypothesis, it might be true that silver maple is more vulnerable to gall infection

thus invest more to signaling and show brighter color. Within one population of red maple (in swamp 1), we found that there is a negative relationship between gall density and red index; this is consistent with the co evolutionary hypothesis in that individuals having stronger signals of defense will deter potential insects thus suffer less. However, in other site and for silver maple, there were no clear relationships between color index and gall density. More over, we could not identify the gall species and have no idea about their life cycles, and we are not sure weather this kind of insect has the ability to detect the color variation or not. In term of aphid, which is better studied and often used to test the coevolution hypothesis, we didn't find any color difference between leaves with and without aphid load. So some of our results support the coevolution hypothesis while others do not.

There are limitations in our one day study and future directions to test the coevolution hypothesis should considered the following: Larger simple size for each population is required to give a higher reliable conclusion; measurement of aphid loading in other green leaves rather than only the red leaves is needed to give a better understanding of aphid damage of the whole tree.

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JUDGE A TREE BY ITS LEAF COLORS IN AUTUMN: THE BRIGHTER, THE STRONGER?
HUIJIE GAN

ABSTRACT

Recently a few hypotheses were proposed to explain the possible adaptive significance of leaf colors change in autumn. I argue that if autumn coloration does have adaptive significance, either through increase nutrient recovery in photoprotection hypothesis or decrease of insect damage in term of coevolution between plants and insects, then trees those can show brighter autumn colors will be “stronger” and have higher fitness. Here I study the coloration of red maples (*Acer rubrum*) and use the growth rate as the measurement of fitness. The result reveals that the timing of coloration has an impact on growth rate probably through lengthening of the growth period. In a habitat with high density of red maples, those with red autumn leaves were found to have a higher growth rate than those with only yellow autumn leaves; while in a more open area, the growth rate is found to be negatively correlated with red percentage. The contradictory results from these two sites may involve tradeoff between growth and reproduction, and the habitat difference of these two sites. Specific Leaf Area (SLA) is found to be negatively correlated with red percentage, suggesting that it costs to show brighter color in autumn.

INTRODUCTION

Leaf colors change from green to yellow or red is one of the most striking phenomenons in many deciduous forests. In Autumn, when temperature decreases, chlorophyll in the leaves begin to degrade and other pigments (e.g. carotenoids and anthocyanins) are unmasked and begin to show the yellow or red colors(Matile 2000). This is the usual explanation of leaf coloration and it is believed that leaf color change in autumn is simply the byproduct of the process of leaf senescence. It is not until recently that ecologists began to consider the phenomena in ecology and evolutionary perspectives and a few hypotheses have been proposed to explain the adaptive significance of colorful autumn leaves(Ougham et al. 2008). From the perspective of possible physiological function of being yellow or red, the photoprotection hypothesis states that senescence-related processes lead to increased vulnerability to damage from visible light; and carotenoids and anthocyanins can serve as antioxidants and protect leaf organelles and ensure foliar nutrients recovery(Lee and Gould 2002).

In contrast to the physiological perspective of the photoprotection hypothesis, the coevolutionary hypothesis (Hamilton and Brown 2001) was proposed in term of the coevolution between plants and their herbivores. This hypothesis argues the bright color may server as a ‘signal’ revealing the level of defensive commitment of the plant to insects that migrate to the tree in autumn and exploit it as a host for the winter. Coevolution of color preference would allow well-defended plants to reduce parasite load and the parasites to locate the most profitable hosts for the winter. After this provocative hypothesis was first brought up in 2001, it has received a lot of attentions and debate; many other hypotheses have been put forward since then(Ougham et al. 2008). Not long after the original coevolution hypothesis, Lev-Yadun et al(2004) proposed the crypsis hypothesis, which postulates that since most of the herbivorous insects are green, the non-green leaf colors would undermine

camouflage of the insects, exposing them to higher predation and thus do good to the plants. In a modification of the coevolution hypothesis, Sinkkonen(2006) proposed the reproductive insurance hypothesis stating that autumn leaf colors warn specialist herbivores that the trees are allocating nutrients to reproduction, thus lowering leaf quality. Another recent hypothesis similar to the original coevolution hypothesis is the defense hypothesis (Schaefer and Rolshausen 2006), which states that anthocyanins and carotenoids shared the same precursors and similar synthesis pathway with various defensive compounds, so the production of pigments also provides elevated defensive strengths against herbivores. While the above hypotheses have quite different mechanisms, they all predict that those trees that are able to brighter color have less insect damage.

While the adaptive significance (physiological and coevolutionary adaptation) of autumn leaf colors is still under hot debate, more and more evidences reveal the existence of the physiological function of the carotenoids and anthocyanins (the photoprotection hypothesis); but there are still very rare empirical or experimental evidences to test those coevolution hypotheses. In a field project prior to this study (Gan et al, 2008), we found that within one population of red maple in George Reserve, there is a significant negative relationship between the redness of the leaves and the gall infection. Therefore, it is reasonable to assume that these two types of adaptive significances exist in colorful autumn leaves, and then we can make a further prediction that trees that show brighter colors will have higher fitness. Here I use the growth rate as a measure of the fitness of trees and I also argue that red color is “brighter” than yellow color and shows more adaptive significance, because it is more costly for a tree to show the red color (red color is resulted from the de novo synthesis of anthocyanins, while carotenoids already exist in the leaves and the yellow color is unmasked from the degrading chlorophyll in the senescent leaves). So I predict that on the intraspecific levels, those trees showing more redness of autumn leaves will have higher fitness (“stronger”) and have higher growth rate; and if the photoprotection function enable higher efficacy of nutrient recovery of the senescent leaves, there will be higher percentage of nutrient transferred to perennial parts of the tree and then lower the mass of the falling leaves. Thus, we can predict that the brighter leaves, if more nutrients are being reabsorbed, will have a larger Specific Leaf Area (SLA, area of leaf/ mass of the leaf) because of the lower remaining mass in the leaf. Alternately, while anthocyanins and carotenoids may help to transfer more nutrients in the chlorophyll, they themselves are hardly reabsorbed before falling. It was found that in *Acer Platanoides* whereas around 95% of chlorophylls are reabsorbed, no more than 50% of carotenoids are recovered before abscission(Merzlyak and Gitelson 1995). This is actually one of the argument used by Hamilton to support his argument that autumn coloration is expensive. Therefore, if the nutrients retained in the non-green pigments are more than those recovered from chlorophylls, the overall weight of those brighter leaves with more non-green pigments will be heavier than those dull leaves.

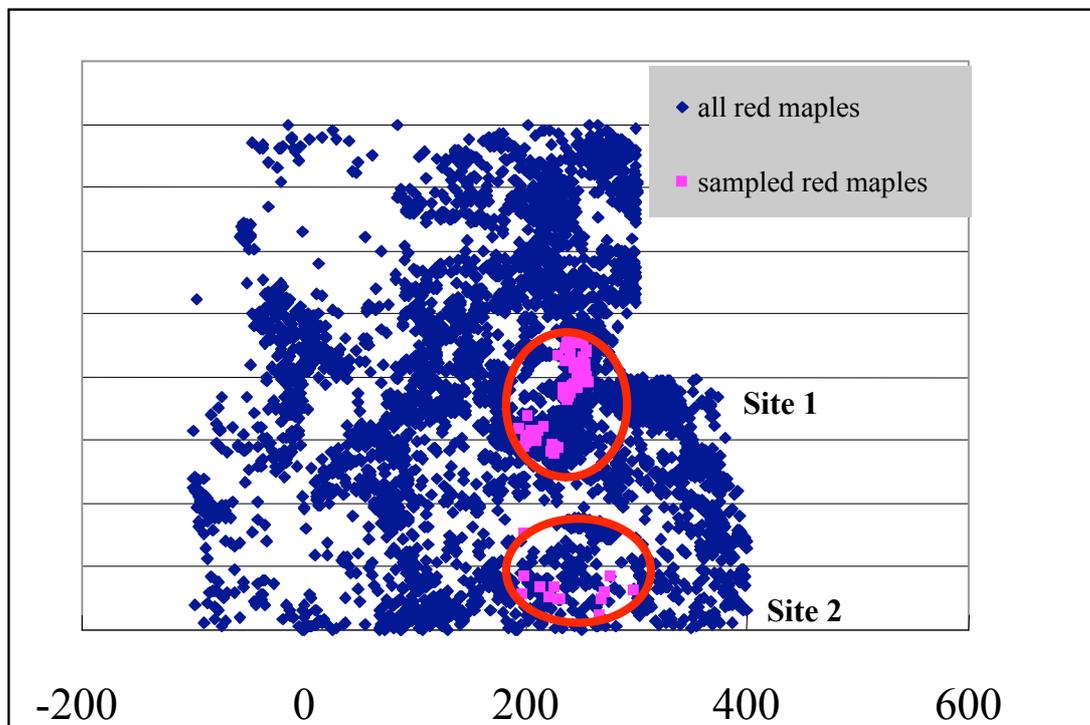
Besides the brightness of the color, the timing of coloration may also have an impact on the growth rate of the tree. Here I assume that those trees change their colors earlier in the autumn have a shorter growth rate, so that we can predict that those trees still green during this sampling will have a longer growth period and then a higher growth rate.

METHODS

Study Site

The E. S. George Reserve is about 25 km northwest of Ann Arbor (approximately 42° 28' N, -84° 00' W). In northwest of the Reserve, there is a Permanent Deciduous Forest Plot, within which most of the trees with GBH (Girth at Breast Height) larger than 10 cm are tagged and their GBH were measured in 2003. I selected two sites in the plot based on whether there were red maple measurements in 2003 or not (Fig 1). The first site is in the north slope of the big plot and is a lowland close to swamp. There is high density of red maples and half of them were still green at the time of sampling. In this site, I measured the DBH (Diameter at Breast Height) of those red maples with tags; I also wrote down whether the tree had changed color or not (1 for color change, 0 for still green). If they already changed color, I differentiated if their colors were red or yellow. If there are over 10% leaves showing red or orange color, I treated the color of the tree as red. The second site is an upland mix forest in south slope of the big plot. It is a much more open area compared to Site 1 and most of the red maples had fully changed colors. In this site, I measure DBH of the red maples. 6 to 10 leaves were collected from each tree for the color analysis. To ensure that the leaves are from the same developmental stage, I shook each tree and only collected the fresh leaves falling after shaking.

Figure 1. Sampling sites in the permanent big plot in E. S. George Reserve. Site 1 is a lowland in the north slope of the plot with high density of red maple; site 2 is a much more open upland mix forest in the south slope .

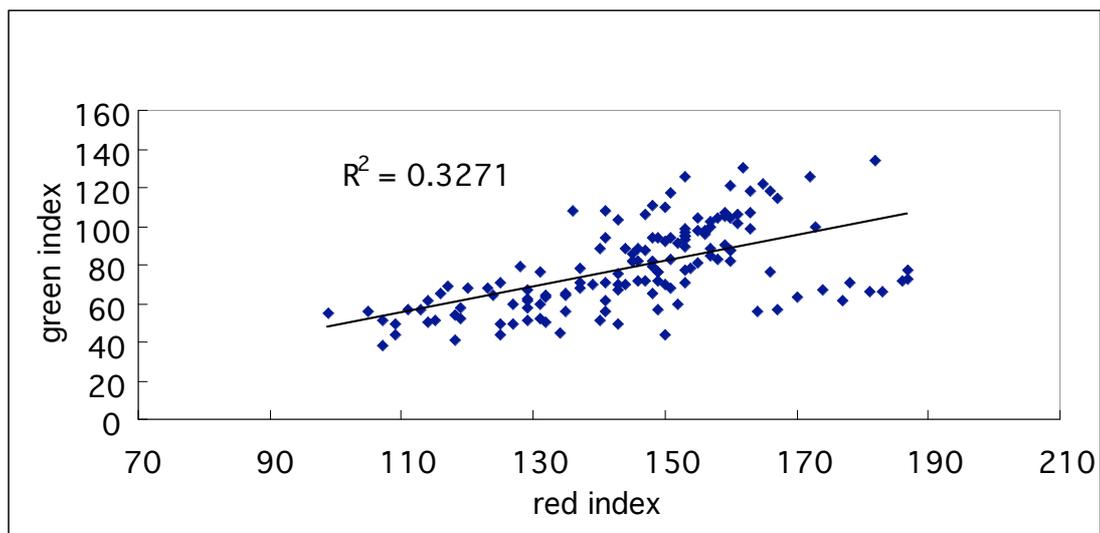


Leaf color and SLA analysis

Every individual leaf was put on a black square (10 cm * 10 cm), photographed from same distance under same lighting condition by using Canon PowerShot SD1100IS 8MP digital camera, and the image size was set to 640*800. Photos were input into Adobe Photoshop 7.0, the leaf area was selected and the red degree (red index) and green degree (green index) of each leaf were determined by the median number obtained from the color histogram (read from red channel for red degree and green channel for green degree). Because the overlay of red color and green color produces the yellow color, and we also find in our leaf sample that there is a strong positive relationship between the green index and red index (Fig 2), I then use the red percentage to be a measure of redness.

$$\text{Red Percentage} = \text{Red Index} / (\text{Red Index} + \text{Green Index})$$

Fig 2. In our leaf samples that there is a strong positive relationship between the green index and red index. Red percentage is then used to be as a measure of redness.



The pixels numbers for the leaf and black square were also recoded. The leaf area were then calculated as

$$\text{Leaf area} = \text{pixels number of the leaf} / \text{pixels number of the black square} * 100 \text{ cm}^2$$

Data analysis

All statistical analysis was performed on SPSS (version 16.0).

RESULTS

There are 98 red maples being surveyed in this study, 18 of them were still green at the time of sampling and 31 have completely changed to yellow or red. Those still green tend to have a higher growth rate compared to those with totally red or yellow leaves, but the difference is not statistically significant (Fig 3). In site 1, among those red maples that have changed colors (not all of them have totally changed); the growth rates were much higher for those trees with the presence of red leaves compared to those with only yellow leaves (Fig 4), the DBHs for the former were also a little higher than the latter, suggesting that those big trees tend to show more red autumn leaves. However, in site 2, the average red percentage per tree in the South Slope also negatively correlated with growth rate (Fig 5), no relationship was found between the red percentage and DBH (data not shown).

Fig 3. Comparison of growth rates of red maples between trees that were still green or have fully changed to red or yellow.

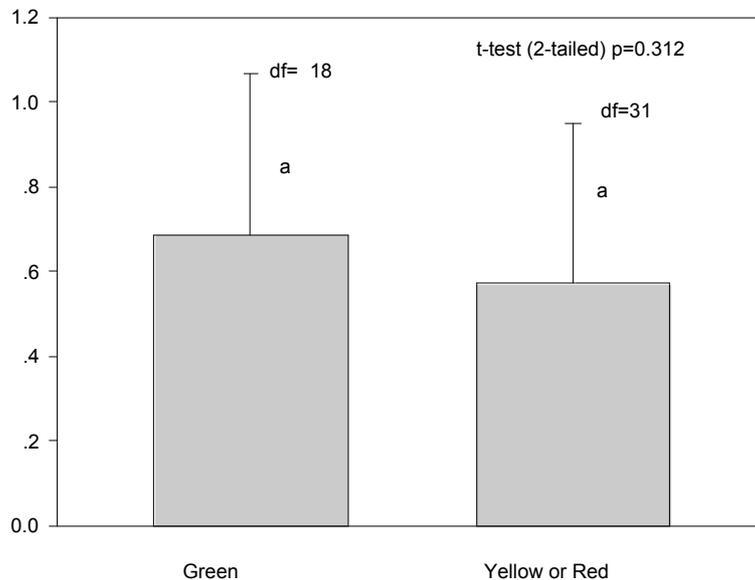
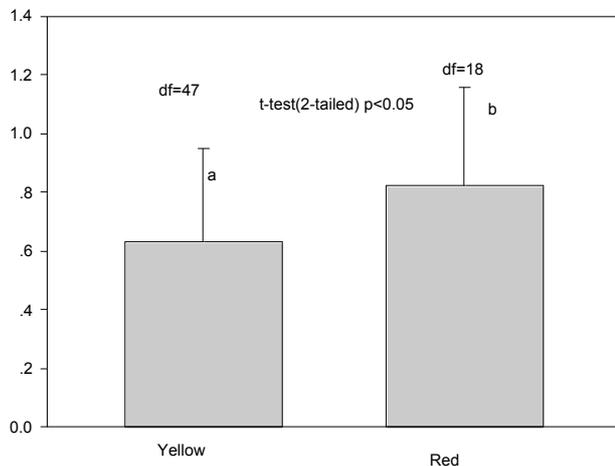


Fig 4 Red maples with the presence of red autumn leaves have a higher growth rate than those with only yellow autumn leaves (top). The DBHs in 2003 were also a little higher for those trees with red leaves (bottom).



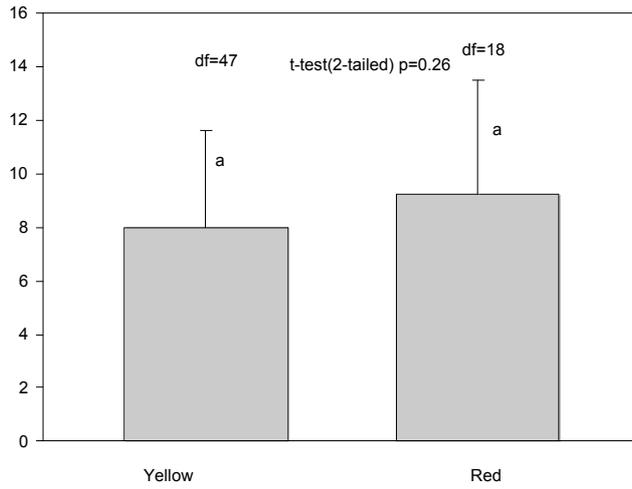
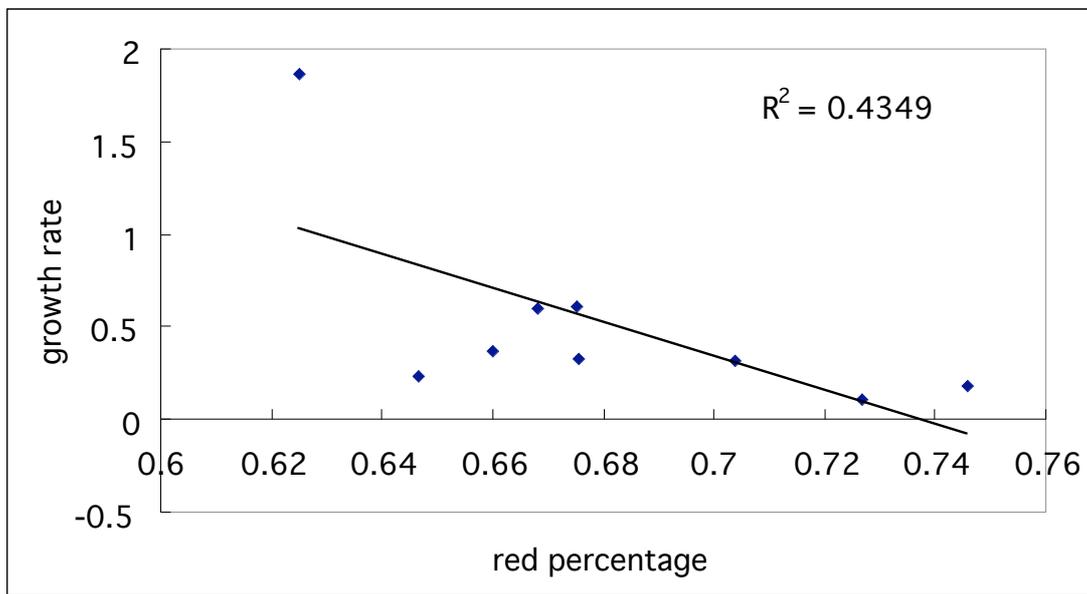
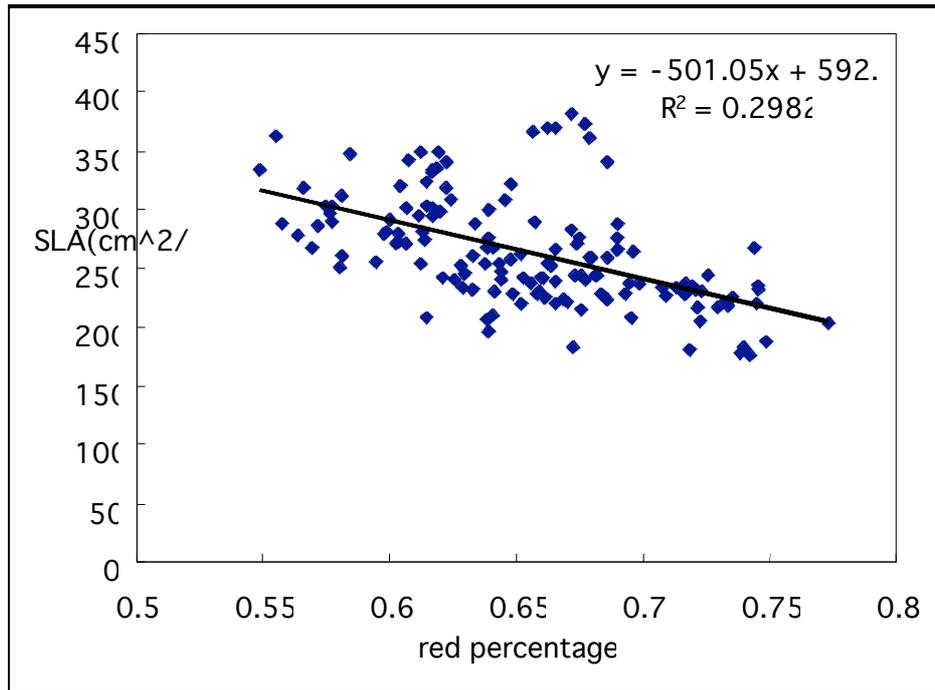


Fig 5 The average red percentage per tree in the South Slope negatively correlated with growth rate



When the red percentage and SLA were attained for leaves samples, a significant negative relationship was found between them.

Fig 6 The negative relationship between red percentage of each leaf and its Specific Leaf Area(SLA).



DISCUSSION

Trees that have later defoliation in autumn are more likely to have higher growth rates if they have longer growth period. In this study, I did find that red maples that were still green had a higher growth rates than those with leaves colors totally changed. However, the difference was not significant and there are some uncontrolled factors may make this comparison result confounding, like asymmetrical sample size and different microhabitat for growth. One of the compelling arguments behind this is that the sprout times among these trees may also be different. It will be interesting see to whether trees those sprout earlier in the spring will defoliate earlier or later in autumn.

In site 1 in the north slope, red maples with the present of red autumn leaves were found to have a higher growth rate than those with only yellow autumn leaves. This finding might be the evidence to support my hypothesis that red leaves are more adaptive to yellow leaves and trees with the presence of red autumn leaves are “stronger” and have higher growth rates than those with only yellow autumn leaves. However, in site 2 in south slope, the growth rate is found to be negatively correlated with red percentage. The contradicted results from these two sites may first reflect that it is problematic to simply use growth rate as the measurement of fitness, which include both survival and fecundity. It might be true that those red maples with brighter autumn colors invest more in reproduction thus slower their growth rate. But then why trees that have higher fecundity show brighter autumn colors? There is actually one hypothesis, the reproductive insurance hypothesis, proposing that autumn leaf colors warn specialist herbivores that the trees are allocating nutrients to reproduction, thus lowering leaf quality (Sinkkonen, 2006). While it is still hard to explain the contradictory results, the habitat difference might also contribute to the

discrepancy from these two sites. In site 1, there is high density of red maples in this site and there might be strong competition for light, DBHs in 2003 were also a litter higher for those trees with red autumn leaves, suggesting that most of them are in the canopy. In contrast to site 1, site 2 is much open and there should not be light limitation for red maples here, and the red percentage is not relative to DBHs at all. So it might be true that in a habitat where there is high competition for light (site 1), red maples will invest more to grow higher for light, once they reach the canopy and get enough light, they will grow faster compared to those still in the understory, they also show brighter color because of the higher light level in autumn.; where light is not a limitation for their growth (site 2), they will invest more in reproduction. That will be very interesting if there is future study to measure the seed production of those red maples next year to test the reproductive insurance hypothesis and to see the tradeoff between growth and reproduction.

Specific Leaf Area (SLA) is found to be negatively correlated with red percentage, which is consistent with my alternate prediction that while anthocyanins and carotenoids may help to transfer more nutrients in the chlorophyll, they themselves are hardly reabsorbed before falling, thus weight per area (inverse of SLA) of those brighter leaves with more non-green pigments will be larger than those dull leaves. This result suggest that it costs to show the red or yellow color, it doesn't necessary mean that the cost of coloration (production of the new pigment) is larger than its benefit (higher nutrient recovery), because what matters here is not the overall mass, but those valuable nutrient (like nitrogen and phosphorous). A more direct way to test the photohypothesis is to measure the nutrient concentration of the autumn leaves when they fall down. Another thing to remember is that the conclusion I get here is based on the assumption that SLAs before coloration are the same. Since the assumption can hardly be met; a more accurate way is to measure the change of SLA, and the nutrient concentration before and after color change.

ACKNOWLEDGEMENTS

I would like to thank Rima Upchurch in the Soil Lab to help me with the SLA measurement.

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MILKWEED AUTOCORRELATION THROUGH SPACE

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COLIBRÍ SANFIORENZO-BARNHARD, MARK HUNTER

ABSTRACT

Spatial Autocorrelation of plant traits and herbivory were assessed in an ecosystem dominated by the common milkweed species (*Asclepias syrica*). The common milkweed species has been reported as self-incompatible and we were interested in assessing its spatial structure. We measured plants traits (e.g. plant height, number of leaves) and also quantified the abundance of herbivores (e.g. aphids). We found strong autocorrelations below 6 meters for plant height, stem diameter, and the aphid *Myzocallis Asclepiadis*. However, no strong autocorrelation was found for the number of leaves, senescence, and density of other insects. We postulate that environmental gradients such as topographical features at our study site may possible limit the strength of autocorrelation. Further studies are needed to evaluate spatial genetic structure of milkweed species and assessment of long-term seasonal changes on the spatial distribution of milkweed species.

INTRODUCTION

Spatial analytical methods have been widely applied in a variety of areas that span geography, ecology, and mining engineering. It has by now been widely recognized that the traditional paradigm of homogeneity in ecosystems can no longer be considered a truism and that ecological processes are in large part influenced by spatial heterogeneity. The emergence of landscape ecology has explicitly focused on spatial pattern and scale that define ecological processes. Thus, ecological processes are consequently spatial in nature while also constraint by environmental factors (Wagner 2005).

The spatial structure of species within an ecosystem may undergo two different spatial processes. In the first case, ecological data subjected to spatial autocorrelation occurs when neighboring species exhibit greater similarity as result of biotic conditions (e.g. dispersal) that cannot be solely attributed to randomness. On the other hand, physical factors can create conditions for spatial dependence (e.g. wind intensity) that drive the mechanisms by which species are distributed in space and time. Spatial interactions in the ecosystem occur at both micro and macro defined scales out of which non-linear interactions can emerge (Levin, 1992). Spatial pattern can either have the same intensity in one particular direction (isotropic) or substantially vary from that direction (anisotropic).

Spatial autocorrelation has been commonly used in approaching ecological phenomena. For instance, spatial autocorrelation has been subjected to annual growth

rates of individual trees, population densities of snowshoe hares throughout the northern hemisphere, and the correlation of climate patterns with species distribution (Koenig 1999). In plant ecological studies, spatial autocorrelation has been applied to determine the spatial genetic structure of self-fertilizing plants, which tend to have less genetic variation within a population. Therefore, spatial genetic structure maybe the result of local genetic drift, limited gene flow (e.g. pollination), and the formation of clonal pattern (Heywood 1991).

Common milkweed species (*Asclepias syrica*) form an ideal system to study spatial autocorrelation because of their distinguished self-incompatible (genetically similar) reproduction system. Although most milkweed species are considered to be self-incompatible, due to late-acting pollen insertion in the stigma chamber of the same genetic individual, several weedy milkweeds have been found to be self-compatible. However, since the common milkweed species grows as a colony of plants developing from a single plant, ramets can produce varying levels of seeds depending on the size of the outcrop that influences the degree of spatial autocorrelation. Pollen dispersal takes place within short distances by Hymenoptera and Lepidoptera species through which self-pollination occurs between stems from the same genetic individual that can produce large clonal patches (Wyatt and Boyles 1994).

Our study focused on whether spatial structure emerges within a homogenous milkweed system at the George S. Reserve. We wanted to evaluate whether there was any evidence of spatial autocorrelation and which factors generate spatial structure in this ecosystem. We measured both plant traits and herbivory on the common milkweed species. We hypothesized that spatial autocorrelation in milkweed plant traits and herbivore density will decline with distance and associated herbivores declined with distance classes. We expected milkweed plants traits (e.g. plant height) to be auto-correlated on a coarse scale, ranging from 5-15 meters, whereas we expected herbivore densities to be more auto-correlated on a much finer scale in the range of 2-8 meters. Similarly, we expected that biotic conditions resulted in positive autocorrelations for herbivore and milkweed traits near the road, whereas we expected a negative association along topographical gradients.

METHODS

Study site

This study was conducted at the E.S. George Reserve in Livingston County, Michigan. The study site was chosen due to the abundance of *Asclepias syriaca*. The site was located in an abandoned field sparse with trees and undulating slightly with low hills and shallow valleys. A road defined one side of the field and the rest was marginally confined by woods. The weather was cool and cloudy throughout the duration of this study. This study was conducted during the month of September towards the end of the flowering season for the common milkweed

Study organism: The common milkweed

An *A. syriaca* population begins with seed dispersed by the wind from a hermaphroditic self-pollinating parent (Gold and Shore 1995). The perennial plant once established and sexually mature produces underground shoots resulting in clusters of clones (Woodson 1954).

Herbivory of *A. syriaca* is controlled by the production of highly toxic cardiac glycosides. However, several species have coevolved with the milkweed and are not only unaffected by the glycoside but can sequester the toxin for their own predation defense. Monarch butterflies, *Danaus plexipus*, and aphids are the most well known associates of the milkweed. However, there are several other primary herbivores of the milkweed including the stem weevil, *Rhyssomatus lineaticollis*, the milkweed leaf miner, *Liriomyza asclepiadis*, and the red milkweed beetle, *Tetraopes tetraophthalmus* (Agrawal and Malcolm 2005).

Spatial distribution and anisotropy study

Two perpendicular transects were aligned with one running east to west and the other running north to south. The east-west transect was 96 meters long and the north-west transect was 29 meters long. To evaluate similarity of clones based on closeness to each other, plant characteristics and the insect communities were measured for each milkweed individual located within 1 meter of the line. The transects intersected perpendicularly to compare plant differences based on anisotropy, conditions dependent on direction.

Characteristics of each plant were measured including height, the number of leaves, the stem diameter, the number of fruit, and the number leaves within three categories of senescence (0, < 50%, >50%). The insect community of each plant was measured by counting the number of individuals from three aphid species (*Aphis nerii*, *Myzocallis asclepiadis*, *Aphis asclepiadis*), the presence or absence of stem borer scars, and the extent of herbivory defined by the percentage of defoliation per leaf in three categories (0, <50%, >50%).

Statistical analysis

Spatial autocorrelations of plant characteristics were analyzed using ArcGis 9.2 with the Kringing Model. Semivariograms were created to reveal the relationship between space and data categories including plant height, stem diameter, leaf damage, number of leaves, number of total insects, number insects excluding aphids, and aphid density. Because aphids usually have exponential growth, we log-transformed the density of *Myzocallis asclepiadis*, calculated as $\log(\text{number of } M. \text{ asclepiadis per leaf} + 1)$, before further analysis. Leaf damage was estimated based on the damage categories using the following equation: $(0.25 * n(1) + 0.5 * n(2)) / \text{number of total leaves}$. Anisotropy was analyzed by comparing direction of each transect to both the plant height and the amount leaf damage using.

RESULTS

We encountered a total number of 77 milkweed plants along our two transects. Semivariances for four plant traits (height, stem, number of leaves and leaf damage) show that there are no significant ranges where semivariance increases linearly. However, for plant height, plant stem, and *M. Asclepiadis*, semivariance within 6 meters show an increasing trend, suggesting that there is similarity occurring at the scale about 6 meters. There is no strong autocorrelation for leaf damage, number of leaves and density of other insects even in smaller scale. The figures show the variances measured as a function of the distances between all the sampled locations.

Fig 1. Semivariograms for plant height (lag size 1.28; number of lags 12; model: spherical) The y-axis represents the variances measured and the x-axis represent the distance classes in meters

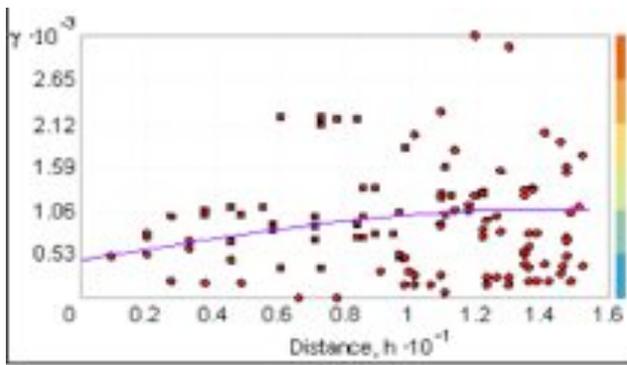


Fig 2. Semivariogram for stem (lag size 1.28; number of lags 12; model spherical) The y-axis represents the variances measured and the x-axis represent the distance classes in meters.

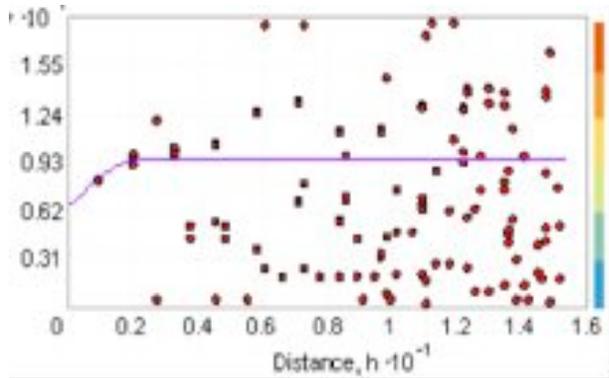


Fig 2. Semivariograms for density of *M. Asclepiadis* and other insects. (lag size: 1.28; number of lags: 12; model: spherical) The y-axis represents the variances measured and the x-axis represent the distance classes in meters.

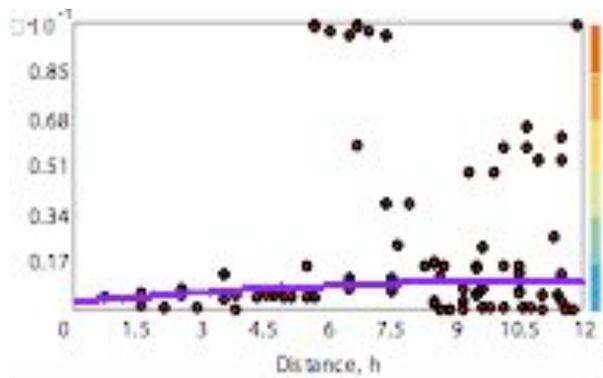
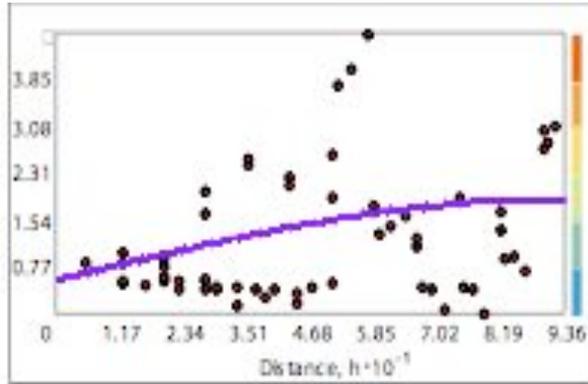


Figure 3. Semivariogram for other insects (lag size: 7.8; number of lags: 12; model: spherical) The y-axis represents the variances measured and the x-axis represent the distance classes in meters.



DICUSSION

The spatial autocorrelation analysis, which was performed using semi-variograms, showed that there was spatial autocorrelation in the insect community, but only at a very local scale (< 6 m). We also found younger plants up the hill, conceivably because the colonial plants receive less water. Furthermore, we found that aphid density was far greater along the road.

This could be due to some intrinsic feature of the insect communities, e.g., dispersal limitation, but could also be explained by spatial autocorrelation in another, unmeasured feature that affects the quality of the milkweed in terms of its suitability as habitat for arthropods. For example, if cardenolide concentrations are spatially autocorrelated at a very small scale, it might be reasonable to expect insect communities to vary in response to this gradient. The spatial autocorrelation of plant height and stem diameter on the same scale (< 6 m) suggests that the aphids may be responding to variation in plant characteristics, but further investigation would be necessary to substantiate this hypothesis.

The lack of clear spatial autocorrelation or spatial dependence in the remainder of the characteristics that we measured could be due to a number of factors. Our study was performed in late September 2008, which was approximately 2 weeks after significant senescence had occurred in this population of milkweeds. Had the study been performed a few weeks earlier, it is possible that spatial autocorrelation would have been present for characteristics that showed no such autocorrelation in our results, such as leaf damage, number of leaves, or any other feature that is significantly influenced by senescence. Therefore, the negative results that we obtained would need to be reevaluated before the onset of significant senescence in order to verify this result. Spatial autocorrelation may also have been obscured by underlying genetic variation that we did not investigate in the study. Although one would expect genetic relatedness to decrease with distance, and

therefore increase spatial autocorrelation, particularly in clonally species such as milkweed, it is not possible to rule out genetic structure in the population that could be counteracting or reversing tendencies towards spatial autocorrelation a priori.

The results from this study suggest that variations in the local microclimate can have a significant influence on milkweed, even at a relatively small scale. While not providing conclusive evidence for or against spatial autocorrelation of numerous other features of this milkweed population, this study will provide a useful baseline for future studies of this milkweed population. These results suggest that future studies should occur earlier in the season in order to increase the likelihood of detecting spatial autocorrelation of features that are modified or obscured by senescence. Studies like this will be important for understanding spatial variation in characteristics of *Asclepias syriaca* and its associated arthropod communities, which is vital information for understanding the role that this plant species plays in ecosystems throughout its extensive range.

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“QUASI-DEER EXCLOSURE-LIKE” EXPERIMENT: THE EFFECT OF WHITE-TAILED
DEER PREDATION ON THE POPULATION GROWTH AND DENSITY OF *ELAEAGNUS*
UMBELLATA (AUTUMN OLIVE)

ANDY MACDONALD

ABSTRACT

Through the use of deer exclosures located in “old field,” regenerating grassland habitats at the E. S. George Reserve, the effects of a large deer population on the population growth and spread of an invasive shrub, *E. umbellata*, were explored. The hope was to assess the possibility that deer are acting as a biological control mechanism for the propagation of populations of *E. umbellata*. Based on the results, the deer population at the E. S. George Reserve does not appear to be playing this role in the system studied. However, based on observations made that were not formally a part of this study, it is clear that the deer are in fact playing a significant role in the formation of the plant community present in the old fields at the Reserve. This has broader implications for future studies that take a community level approach rather than a single species level approach, the hope being to elucidate further the interactions, more broadly, between large herbivores and invasive plant species that now inhabit their natural ranges.

INTRODUCTION

The spread of invasive species across North America has been accelerating throughout the past few decades, compounded by international trade and climate change, which has caused species’ ranges to shift and expand. As a result, many species that once could not survive in North America are now thriving, though the primary means of invasive species introduction is by way of human activities. Invasive species, defined as non-native or alien to the ecosystem under consideration and whose introduction to that ecosystem causes economic or environmental harm or harm to human health (USDA), can be plants, animals, or other organisms like microbes. It is estimated that invasive species cause environmental and economic losses valued at up to \$120 billion a year in the US alone (Pimentel et. al. 2004). On top of the economic and environmental costs associated with the introduction of invasive species to fragile ecosystems, their presence introduces significant problems for conservation of species. In fact, 42% of all the species on the threatened or endangered species lists are at risk primarily due to the effects of invasive species, such as competition for resources, introduction of disease, or predation for example (Pimentel et. al. 2004).

Despite significant attempts at management of invasive species, they continue to spread rapidly and the ecological and economic effects associated with them persist. The identification and promotion of a biological control mechanism may prove to be a more worthwhile and successful endeavor than would continued human mitigation. This has been precisely the hope for Zebra Mussels (*Dreissena polymorpha*), which have been causing massive amounts of ecological damage in the Great Lakes basin and region of North America. The hope has been to identify a predator (the Log Perch has been identified as a potential predator) capable of stemming the spread and population growth of the Zebra Mussel (Gan et. al. 2008).

The primary focus of this study originated with this idea of biological control of invasive species in mind. Autumn Olive (*Elaeagnus umbellata*) is an invasive shrub that has spread

widely across the Eastern US where it vigorously outcompetes native species in regenerating fields and other disturbed habitats as well as raises soil nitrogen levels to the detriment of local plant communities (Autumn Olive Fact Sheet). It has been reported that elk and other large North American herbivores will eat *E. umbellata* (Schneider 2006). Predation-induced defenses such as thorn production or toxic chemical release have been observed in various plant species and may provide a potential metric for identification of predation events on individual *E. umbellata*. This could signal the extent to which predation might be affecting populations of *E. umbellata* and their spread or success of invasion. As such, the potential for the biological control of *E. umbellata* by local populations of deer in southeastern Michigan was the central focus of this study.

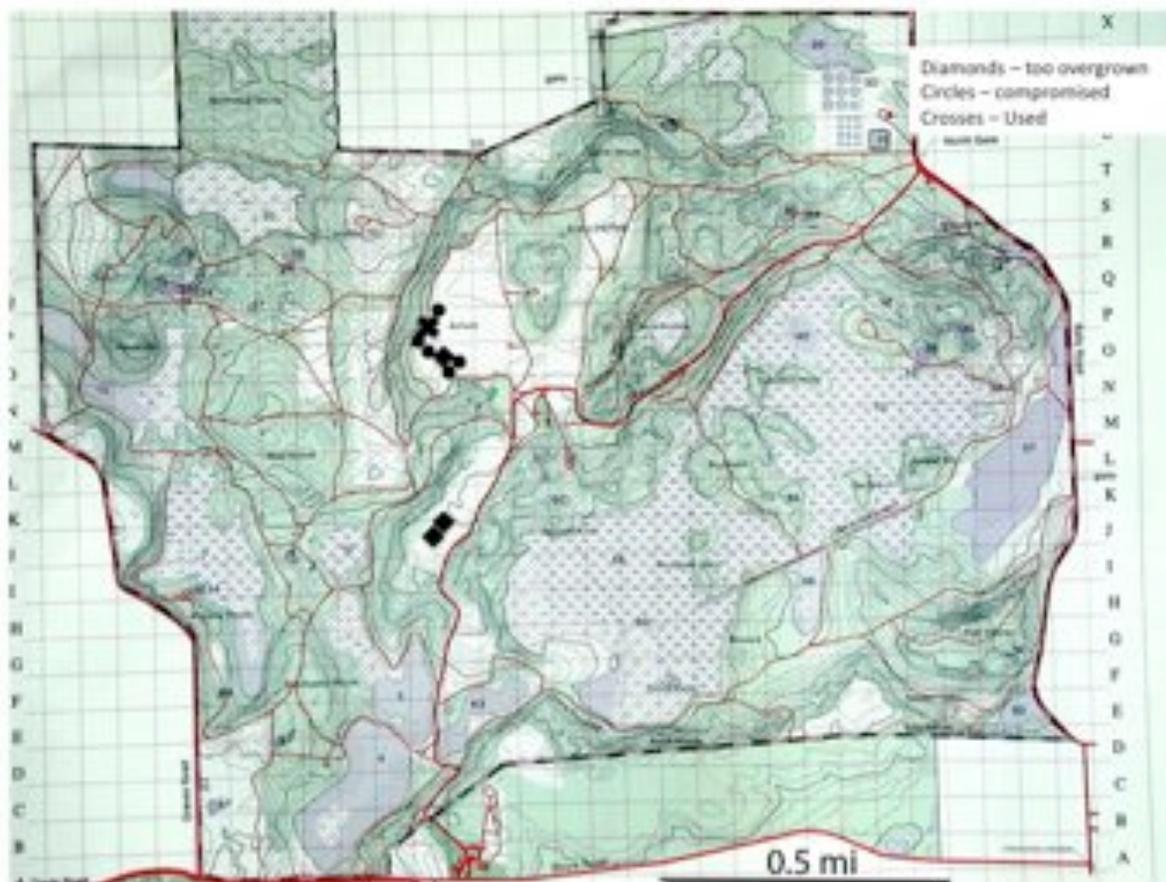
Using pre-existing deer exclosures at the E. S. George Reserve in Livingston County, Michigan, the effect of white-tailed deer predation on *E. umbellata* was assessed. Plots in the old field where the deer exclosures are located were compared with plots within the exclosures to make this assessment. Based on the assumption that the deer population at the E. S. George Reserve is controlling the population of *E. umbellata* in the old field studied, a few predictions were made: a higher density of *E. umbellata* (particularly of seedlings) was expected inside the exclosures as compared to outside; fewer seedlings per area and per adult as well as fewer adults in general were expected outside the exclosures as compared to inside; and, under the assumption that *E. umbellata* produces thorns in response to predation, a higher incidence of thorn production was expected outside of the exclosures as compared to inside.

MATERIALS AND METHODS

Study Site

This study was undertaken at the E. S. George Reserve in Livingston County, Michigan. The “Air Field,” an old-field located near the center of the Reserve containing multiple deer exclosures, as well as another old-field south of the “Air Field” also containing deer exclosures were utilized for this study. Both fields are characterized by successional “grassland” vegetation such as big and little bluestem, queen ann’s lace, *Desmodium spp.*, *Rubus spp.*, and iron weed as well as patches of *E. umbellata* and other woody plants like *Quercus spp.* The deer exclosures utilized were constructed in 1997 by Jacqueline Courteau, a University of Michigan student, for the purposes of field studies and experimentation associated with a dissertation completed in 2005 (Courteau 2005). The exclosures are located near the forest edge within the fields and each measures 10 by 15 meters and approximately 3 meters in height. Out of 9 exclosures found, only one was in good working condition for the purposes of this study (see figure 1).

Figure 1. Each shape represents an individual deer enclosure (Circles = “compromised” or falling apart, Diamonds = too overgrown to utilize, and Crosses = utilized in this study). The field to the north with 7 individual shapes is the “Air Field” and the field to the south with 2 individual shapes is the other field utilized in this study.



Study Organisms

Elaeagnus umbellata (Autumn Olive) is a deciduous shrub initially introduced from Asia in the 1830’s. It has been widely planted as wildlife habitat (for food and cover), as an ornamental or hedge on residential properties, as screens or barriers along highways, to stabilize and revegetate loose soil or road banks, and to reclaim mine spoil (Jackson). It grows rapidly and outcompetes native species, particularly in disturbed habitats and fields in the process of regeneration to forest. It can reach heights of up to 7 meters and attain substantial girth (many meters in diameter). It propagates via production and dispersal of a large number of seeds contained within a small fleshy fruit. In North America, dispersal is likely undertaken by various bird species by and large. Autumn Olive, when it reaches adulthood, is capable of shading out all other competing species in the vicinity due to its dense “canopy” growth. It also increases soil nitrogen levels, often to the detriment of local plant communities (Autumn Olive Fact Sheet).

Experimental Design

One deer enclosure located in the “Air Field” was utilized in this study, as all others encountered were deemed unfit for use. Within the enclosure (10x15 meters), a grid was created with 10, 3x5 meter rectangles. This grid was created to facilitate the mapping of *E. umbellata* and other woody plants present. Each plot in the grid was systematically mapped with the location of *E. umbellata* adults and seedlings (adults were characterized as any individual plant measuring over 1 meter in height and seedlings were characterized as any plant measuring under 1 meter in order to ensure all individuals were taken into account) as well as location of any other woody plant species present regardless of size. Basal circumference of each individual *E. umbellata* was measured, as was number of sprouts from the base, presence or absence of thorns, and evidence of predation. The number of adults and seedlings as well as other woody plants was also noted for each plot within the grid and for the entire enclosure as a whole.

This process was repeated for a 10x15 meter grid adjacent to the deer enclosure as well as for a 10x15 meter grid chosen at random located near the middle of the “Air Field.” The location of the “random” grid was determined before the study was undertaken (50 meters directly toward the center of the “Air Field” from the grids established adjacent to the enclosures used). These two grids were used as comparisons to measure the difference between the vegetative structure and assemblage within the enclosures (with particular attention paid to *E. umbellata*) and that found outside the enclosures.

Statistical Analyses

Chi squared analyses were conducted to measure the difference between the vegetative composition within the deer enclosure and outside the enclosure. This analysis was undertaken to assess differences in *E. umbellata* density overall and ratios of *E. umbellata* adults to seedlings as well as other woody plant density.

RESULTS

A map of each grid studied can be found below (figures 2-4). Based on these representations, the difference in density of other woody plants between the enclosure and the two grids outside the enclosure is striking. In fact, a significant difference was found between these two data sets (inside vs. outside the enclosure with outside averaged between the two grids in terms of other woody plant vegetative density) with a P-value of 0.018. The difference in *E. umbellata* densities overall however, was not significant (P-value of 0.235) nor was the difference in terms of adult to seedling ratios of *E. umbellata*. (See figure 5 for a graphic representation of these differences between the two data sets).

Figure 2. This scatter plot represents the locations and density of *E. umbellata* (represented by blue squares with shaded areas representing significant *E. umbellata* “canopy” cover) and other woody plant vegetation (represented by the red circles) for the enclosure.

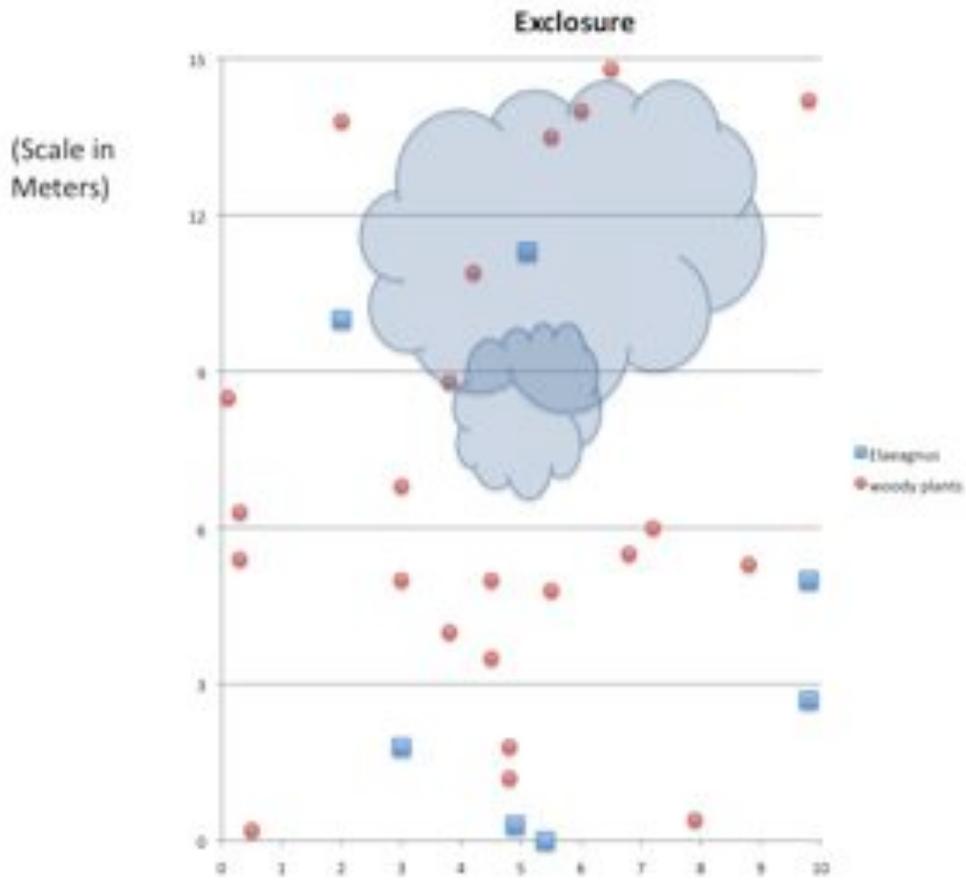


Figure 3. This scatter plot represents the locations and density of *E. umbellata* (represented by blue squares with shaded areas representing significant *E. umbellata* “canopy” cover) and other woody plant vegetation (represented by the red circles) for the grid adjacent to the enclosure.

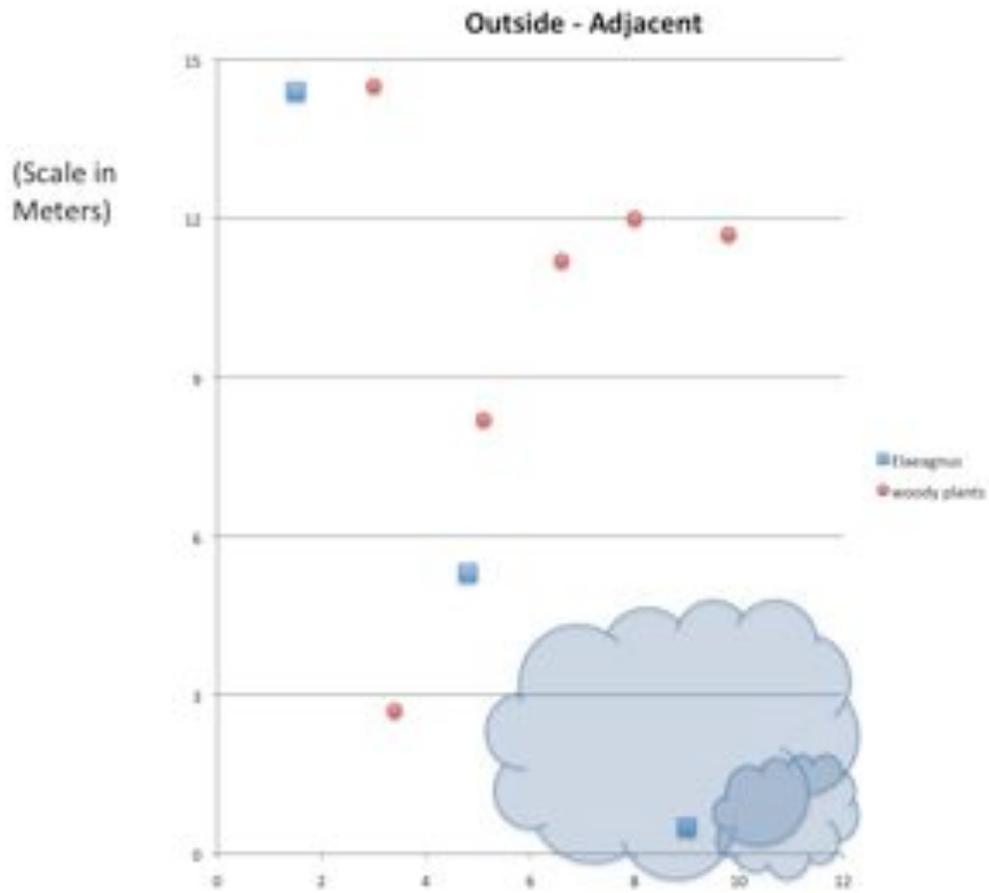


Figure 4. This scatter plot represents the locations and density of *E. umbellata* (represented by blue squares with shaded areas representing significant *E. umbellata* “canopy” cover) and other woody plant vegetation (represented by the red circles) for the randomized grid outside of the enclosure.

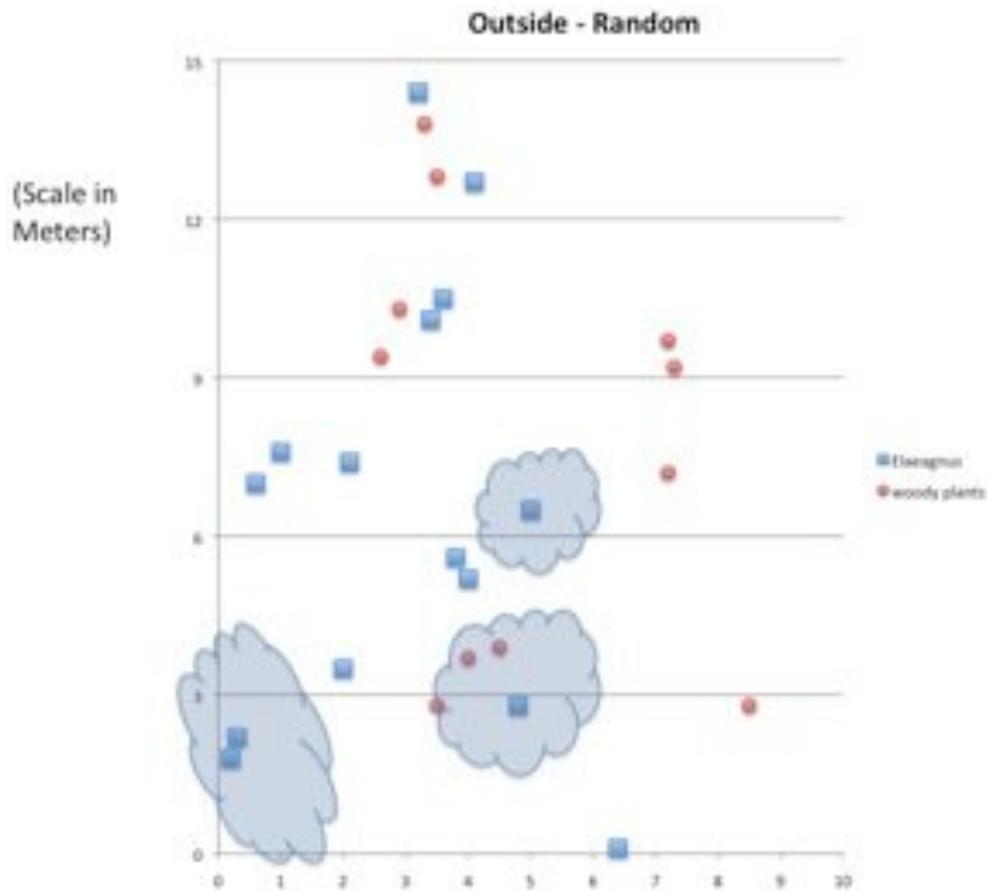
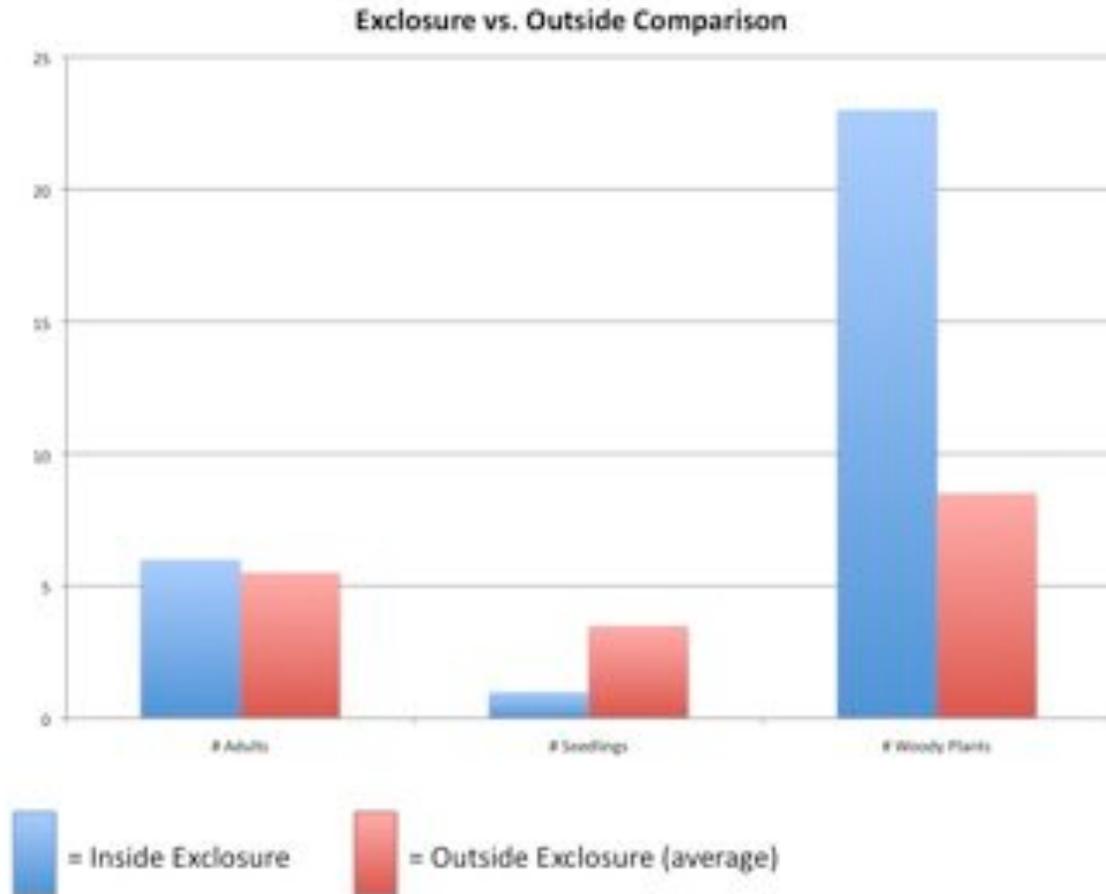


Figure 5. This is a graphic representation of the numbers and relative densities of each data set (within and outside the enclosure) in terms of *E. umbellata* and other woody plant vegetation. Note the significant difference in number/density of woody plants.



It was also found that 95% of all adult *E. umbellata* and 0% of all seedlings (both within and outside of the enclosure) had produced thorns. This yielded no significant difference between the two data sets (within and outside of the enclosure) in terms of thorn production.

DISCUSSION

Expectations based on background research and consequent assumptions made about the system under consideration were not supported by the findings of this study. There was not a significant difference between the two data sets (within and outside the enclosure) in terms of density of *E. umbellata*, adult to seedling ratios, and thorn production as expected (thorn production may thus simply be a product of age or size rather than predation). Given these findings, the deer population on the E. S. George Reserve does not appear to be managing the population growth or spread of the invasive shrub, *E. umbellata*. The only other potential explanation of this finding has to do with the limitations of this particular study. It could simply be that the grids studied, both within the enclosure and outside of it, were not representative samples. Therefore, this conclusion is tenuous due to the limited data set (only a single comparison was made), which is largely the product of the limited availability of functional deer exclosures as well as the limited time frame of the experiment. More replicates are clearly

needed to make any sort of definitive statement about the effects of deer predation on *E. umbellata*. It would also be useful to perform this same study at different times of the year when food availability is different to assess more comprehensively the potentiality of deer as a native biological control mechanism for invasive plants such as *E. umbellata*.

Despite the lack of significant results as pertained to the initial research question, several significant findings and observations were made about the study system that merit future research. The fact that a significant difference was found between the two data sets in terms of density of other woody plants suggests that the deer may be managing the grassland vegetation found in more abundance outside the enclosure. For example, it is evident based purely on observations made in the field that there exists a very significant difference in the overall composition of the plant communities that exist within and outside the deer enclosures. The plant community within the enclosure is dominated by woody plants and *Rubus spp.* while the plant community outside of the enclosure is dominated by big and little bluestem, iron weed, queen ann's lace, and *Desmodium spp.* Based on this observation it may be that the deer population is maintaining in some way the grassland vegetation found in the old fields of the E. S. George Reserve. A plant community level approach would thus be much more practical in assessing the effects of deer or other large herbivores on the plant communities present rather than a single species level approach.

While no definitive conclusions can be drawn regarding deer as a biological control mechanism for the spread of *E. umbellata*, it is clear that populations of large herbivores do have a significant effect on the composition of plant communities and perhaps studies at the community level could elucidate the interaction between these large herbivores and invasive plant species that have populated their natural ranges.

ACKNOWLEDGEMENTS

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EXTENSIVE SEED PREDATION BY A NEW INVASIVE LEPIDOTERAN,
SITACHROA PALEALIS, ON THE WILD CARROT, *DAUCUS CAROTA*

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ABSTRACT. A palearctic lepidopteran, *Sitachroa palealis*, has recently become established in the United States. Significant infestation of the wild carrot population, *Daucus carota* (Apiaceae), and damage to infructescences of individual plants by *S. palealis* was observed at six sites in the E.S. George Reserve, Livingston County, Michigan. This study assessed the distribution of *S. palealis* larvae between sample sites and characteristics of the damage. The results revealed that all of the sampled patches had heavily damaged inflorescence with frequencies of ranging from 76 to 100%. Further research is necessary to determine the rate of invasion, abundance, and biology of *S. palealis* in order to assess potential negative and positive impacts of its establishment. *S. palealis* may have a positive affect as a biocontrol for its host plant, the noxious weed *D. carota*, and negative affects by the potential reduction of seed production in native Apiaceae species and the cultivated carrot *D. carota sativa* if host switching occurs. In addition, the identification of other potential host plants in the Apiaceae family that may serve as conduits for invasion is necessary to control and predict pathways of *S. palealis* introduction and establishment.

INTRODUCTION

The invasive lepidopteran, *Sitachroa palealis* (Karsholt and Razowski 1996) and its host plant, *Daucus carota*, are native to Europe. While the introduction of *D. carota* is unknown, one of the first documentations of the naturalization in the United States of *D. carota* was in 1826 (Columbus Horticultural Society 2007). *S. palealis* is a recent introduction as of 2002 to the United States (Passoa et al 2008). An invasive species is more likely to have pre-adaptations to interact with an organism that it has previously coevolved with (Thompson 2005). The longer an organism has coevolved with another organism, the more adapted it is to that organism and thus may lead to a predictable pattern of successive invasions. *D. carota* invaded the United States and 180 years later was followed by its European associate, *S. palealis*, pre-adapted to consume its toxic seeds, a previously untapped abundant food resource in the United States.

As host plants and seed predators spread to different geographic areas at different rates, virulence and resistance become mismatched in accordance with the geographic mosaic hypothesis (Thompson 2005). For example, when the parsnip webworm, *Depressaria pastenelli*, a species similar to *S. palealis*, and its host plant, the parsnip (Apiaceae), were separated in a region where the parsnip invaded and *D. pastenelli* did not, the parsnips produced lower amounts of furanocoumarins. Furanocoumarins are toxins that interfere with the synthesis of DNA and are found in many species of the Apiacea family including the parsnip and *D. carota*. In addition, when the parsnip webworm was then re-associated with the parsnip, the parsnip webworm was not only pre-adapted to consume the toxic seeds of the parsnip but was also found in *Heracleum lanatum* (Apiaceae), a closely related species located in the same regions as the parsnip but with lower levels of furanocoumarins (Berenbaum and Zangerl 2006).

D. pastenelli and *S. palealis* have such subtle morphological differences that the larvae of *S. palealis* are often misidentified as *D. pastenelli*. While *D. pastenelli* and *S. palealis* are similar in the ability to detoxify furanocoumarins, seed predate on Apiacea species, mature within Apiaceae umbels, and larval appearance, the two differ in taxonomic structures and life cycles. The most easily recognized difference is that *S. palealis* has a bisetose prespiricular pinaculum and *D. pastenelli* has a trisetose prespiricular pinaculum (Passoa 1995; Hassenfuss 1960). In addition, *D. pastenelli* and *S. palealis* also exhibit a considerable difference in pupation behavior. *D. pastenelli* burrows into the stem of the host plant (Berenbaum and Zangerl 1991) while *S. palealis* pupates in the soil.

In 2008 the wild carrot population, *D. carota*, was heavily infested by a lepidopteran seed predator, *S. palealis*, on the George Reserve in Livingston County, Michigan. The range of the host plant, *D. carota*, extends throughout the entire United States (Figure 1; USDA 2008). However, the seed predator, *S. palealis*, has recently been reported beginning in 2002 in only four states: Michigan, Illinois, Indiana, and Wisconsin (Figure 1). A six year survey of *S. palealis* indicated that the organism is established in Michigan as *S. palealis* has successfully overwintered, bred and survived for at least six univoltine generations (Passoa et al. 2008). *S. palealis* was previously collected in four counties in Michigan: Charlevoix, Eaton, Cheboygan, and Allegan (Figure 2). This is the first report of *S. palealis* on the E. S. George Reserve in Livingston County.

Figure 1. The range of *D. carota* is highlighted in green (USDA 2008). The states with the red stars, Michigan, Illinois, Indiana, and Wisconsin have the only documented populations of *S. palealis* in the United States.

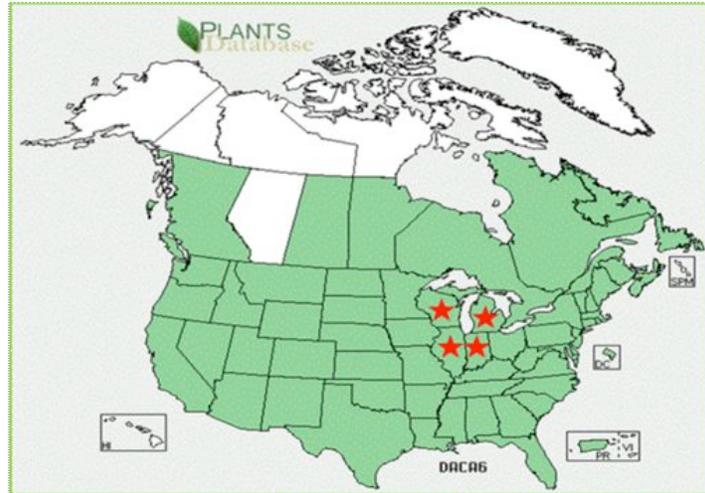


Figure 2. *S. palealis* has been documented in the following five counties including the recent addition by this study of the George Reserve in Michigan: Charlevoix, Eaton, Cheboygan, Allegan, and Livingston.



D. carota population on the George Reserve is in transition from low seed predation due to a previously low level of herbivory to high seed predation by *S. palealis*. This study investigates the extent and distribution of damage by the recent invasion of *S. palealis* on the population of *D. carota* at the George Reserve by comparing the amount and variance of damage at six sites. We tested the hypothesis that *D. carota* would be heavily predated upon at all six sites because the invasion is in its initial stage, the lepidopteran was pre-adapted to consume the toxic seeds and thus filled an unoccupied niche, and invasive lacked a predator. By sampling six sites and analyzing umbel damage, the results elucidate the potential positive and negative impacts of the establishment of *S. palealis* populations as 1) a biocontrol for the noxious weed, *D. carota*, 2) an agricultural pest for the cultivated carrot, *Daucus carota sativa*, and 3) a pollution source point as pesticide use increases to prevent seed destruction on *D. carota sativa*.

METHODS

Study site and organism

Lepidopeteran infestation of *Daucus carota* infructescence was examined in the E. S. George Reserve, a 1500-acre preserve located approximately 25 miles from Ann Arbor, MI. Individual plants were sampled within the Airfield, an expansive field within the reserve. Prior to reserve designation in 1927, the Airfield was most likely used for the agricultural production of row crops and livestock grazing. The current plant community within the Airfield is characterized by a grass-shrub demography dominated by *Juniperus virginiana*, *Elaeagnus umbellata*, and *Schizachyrium scoparium*.

D. carota is a biennial weed native to Europe and Asia. It is extremely common in most temperate regions of the United States (Thieret 2001). Individual populations frequently colonize abandoned fields and other disturbed areas. Seed production in *D. carota* occurs from June to August. After the plant has gone to seed, mature umbels curve upward and inward (Thieret 2001).

Field Sampling

D. carota umbels were collected from the Airfield on September 14, 2008. Six patches of *D. carota* were randomly selected as sample sites, with five being in the airfield and one adjacent to the airfield. Sample sites varied in size and were based on cluster perimeters. Clusters were approximately 12 meters by 12 meters. From each site ten individual plants were randomly selected. For each individual plant sampled, the total number of umbels was recorded. One green umbel and one brown umbel were collected from each plant. If only brown umbels were present, then a green umbel was not collected. Umbels were placed in labeled Ziplock bags and transported to an onsite location for further analysis on the same day.

Laboratory Measurements

Umbels were carefully examined under a bright light using a hand lens. For each umbel collected, we measured the length of the longest pedicel, the developmental stage of the umbel as green or brown, the presence of lepidopteran larvae, the length and identity of each lepidopteran larvae, and damage as evident by the presence of frass.

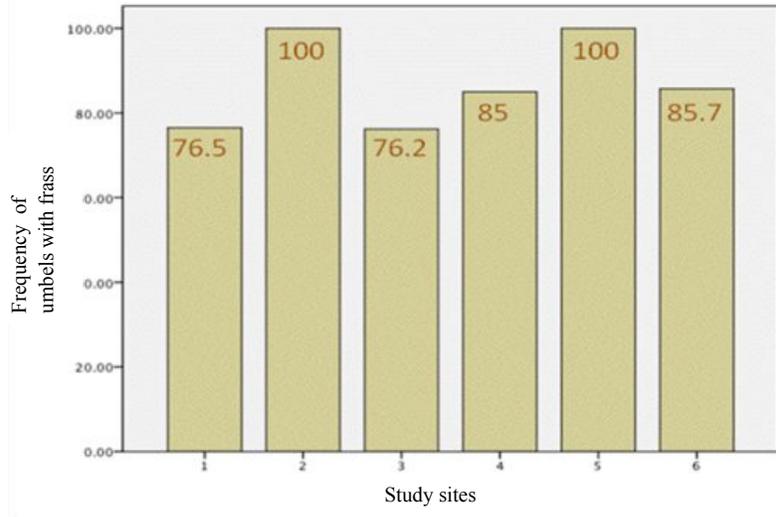
Data Analysis

All data analysis was performed using SPSS 16.0 GP. Chi-square Goodness of Fit tests were used to compare the frequency of damage between each of the six patches, the frequency of damage in umbels at different developmental stages, and the frequency of lepidopteran larvae observed in umbels at different developmental stages.

RESULTS

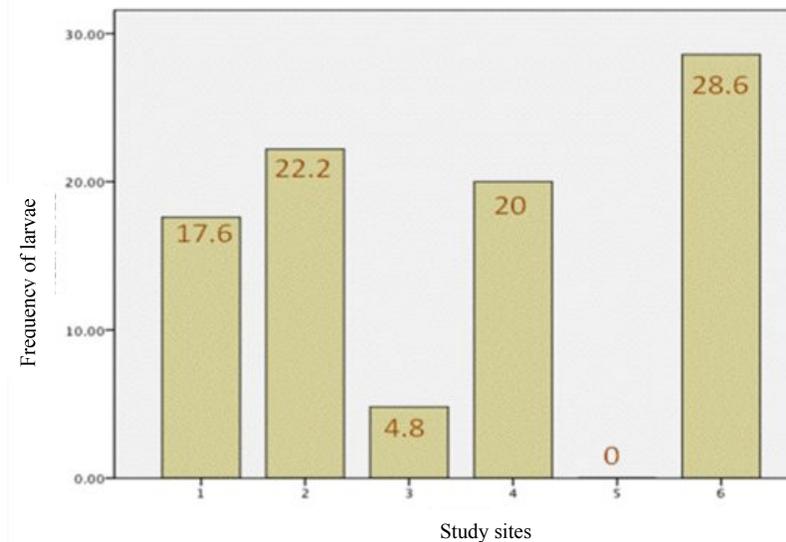
The frequency of umbel damage ranged from 76.2% to 100% by *S. palealis* and was extremely high at each of the six study sites (Figure 3). No significant variation in damage was observed between the six sites ($n=105$; $df=4$; Chi-Square=6.450; $p=0.265$), indicating the extensive damage to the population of *D. carota* is evenly distributed at the George Reserve.

Figure 3. Frequency of *D. carota* umbels with frass from each of the six study sites.



S. palealis larvae were not evenly distributed between the six patches ($n=105$; $df=4$; Chi-Square=1.632E-1; $p=0.003$). The larvae presence frequency was much lower than damage frequency and ranged from 0.0% to 28.6% (Figure 4).

Figure 4. Frequency of larvae at six study sites.



In this study, a brown umbel and a green umbel were collected from each plant as a measure of different stages of maturity. The percentage of damage in brown umbels tended to be higher than in green umbels. However, only a slightly significant difference was found between

the umbel stage of brown or green and damage status (Figure 5; $n=105$; $df=1$; Chi-square=3.571; $p=0.059$). However, larvae were significantly more present on green umbels than on brown umbels (Figure 6; $n=105$; $df=1$; Chi-square=5.828; $p=0.016$).

Figure 5. Frass was more frequently present in older browner umbels than in younger greener umbels.

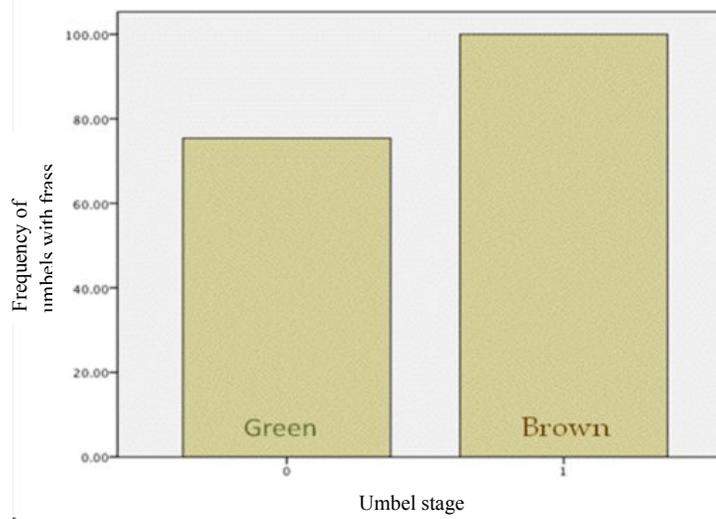
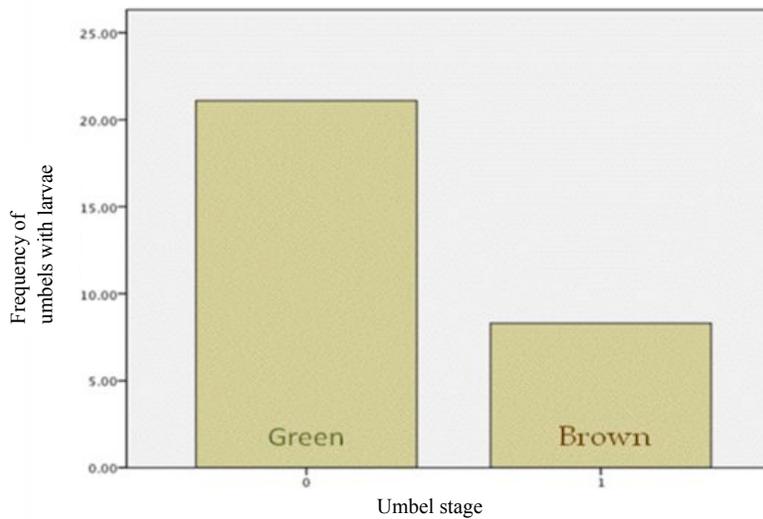


Figure 6. Larvae were more frequently present in younger greener umbels than in older browner umbels.



DISCUSSION

Based upon the casual field observation between an abundance of *S. palealis* and damaged infructescence of *D. carota* prior to formal sampling, the results were not surprising. The evidence of seed predation was extremely high and significantly evenly distributed at all study sites. Evidence of seed predation by *S. palealis* larvae was not always accompanied by the presence of larvae. This may be because the larvae migrated to other seed abundant umbels or

relocated to the soil for pupation. The non-random sampling of this study may have lowered the amount of larvae collected for analysis. By selecting one brown umbel and one green umbel from each plant, the intermediate stage was omitted. It is most likely that the larvae are more frequently found in the intermediate umbel as it is the stage when the seeds are most abundant and the accumulation of brown colored frass and senescence of umbels is just beginning. In addition, the greener umbels may still be in flower while the seeds of the browner umbel may have dispersed or been consumed making the seed abundant intermediate umbel preferable to the seed predator. Despite the omission of an intermediate, larvae were present within green umbels more frequently than brown umbels as expected. In addition, our *a priori* hypothesis that *S. palealis* was aggressively invading and destroying the seeds of *D. carota* was supported by the overwhelming evidence of damage to the umbels at all sites.

The most valuable outcome of this study was discovering the population explosion of *S. palealis* for the first time within the E.S. George Reserve and Livingston County, MI. The dearth of literature on the subject species within the United States suggests little is known about the population dynamics and biology of *S. palealis*. The introduction of *S. palealis* at the research station, E.S. George Reserve, provides the opportunity for study of the invasive as well as the mechanisms, characteristics, and long-term effects of an invasive.

Further studies of *S. palealis* are strongly recommended both within the E.S. George Reserve and Great Lakes Region where its distribution appears to be centered. Studies may include monitoring the distribution of the species, its affect on populations of *D. carota*, and confined laboratory studies to determine if other members of the Apiaceae family are potential hosts for *S. palealis*. As *D. carota* is a biennial species, the major effect of the 2008 seed predation will not be evident until the 2010 growing season.

The establishment of *S. palealis* has both positive and negative potential in the United States. It's host plant, *D. carota*, also a non-native species, is classified as a noxious weed. The re-association of *S. palealis* and its host plant may provide an accidental but positive affect as a biological control for undesirable populations of *D. carota*. However, the potential for host switching and heavy seed predation may have a negative effect on seed production for cultivated commercial varieties of garden carrot, *D. carota sativa*. While the mature plant and the commercially valuable root are not known to be negatively impacted by the larvae, future seed production may be impacted by reduced seed availability. As importantly, a surge of pesticide use may ensue if *S.palealis* host switches from the wild carrot to the cultivated carrot. Lastly, *S. palealis* may have a range of host plants within the Apiaceae family which may include native species.

In addition to monitoring *S. palealis* abundance, host preference, and distribution, chemical analysis of furanocoumarins in *D. carota* should be monitored for a response to heavy

seed predation. Will the population of *D. carota* become increasingly more toxic as natural selection favors highly toxic variants and may thus control the population explosion of *S. palealis*? This initial invasion may be the beginning of an arms race and elucidate the mechanisms of coevolution and the geographic mosaic hypothesis as it is happening from the alpha to the omega of the relationship between *S. palealis* and *D. carota* coexisting at the George Reserve.

ACKNOWLEDGMENTS

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THE INVASION, DISTRIBUTION PATTERN AND SEED PREDATION OF *SITOCHROA PALEALIS* ON THE INVASIVE WILD CARROT, *DAUCUS CAROTA*

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Abstract. A new invasive lepidopteran, *Sitochroa palealis*, has caused extensive damage to its host plant, the noxious weed *Daucus carota*, in the E.S. George Reserve. This study investigates distribution patterns and oviposition preferences of *S. palealis* by evaluating the percent of larvae induced damage per plant based on the number of umbels per plant and its location relative to population density. Results reveal that plants with many umbels are more damaged than plants with fewer umbels. In addition, the percentage of damage to *D. carota* individuals was not dependent on population density. The adult female *S. palealis* may be assessing plants for oviposition suitability based on the characteristics of the individual plant and not its placement in a cluster of plants.

INTRODUCTION

Bring war material with you from home, but forage on the enemy. Thus the army will have food enough for its needs. Sun Tzu, the father of invasion biology, observed in ~ 300 B.C. that for an invasion to be successful, his model organism should arrive unannounced, forage on local foods, bring defenses from home, and not destroy the invaded region (Giles 1910). His astute observations and concisely written principles are still true today and applicable to the invasion biology of animals.

Invasive species can cause considerable damage to regions where they become established resulting tremendous ecological and financial losses. The economic burden of responding to invasives of negative impact such as zebra mussels, leafy spurge, face flies, and chestnut blight fungus is approximately 120 billion dollars a year in the United States (Pimentel et al 2005; Trammel and Butler 1995; Campbell 1994; Benson and Boydston 1995). The most invaluable loss facilitated by invasives is the endangerment or extinction of native species. The classification of 42% of 958 species as threatened or endangered by the Endangered Species Act is due to displacement, predation, or out-competition by invasive species (Wilcove et al. 1998).

However, invasives are not always a doomsday warning. Sometimes invasive species have a positive role in their non-native ecosystems when used as biocontrols. Herbivorous insects have been used to control the invasion of weedy plants as an alternative to toxic herbicide control and ineffective manual removal. In addition, sometimes the control of a devastating invasive plant can only be accomplished by an introduced non-native insect. For example, the seedlings of *Melaleuca quinquenervia*, an invasive tree introduced to Florida that desiccates

wetlands and destroys native species in the process, demonstrate significantly lower growth and survival following the introduction of insect herbivores *Boreioglycaspis melaleucae* and *Oxyops vitiosa* (Franks et al 2006).

Daucus carota, a noxious weed, was introduced to North America ~ 200 years ago and has become successfully established in all states (Columbus Horticultural Society 2007; USDA 2008). It has remained uncontrolled and with scarce herbivory until now. A six year survey of a palearctic lepidopteran, *Sitochroa palealis*, first identified in 2002 determined that *S. palealis* is now established in four states of the United States (Passao et al. 2008). While the biology of *S. palealis* is mostly unknown, it is verified that *S. palealis* closely associates with *D. carota* (Bollman 1955; Allyson 1981, 1984; Goater 1986; Passao et al. 2008). *S. palealis* adults have been documented as being active at night (Truscott 2008) and present upon communities of mature *D. carota* during the day (Phillip 1987). In addition, the larvae are known to consume the seeds of *D. carota* (Balachowshy 1972).

The recent documentation of *S. palealis* at the E. S. George Reserve adds Livingston County to the list counties in Michigan where *S. palealis* is established which includes Charlevoix, Eaton, Cheboygan, and Allegan (Hessler et al. 2008). In addition, this study investigates the distribution pattern of umbel damage within a population of *D. carota* and upon individual plants, and further elucidates the biology of *S. palealis*. Because the adult female leads the invasion by carrying and depositing eggs into new regions, oviposition is the first and most determinant act of successful invasion. As the mobility of larvae is limited, the survival of the larvae depends on the food source available at the oviposition site. I considered the damage patterns by larval seed predation and pupation within the umbels of *D. carota* as indicators of oviposition preference with the hypothesis that plants with many umbels will have more damage than plants with few umbels.

METHODS

Study site

The location of the study site is in a disturbed and abandoned field within the E.S. George Reserve in Pinckney, Michigan. Throughout the field, populations of *Daucus carota* are common and interspersed with plant species such as *Juniperus virginiana*, *Elaeagnus umbellata*, and *Schizachyrium scoparium*.

Observations of Sitochroa palealis

Larva of varying life stages were found in the closed infructescences of mature *D. carota*. Early instars of the larvae were observed consuming seeds (Plate 1). Frequently more than one larva was present in an umbel. Webbing produced by the molting of *S. palealis* late instars wove the pedicels of the umbel together limiting access to the interior and preventing seed dispersal of any seeds that were not damaged. When the webbed cases were opened, a late instar *S. palealis*

was inside. A very limited number of individuals from a few other species were observed on *D. carota*. However, none were as omnipresent by the hundreds as *S. palealis*.

Plate 1. The presence of *S. palealis* inside the umbel of *D. carota* consuming seeds.



Signs of damage included the presence of copious frass accompanied by desiccated and malformed seeds, unopened and blackened infructescences with tightly woven umbel pedicels, and frass laden skeletons of pedicels lacking seeds (Plate 2).

Plate 2. Damaged umbels of *D. carota*.



Study design

On October 12, 2008 a twelve by twelve meter grid with two meter intervals was laid containing all the individuals of one population of *D. carota*. Individual plants were mapped within the grid. Each plant was measured for number of umbels and the number of umbels with signs of damage.

Data analysis

Statistical analysis of the relationship between the number of umbels and presence of damage was completed using SPSS GP 16.0. Distribution of damage and plant density patterns were analyzed using Matlab. Distribution maps were created with Microsoft Excel 2007.

RESULTS

77% of the 1126 umbels evaluated from 212 individual were damaged. There is a significant correlation between the number of umbels per plant and the amount of damage sustained by each plant (Pearson's correlation, $N = 211$, $\text{sig.} = .003$).

There is a positive linear relationship between the number of umbels and the amount of damage per plant. The frequency of damage per plant is significantly dependent on the number of umbels per plant (linear regression, $df = 211$, $\text{sig.} = .003$).

The distribution of plants without damage (Figure 1) and with 100% damage (Figure 2) was not significantly different from their distributions within the population (Figure 3). However, there was a trend of undamaged being further away from the center.

Figure 1. Individual plants without damage in a population of *Daucus carota*.

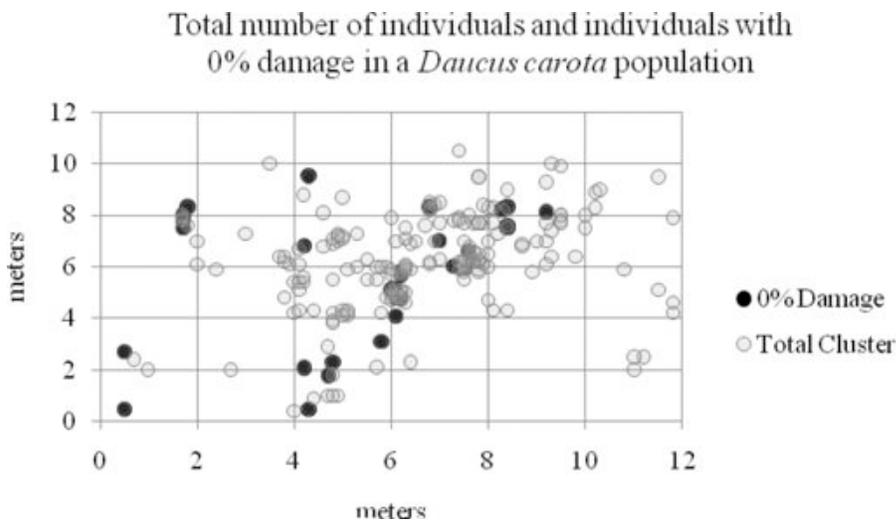


Figure 2. Individual plants with 100% of the umbels damaged in a population of *Daucus carota*.

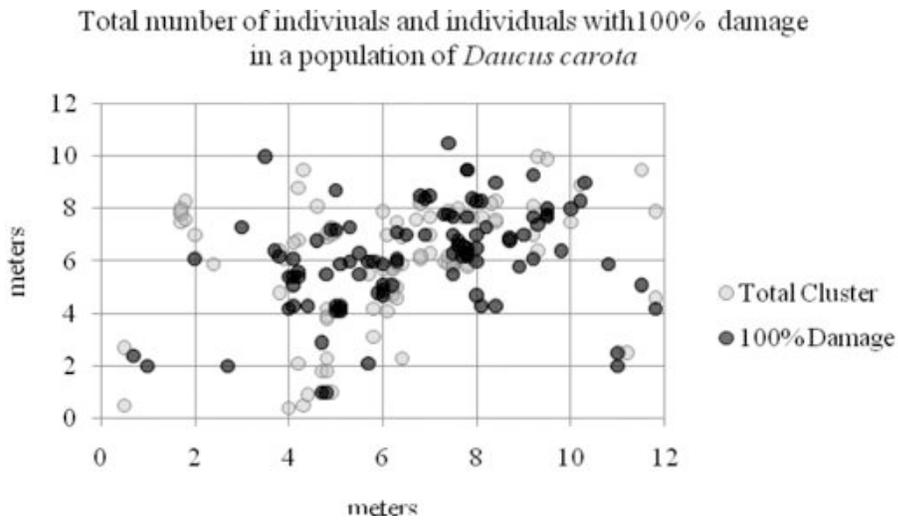
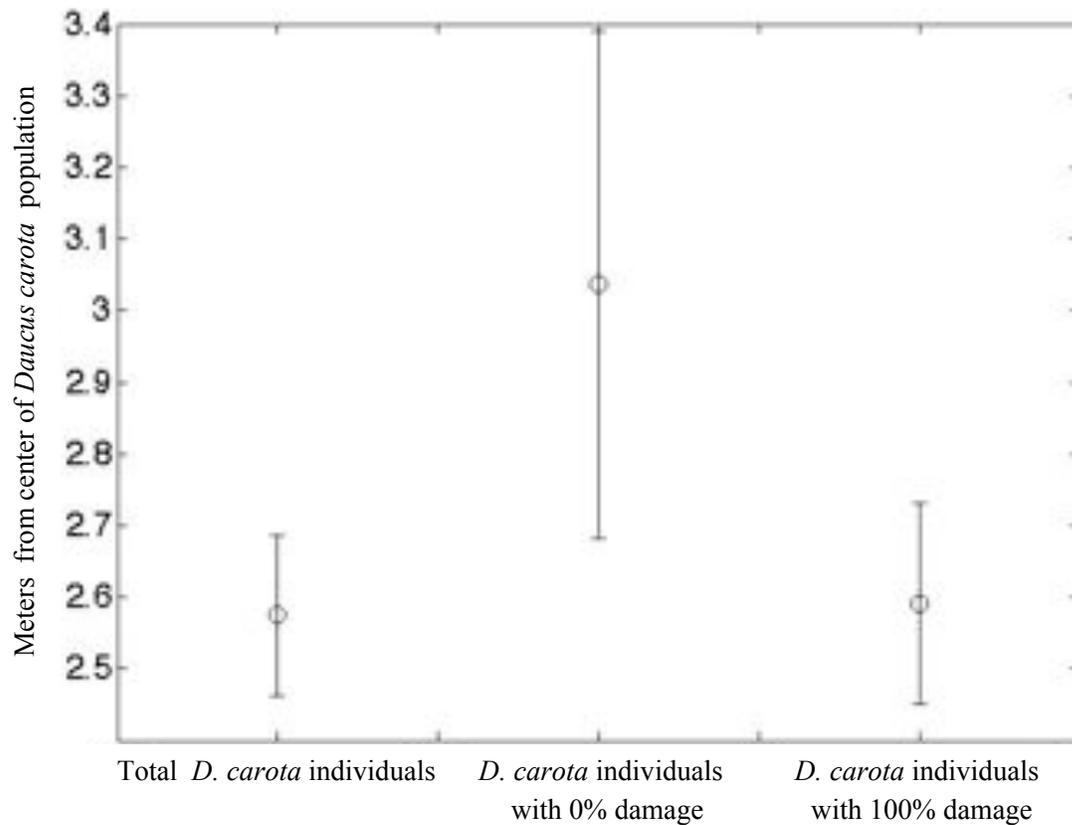


Figure 3. The distance of three groups from the center of cluster: total individuals, individuals with 0% damage, and individuals with 100% damage.



DISCUSSION

The hypothesis that the adult female *S. palealis* may prefer to oviposit on plants with more seed heads was supported by the results that the more umbels a *D. carota* has, the more likely it is to have damage to its umbels. In addition, it appears oviposition site assessment is based on the number of umbels on the individual plant and not by the umbel's location within a cluster of plants. The idea that females would prefer plants with more umbels was based on the fact that the survival of the larvae depends on the food abundance and protection provided by the oviposition site. Where the female lays the eggs is paramount to regeneration. If the trait to visually or chemically sense seed abundance on an individual plant is inheritable, then natural selection would favor the trait to discern between optimal and less than optimal oviposition sites.

This study assumes that all of the damage measured on the umbels was from *S. palealis*. It is possible that some of the damage was from another seed predator though the presence of *S. palealis* was overwhelming. It is also possible that had more study sites been established, the location of the individual *D. carota* within the cluster would have significantly affected the amount of damage incurred. Despite the shortcomings of the study, this investigation provides important data for future studies and information on the life history of this productive and abundant invasive species. In addition, this study definitively documents the extensive damage to *D. carota* infructescences coinciding with the introduction of *S. palealis* to the E. S. George Reserve.

The long term effects of *S. palealis* generates many considerations concerning the initiation and continuation of an arms race from the reunion of the furanocoumarin producing host plant and its seed predator. Furanocoumarins, a defense toxin in *D. carota* that interferes with DNA synthesis, is expensive in terms of sequestering amino acids. Because the *D. carota* population in the United States had little seed herbivory prior to *S. palealis*, the *D. carota* population was able to explode not just from a lack of herbivory but also from the ability to invest in growth and seed production because amino acids were not sequestered for defense in the production of furanocoumarins.

While *S. palealis* may initially appear as a beneficial biocontrol for the noxious weed, it is likely that herbivory will increase the toxicity of *D. carota* by stimulating and thus increasing the production of furanocoumarins. The relationship between furanocoumarin production and plant growth was demonstrated in a close relative of *D. carota*, the wild parsnip. Wild parsnips and *D. carota* are both members of the Apiaceae family and both produce furanocoumarins. When wild parsnips are protected from their dominant seed predator, *Depressaria pastnelli*, the plant more than doubles its investment in seed production compared to plants with heavy seed predation (Berenbaun and Zangerl 1994).

As *D. carota* responds to herbivory with the increase of furanocoumarin production, plants may become smaller as less amino acids are invested in growth. Perhaps the size of the plant is an indicator of furanocoumarin production as larger plants with more seeds have lower furanocoumarin because the amino acids were invested in growth and not defense. It is possible that while the hypothesis that females prefer ovipositing in plants more umbels appears correct, it

is correct for the wrong reason. Perhaps females prefer to oviposit in larger plants not because of food abundance but because of lowered furanocoumarin levels.

Future research should focus on the driving forces of invasion specifically oviposition behavior using the biology of *S. palealis* and the furanocoumarin production in *D. carota* as a model system. Field work is essential to understanding how, when, and where the female oviposits. This should be followed by chemical analysis of the furanocoumarin levels that distinguish oviposition site preference and the potential stimulation of oviposition by a specific level and type of furanocoumarin. Chemical analysis is also necessary to measure furanocoumarin levels in *D. carota* 1) prior to seed predation, 2) after seed predation and 3) at various life stages in the same plant to determine if the plant maintains the same level of toxicity throughout its life or if toxicity triggered by seed predation. In addition, molecular analysis may reveal which genes are responsible for the regulation of furanocoumarins and if the gene is fixed or varied in the population. If furanocoumarins are so costly then it seems that the plant would have a developmental gradient investing the most protection at the site most crucial towards the propagation of the next generation and investing less in less vulnerable and essential areas.

The recent invasion of *S. palealis* on the invasive weed *D. carota* marks the beginning of an evolutionary reunion between two species pre-adapted to co-exist. This is invasion succession. While both species are successful invaders, they will now continue their evolutionary journey throughout the United States together and may act as a building force that changes environmental conditions enabling other symbiotic palearctic species to successively and successfully invade.

ACKNOWLEDGEMENTS

I thank Ivette Perfecto and Beverly Rathcke for the photographs of the specimen and guidance, May Berenbaum and Terry Harrison for positive identification of *S. palealis*, and the E.S. George Reserve for use of supplies and access to the study site, and David Allen for assistance with Matlab analysis

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POLLINATOR FORAGING PREFERENCES IN E.S. GEORGE RESERVE

ELISSA CHASEN, HANNAH FOSTER, ASHLEY LARSEN
EMILY SLUZAS, LEILING TAO

ABSTRACT

Pollinators play valuable roles in providing services to ecological and agricultural systems. This study looked at foraging preferences of three wild bee pollinators in the E.S. George reserve, honeybees (*Apis mellifera*), bumblebees (*Bombus spp.*), and sweat bees (family Halictidae). Pollinators showed strong preferences for particular plant species including native thistle (*Cirsium sp.*) and purple aster (*Aster novae-angliae*). They also were more likely to visit plots where flowers were denser. Pollinator activity was lower in sites closest to forests and peaked at mid-range distance from the forest. Interactions between foraging *Bombus spp.* and *Apis mellifera* were documented in which *A. mellifera* may be having negative effects on foraging success of *Bombus spp.*

INTRODUCTION

Pollination is an essential ecosystem service provided by animals to plants, which reproduce sexually. Pollination services are required to produce most of the fruiting crops cultivated by man and hence interest in pollinators has intensified with the recent development of “colony collapse disorder” (CCD). CCD affects honeybees, *Apis mellifera*, which are heavily relied upon to pollinate crops. The growth of this issue has renewed interest in native pollinators, which have different social systems, high diversity, and are not subject to CCD. Recently, systems have been identified in which wild bee pollinators actually pollinate the majority of crops (Winfrey et al. 2008). Scientists have long sought to understand what attracts particular pollinators to particular plant species and areas of floral availability. With the advent of CCD there is an increasing urgency to our quest to understand the foraging behavior of pollinators.

Many factors can impact the visitation rates of pollinators to a particular plant. The plant must provide a perceived benefit to the pollinator, and pollinators attempt to acquire resources as efficiently as possible. This is reflected in a study examining the effects of plant population size and density on pollinator foraging (Kunin, 1997). This study found that the number of individual plants available in a given space had no impact on the number of forager visits. However, the density of plants, plants per area, in experimental plots had a remarkable effect on visitation rates and reproductive success. The pollinators in this study were also found to be more “flower constant” at higher plant densities, meaning that pollinators were more likely to visit flowers of the same species and thus appropriately transfer pollen within a species. In addition, distance from intact suitable nesting habitat may impact pollination rates. A study by Ricketts et al. found a steep drop off in pollinator visitation rates at just 0.6 km from natural habitat (Ricketts et

al. 2008). Thus the attractiveness of a floral resource may depend not only on its density but on its location in the landscape.

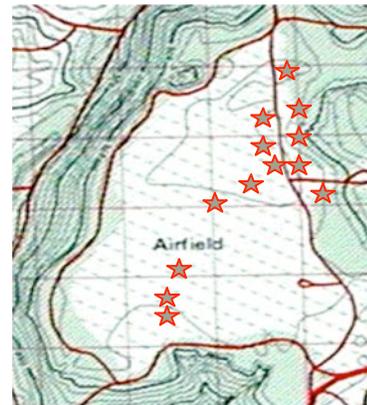
An additional layer of complexity when studying foraging behavior of pollinators is added by inter and intra specific competition. Some pollinators are specialists under some conditions, and generalize more as density of conspecifics increases (Fontaine et al 2008). Hence while some species of pollinator may be thought to only visit certain plants, they may be induced to pollinate other plant species at higher foraging bee densities. With all of these factors to consider, we sought to address several questions about foraging behavior within a disturbed area of the ES George reserve. We wanted to examine whether the number of plant species available or the abundance of flowers within a plot impacted the number of pollinator visits, whether pollinator species were specializing on particular plants, and whether the presence of more than one pollinator species impacted foraging behavior.

MATERIALS AND METHODS

Study Site

This study was conducted in the Airfield area of E.S. George Reserve in Michigan. The airfield is an open area which is surrounded by forests. After abandoned in the 1950s, it was turned into a grazing place and since then many grasses and flowers encroached the old field. We selected 13 2m by 2m plots in the airfield by looking for areas in the field with either diverse floral composition or greater floral abundance (shown in Fig.1), with different flower composition and abundance in each plot.

Fig.1 Study site and plot distributions



Methods

At each plot site, we noted which species were present and how many total flowers were present (Table 1). The distance from each plot to the forest was estimated by pace. From 10:08 am to 11:50 am, 2 or 3 10-minutes periods of observation were taken in each plot. We observed honeybees, bumblebees, and sweat bees. We recorded which pollinator visited which flower and the duration of visits to different species of flowers. For plots that had more than 1 pollinator, the interaction between the pollinators was also recorded.

RESULTS

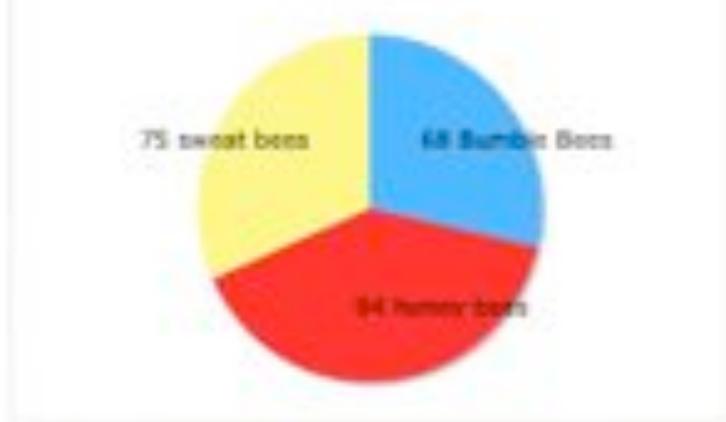
Flower species and abundance

For the 13 plots, a total of 6 species in flower were found: *Centauria sp.*, *Cirsium sp.* (thistle), *Solidago sp.*(golden rod), *Liatrus sp.*, *Aster novae-angliae* (purple aster) and white aster.

Pollinator species and abundance

Between 10:08 am and 11:50 am, a total of 86 bees from three groups of pollinators (honey bee, *Apis mellifera.*; bumble bee, *Bombus spp.*; sweat bee, Halictidae) were found in the plots. They had a total number of 237 visits to the flowers, with 94, 68, 75 times of honeybee, bumble bee and sweat bee respectively (Fig.2).

Fig 2 Total times of visits by different species of bees



Pollinator's preference

There were strong floral preferences for each bee species, as shown in Fig.3-5. For honeybees and bumblebees, the preferred flower is thistle (*Cirsium sp.*), and more than 60% of visits were made to thistle flowers. Sweat bees, on the other hand, preferred to visit purple aster (*Aster novae-angliae*).

Fig 3. Floral preference of bumblebee

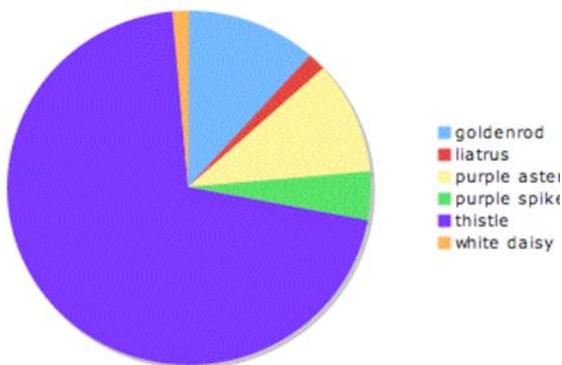
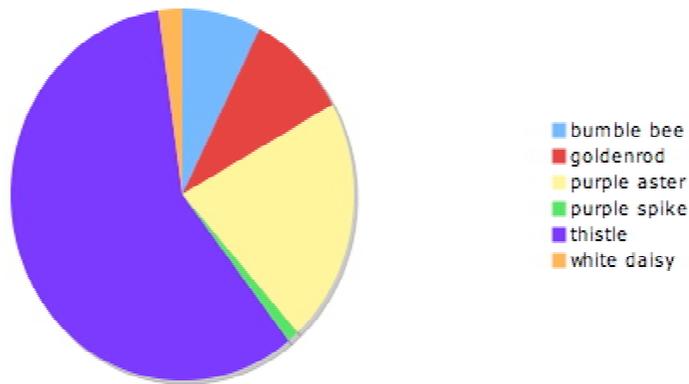


Fig 4. Floral preference of sweat bee

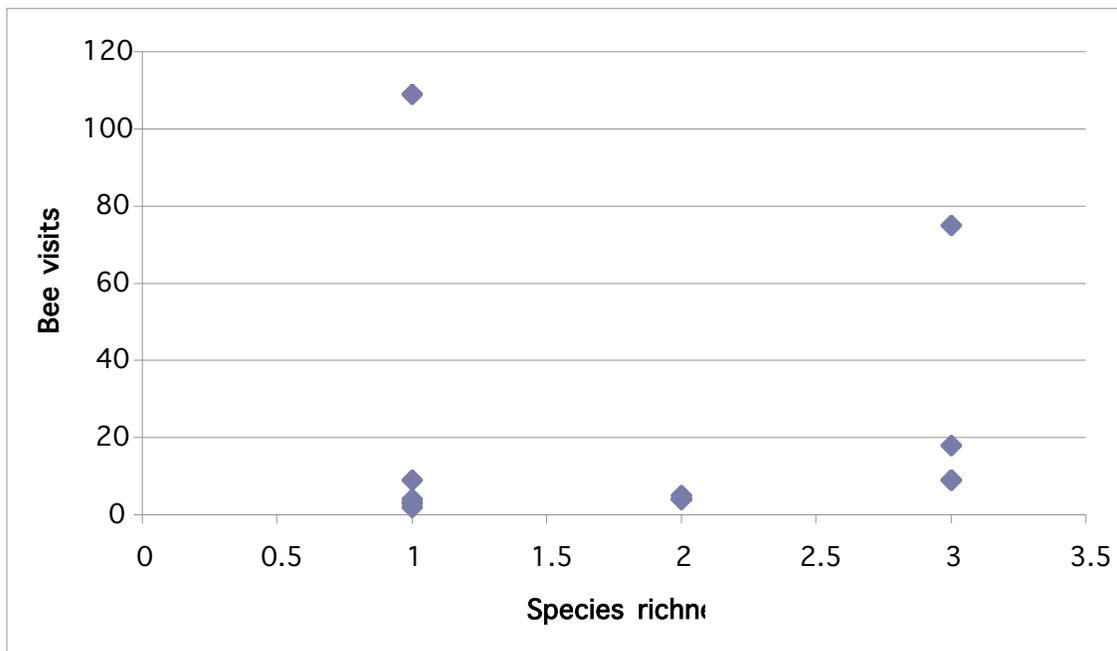


Fig 5. Floral preference of honeybee



Floral species richness, abundance and number of visits

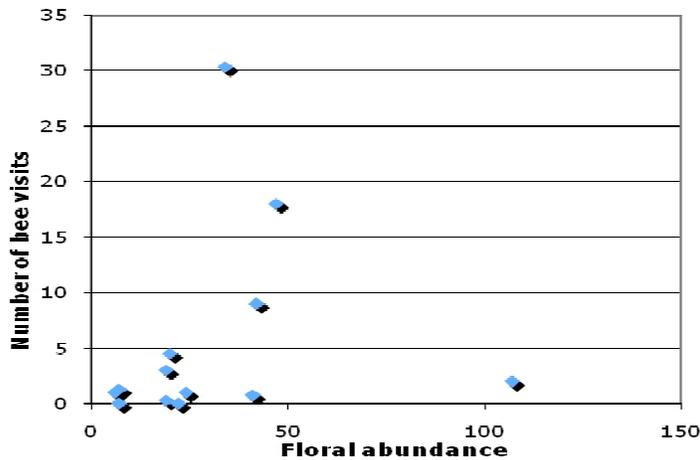
Fig 6 Plant species richness and number of visits



There is no correlation between floral species richness and total number of visits by bees, as shown in Fig.6. Because different bees have strong preference in selecting flowers, the species composition might be more important than species richness in attracting bees. For example, plot 4 only has thistles thus the species richness is 1, but since thistle is the favorite for bumblebee and honeybee, it had the most bee visits. Similarly, there is no correlation between floral species richness and total durations of bees.

Although bees do not seem to prefer plots rich in floral species, they do show a preference to plots with higher abundance of flowers (Fig.7). This is in correspondence with Kunin's discovery in 1997. The similar pattern is also found in correlation between plant abundance and bee numbers and durations.

Fig 7 The floral abundance and average number of visit per plot



Distance from forest affects the number of floral visit by bees

Along with plant species and abundance, the distance of the plots from the forests also affected bee visits. Shown in Fig. 8 and Fig. 9, as distance from plots to forests increases, the number of bee visit first increases, but after reaching the peak at about 20 meters, the number of visit goes down.

Fig.8 Distance of plots and number of visits

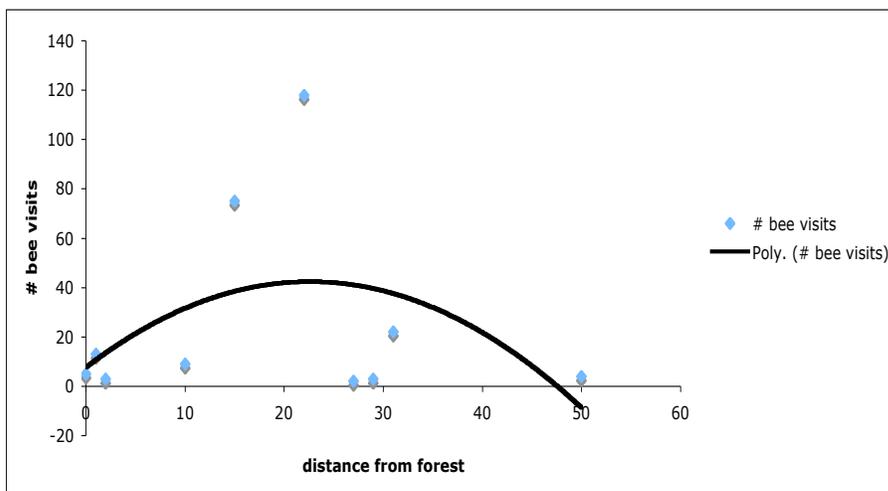
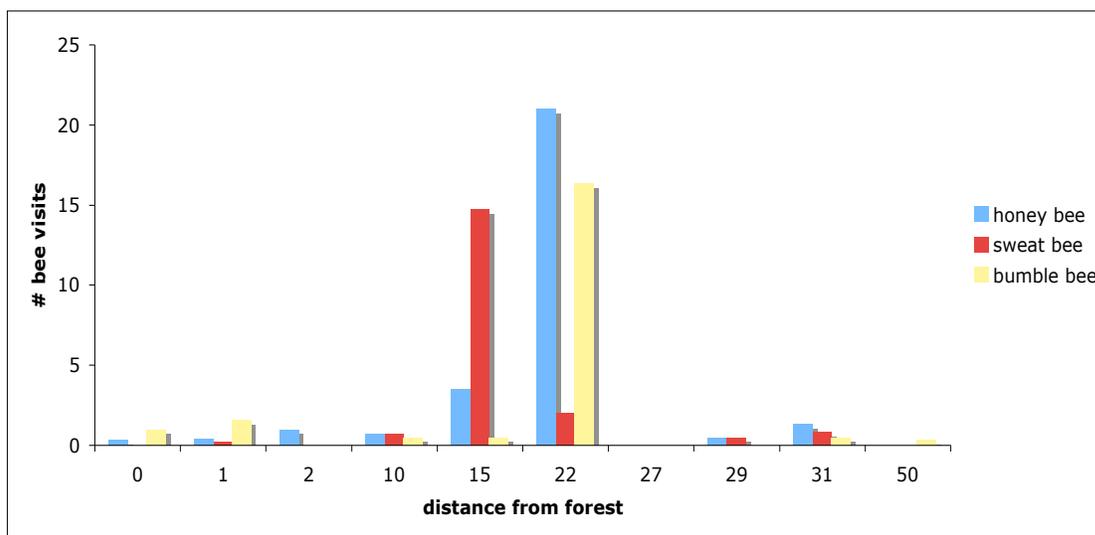


Fig.9 Distance of plots and number of visits of different species



Interactions between pollinator species

We did not encounter many interactions between species. In general the different species and individuals ignore each other. In several instances though, we did witness honeybees foraging on the pollen sacs that bumblebees had gathered. The bumblebees continued foraging as usual, seemingly without even noticing the presence of the honeybee gathering the pollen already collected by that individual.

DISCUSSION

In this study we looked to find patterns of foraging behavior among different pollinators. We saw that different pollinators showed strong preference for individual flowering species; both bumblebees and honey bees were more likely to visit thistle flowers, while sweat bees were more likely to visit purple aster. Pollinators also showed a preference for areas with more abundant floral resources. However they did not have a preference for areas with more diverse floral resources. This is likely due to the fact that they did have such strong tendencies toward individual flower species; they were more interested in a single species than in a diversity of species. The distance from the forest of the plots we looked at did relate a pattern of foraging preferences. We saw optimal foraging at medium distances from the forest and this may be due to the fact that sites we observed that were closer to the forest edge remained shaded and colder, and possibly too cold for the pollinators to move in. On the other hand, sites that we observed which were

furthest from the forest may have received less attention because they were possibly farther from nest sites.

Pollinators are necessary components of ecosystems and provide services toward ecosystem functioning and stability. As well they provide services to agricultural systems. As seen in one New Jersey study, wild bees were the majority of pollinators that visited their crops (Winfree et al. 2008). Understanding how these pollinators decide to visit floral species will be of great benefit to agricultural systems.

In this study, we saw that pollinator foraging behavior was determined by the presence of particular species of flower, the abundance of floral resources in a given site, and the distance of the patch of flowers from the forest. There was no discernable impact on foraging behavior by flower species richness.

If we apply this study's findings to agricultural systems, we can recommend that specific wildflowers be planted along or throughout home gardens or farms to increase pollinator visitation. Namely, if one wants to increase honeybee or bumblebee visits to their crops, plant thistle (*Cirsium sp.*) and if one wants to increase sweat bee visits, plant purple aster (*Aster novae-angliae*).

In the future, this study could be built on by completing similar experiments in the spring and summer to determine if foraging behavior changes through the seasons.

In regards to the interactions between bumblebees and honeybees, a brief literature search leads us to believe this is the first record of such interactions. In 2004, Thomson detected negative effects on *Bombus occidentalis* foraging and reproductive success by the presence of *Apis mellifera* hives but does not note interactions such as the ones we saw. This could be a very important avenue of future research because *Apis mellifera* is an introduced species while *Bombus spp.* are native and are important pollinators for many native plants. If these interactions are the reason for the negative effects on *Bombus spp.* then it will prove to be a very interesting window to pollinator behavior.

ACKNOWLEDGEMENTS

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POLLINATOR FORAGING BEHAVIOR AND CLIMATE CHANGE

EMILY SLUZAS

ABSTRACT

Global warming threatens to disrupt a huge range of species interactions. Pollinators provide essential ecosystem services, and the plant-animal interactions these services depend on are very likely to respond to climate change. Not only will plant phenology and distribution be impacted by warming temperatures, but pollinator foraging activity may change with increasing temperature. This experiment sought to use an unusually warm day in October to provide an example of a global-warming like scenario. Few floral resources were found and high levels of pollinator activity were observed. These results have implications for the pollinator species, the plants they pollinate, and the humans whose agricultural system depends on these pollinators.

INTRODUCTION

Pollinators are necessary for the reproduction of a huge number of plant species and provide essential ecosystem services to humans in the form of crop pollination. An estimated 70% of agricultural crops are pollinator dependent (Ricketts et al 2008). Native pollinators are under increasing threats from habitat destruction. Strong exponential declines in both pollinator richness and visitation rate have been observed with increasing distance from natural habitat (Ricketts et al 2008). In addition, in the United States, an important introduced pollinator, the European honeybee (*Apis mellifera*) is under threat from a phenomenon called Colony Collapse Disorder. CCD has damaged up to 25% of commercial hives in the United States. The impact of this loss is immeasurable as large agricultural producers are dependent on commercially supplied honeybees to pollinate their crops. All pollinators, both native and introduced have been under increasing stress from pesticides.

An additional problem for pollinators may arise as global warming increases the average temperature through earth's seasons. Pollinator biology is highly temperature dependent, with species responding variably to temperature increases. Honeybees will not forage below particular temperatures, 16°C in one study (Currah and Ockendon 1984). In this study the honeybees remained consistently active at all temperatures above 16°C. Bumblebees, on the other hand, have been shown to forage optimally at particular temperatures, and decrease in activity above certain temperatures (Kwon and Saeed 2002). Very little is known about the temperature response of the many native pollinators which in some cases are responsible for up to 80% of crop pollination (Winfree et al 2008).

If pollinators are in fact more active later into the fall as temperatures rise, there may be increasing competition for limited floral resources. It has been proposed that increased carbon dioxide alone will cause a phenological shift that may reduce the floral resources available to 17-50% of all pollinator species (Memmot et al 2007). The concentration of atmospheric CO₂ is predicted to double between now and 2070-2100 (IPCC 2001). Memmot et al used observed phenological shifts from multiple studies in temperate regions over the past century to calculate a mean 4 day phenological shift (advancement in flowering) per degree Celsius increase in

temperature. Current climate models for northeastern North America predict a 3.5-5 °C/year increase in mean temperature under doubling of atmospheric CO₂ (IPCC 2001). With simple multiplication this predicts an average phenological shift of about two weeks. Memmott et al used these observations to calculate hypothetical shifts in phenology of plants and pollinators and found that pollinators using flowers of few plant species were likely to be left with no food supply after a phenological shift of two weeks. Generalist pollinators experienced reduced diet breadth following phenological shifts.

Because there will be disconnect between the behavioral adaptation of pollinators and the phenological adaptation of plants, we might expect to see some pollinators outcompete others and eventually cause the extinction of certain species through the competitive exclusion principle. We may also observe the disruption of long evolved niches which have allowed many native species to coexist. This study examined pollinator activity on extremely limited floral resources on an unusually warm day in mid-October. Because current climate models predict a 3.5-5°C/year increase in mean temperature, expected temperatures could easily rise to those experienced during this study. Based on the observation that generalist pollinators would experience a reduced diet breadth, it was hypothesized that high levels of activity would be seen on the remaining flowering plants and that both intra and inter-specific competition would be observed. It was also predicted that plant species previously not preferred or heavily utilized by pollinators would experience increased visitation due to the reduced breadth of species available.

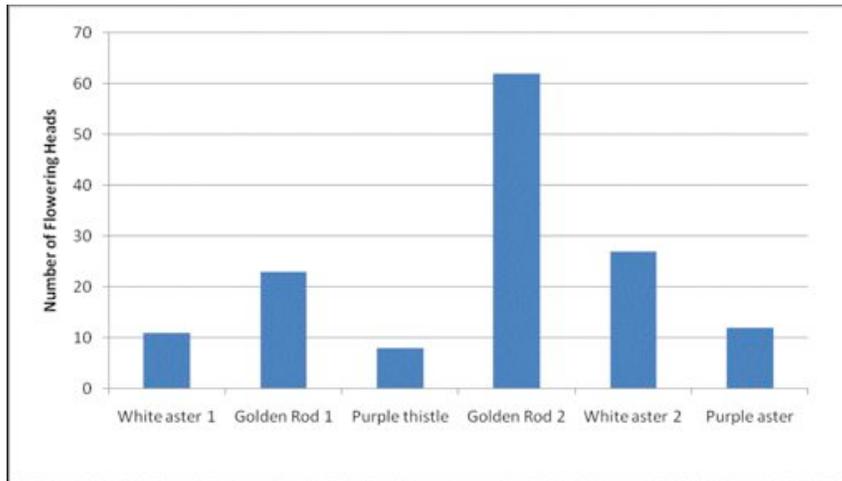
MATERIALS AND METHODS

This study was conducted at the ES George Reserve on October 5th, 2008. Six flowering plants were identified in the old Airfield. Two plants were of one goldenrod species, two were of one white aster species, one was a non-native purple thistle, and one was a purple aster species. The number of flowering heads on each plant was counted. The first three plants were observed from 10:20am to 12:30pm. Ten minute focal observations of each plant were conducted and each plant was observed four times. The second set of three plants was observed from 12:50pm to 3:00pm. Again, four ten minute focal observations of each plant were performed. At each plant, any observed pollinators were recorded including the time arriving at the plant and the time leaving the plant. For the most active site, number of pollinators present every two minutes was recorded. Interactions between pollinators were documented only if one pollinator arrived on an already occupied flowering head, and the occupant immediately departed.

RESULTS

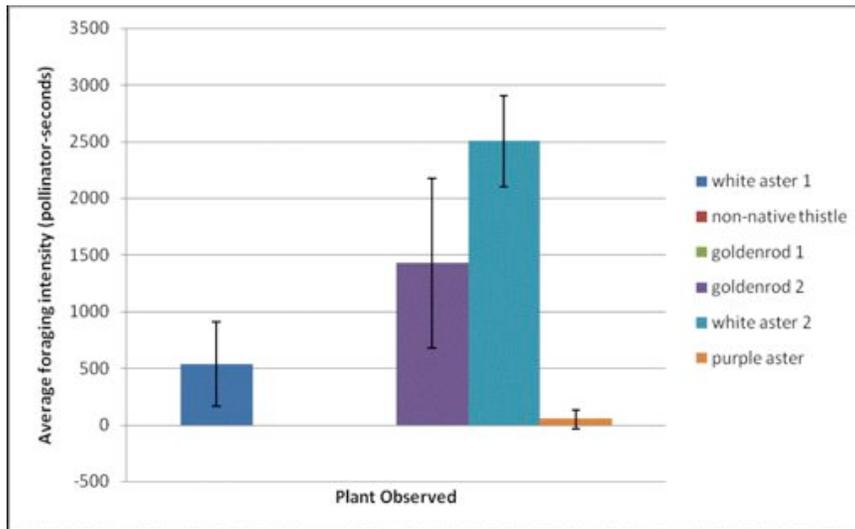
Flowering resources were scarce in the George Reserve in early October, as seen in Figure 1. The number of flowering heads on golden rod in previous studies was much higher.

Figure 1. This figure shows the number of flowering heads on each observed plant.



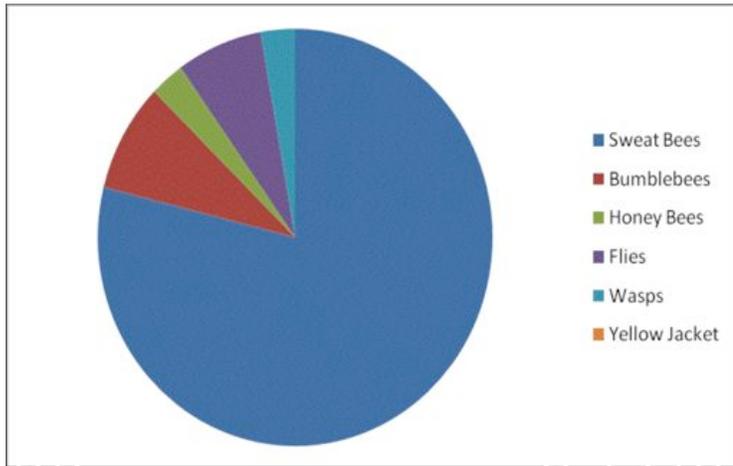
No pollinator activity was observed on two of the six observed plants. On plants where pollinators were observed, there was a high intensity of foraging behavior (Figure 2).

Figure 2. Though no pollinator activity was observed on two of the six plants, overall foraging intensity (pollinator*seconds) was high, especially on white aster and goldenrod.



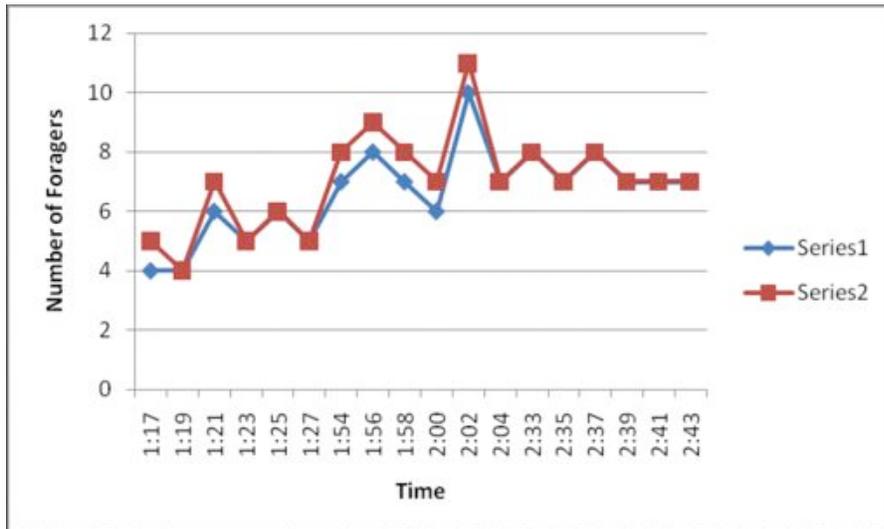
Many different pollinator species were observed at the flowering plants, as seen in Figure 3. The most dominant species observed was the sweat bee, which was actually a grouping of small native bees for which species level identification was not possible. In an earlier study at the George Reserve, which grouped sweat bees in the same manner, only three species were identified. Of the species observed, all were seen on white aster, whereas only bumble bees and sweat bees were observed on golden rod, and only sweat bees were seen on purple aster.

Figure 3. Observed pollinators by species.



On the most active plant, white aster 2, a high level of foraging activity was seen at all time points, as demonstrated in Figure 4.

Figure 4. The total number of foragers over time on white aster is represented in Series 2, while the number of small native bees present over time is seen in Series 1.



High levels of intraspecific competition could be inferred from the number of sweat bees (small native bees) foraging on white aster over time as also seen in Figure 4.

Four instances of interspecific interactions were observed. The interactions were of two types. In the first two interactions, a honeybee moved a small dark native bee. In the second two observed interactions, a bumblebee moved a helictid. In both cases, a larger bodied non-native bee landed on a flowering head where a smaller native bee was foraging, and the smaller native bee immediately left the foraging site.

DISCUSSION

Floral resources were scarce in the ES George Reserve in early October. Though no comparative data was available for quantifying floral ability, the observer had difficulty even finding flowering plants to include in this study. This was qualitatively significantly different from the study conducted in September, during which many species of flowering plants were easily found. Pollinators were observed heavily using a resource, the white aster, which was not preferred in the September study. This difference in usage could be explained either because pollinators are willing to visit a lower quality resource only when there is not much else available, or because the white aster has a phenological difference which allows it to release more nectar later in the fall. Indeed, an evolutionary strategy could be inferred here because as fewer floral resources become available, a plant could offer a lower quality nectar reward and still receive pollination services.

Though high levels of pollinator activity were observed, fewer honeybees were seen than expected. Because some honeybees were seen, it was certainly warm enough for this species to be foraging, and it is possible that another, higher quality floral resource was available somewhere within the Reserve which was not encountered by the observer. Competition was observed both within and between species. It was particularly interesting that the four interspecific interactions observed were all instances of a non-native, large bodied bee moving a small native bee from a flower. More observations would be required to see if this pattern were consistent. Further experiments could be designed to see if this competition actually impacts the fitness of the native bees involved. This study could be significantly improved by identification to the species level of small native bees. Though both types of competition were certainly observed, they could be better quantified by an observer versed in Michigan bee taxonomy.

Global warming raises significant concerns for a wide range of species interactions. In the case of pollination, a critical ecosystem service, the shift in plant communities and changes in pollinator activity may cause disruption of a system that humans largely depend on for food production. Further research and long-term comparative studies are needed to determine whether competition is actually increasing among pollinator species as the average temperature rises during the fall season in temperate zones. This study has provided a small snapshot of the high pollinator activity levels we might expect well into October as the climate warms.

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MICRO-HABITAT SELECTION IN THE WHITE-FOOTED MOUSE,
PEROMYSCUS LEUCOPUS

EMILY SLUZAS, ELISSA CHASEN, HANNAH FOSTER, TAMATHA PATTERSON,
and CATHERINE BADGLEY

ABSTRACT

Peromyscus leucopus, the white-footed mouse, is a small mammal commonly found throughout the eastern United States. In this study we examined the distribution of *P. leucopus* in the ES George Reserve in relation to habitat type and food availability. We found a strong relationship between habitat type and *P. leucopus* presence. We did not find any difference in the amount of food available between sites with *P. leucopus* and sites without *P. leucopus*. We theorize that the *P. leucopus* population in the ES George reserve is not food limited this year, and that trapping success should be higher next year as a result of abundant food resources this year.

INTRODUCTION

For most mammals, food resources are key to survival. Some species are more or less affected by changes that affect their feeding options. The white-footed mouse, *Peromyscus leucopus*, is a species particularly sensitive to available food resources. This mouse has also been shown to be selective of its food choices (Lewis, 2001). This species relies predominately on nuts and seeds from maples, oak, beech, hickory, pine, grass grains, and berries and secondary grubs and caterpillars. *P. leucopus* relies on hoarded food for winter consumption. Higher densities and greater reproductive success in this species has been attributed to food availability (Wilder, 2003). Other studies have shown negative effects on male reproductive fitness regardless of food availability due to botfly parasitism (Baudoin, 1976).

P. leucopus is common in deciduous forest with moderate herbaceous cover and decaying logs. The leaf litter and fallen logs of this habitat type provides cover from the many predators of the mouse including hawks, owls, foxes, and mink. Individuals are generally solitary and hold territories of approximately 10 square meters (Kurta, 2001). *P. leucopus* has a short life-span with only 2% surviving past 1 year. This species also has a rapid regeneration time as females can produce four or more litters with the average size of 4 pups per season, and has uncomplicated connections between lower and upper trophic levels (UMBS unpublished data). In this study, we will investigate food availability and habitat preference on the micro-scale for this species. We seek understand whether food resources in a given area influence the presence of *P. leucopus*. In addition we will look for the impact of habitat type on the presence of *P. leucopus*. We expect that mice will prefer and be more frequently trapped in habitats which provide both adequate coverage for predator avoidance and abundant food sources. On the reserve, oak and hickory forest habitat is expected to harbor the largest concentration of *P. leucopus*. The results of this study will be compared to those of previous field courses and with data from the Biological Field Station (UMBS) to determine if there is a pattern in population fluctuations of *P. leucopus*.

METHODS

Peromyscus leucopus, the white-footed mouse is rodent of the family Muridae, class sigmodontinae. The species is widely distributed in central and eastern North America with the Great Lakes as its northern border in Michigan. It is generally 145-195mm in length and 16-30 grams in weight. Adult mice are characterized by large dark grey to black ears and large bright black eyes. Their dorsal fur is russet with a darker band along the midline. The ventral fur is white to cream and the tail is dark brown on top and light grey on bottom. Young are grey and develop adult coloration in 40 days. (Kurta, 2001).

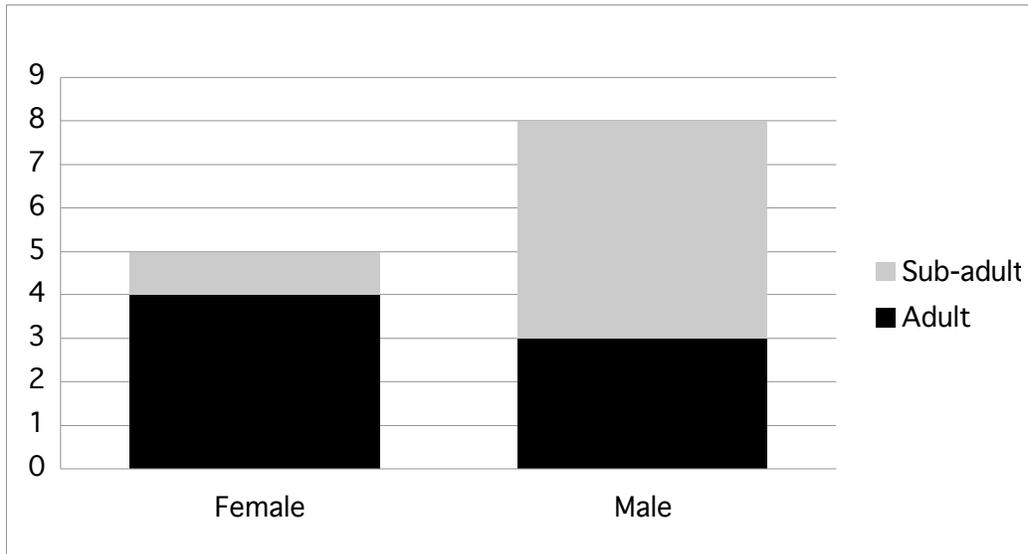
This survey took place at the E.S. George Reserve near Pinckney, MI. The survey began in the middle of the old field. Four 500 m transects were set up that radiated from this central point. Each transect was directed in a cardinal direction as much as possible considering topography and vegetative obstructions. One mammal trap was set approximately every 10 meters for a total of 50 traps per transect. The traps were set between 2:00 pm and 4:30 pm on Saturday, October 4, 2008 and were cleared the following day between 7:45 am and 1:00 pm.

At each trap, the presence or absence of mammals and the habitat type was recorded. When *P. leucopus* was found, its weight, colorations, gender based on the ano-genital distance, presence of parasites such as bot flies, and reproductive status was recorded. The age was determined from the coloration of the mouse and the gender was decided from the ano-genital distance. Reproductive status was assessed based on the presence of visible nipples in females. Additionally, each site where a mouse was trapped, three 1 square meter plots were used to quantify food resources within the territory. The number of acorns, hickory nuts, autumn olive berries and grass seeds were recorded. As a control, another set of three 1 square meter plots within the same habitat type and within 20 meters from the capture trap was sampled for food resources.

RESULTS

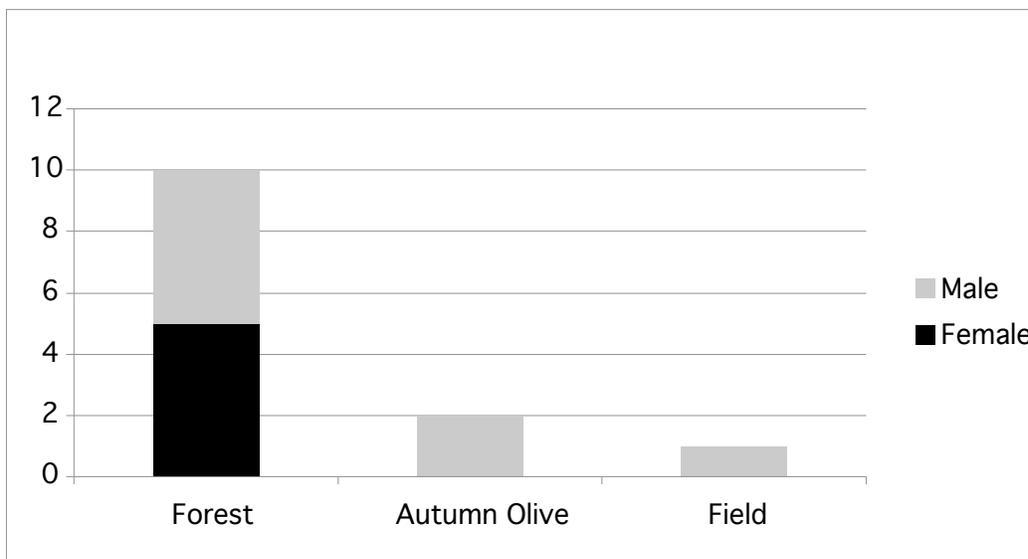
16 small mammals were captured in our traps: 14 *P. leucopus* and 2 chipmunks. One *P. leucopus* escaped before we were able to ascertain data on its sex and weight, so it was not included in the data analysis. Of the 13 *P. leucopus* remaining, five were female, and eight were male. The proportion of sub-adults to adults was greater among males at 5:3. Among females, we found only one sub-adult to four adults (fig. 1). We observed two sub-adult male individuals with botfly infections.

Fig. 1. Number of sub-adults and adults captured for male and female *P. leucopus*.



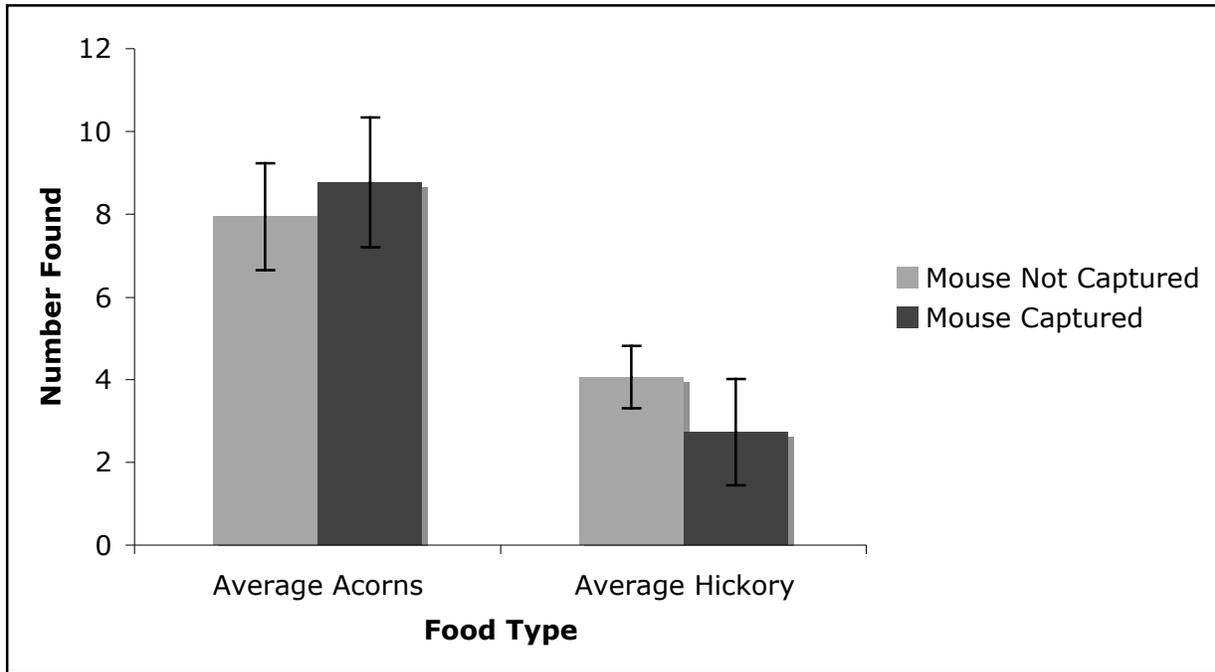
76.9% of *P. leucopus* captures were in forest habitats, as compared with 15.4% in autumn olive thickets and 7.7% in old growth fields. All females were found in forest habitats (fig. 2)..

Fig. 2. Number of male and female *P. leucopus* captured in three different habitat types: forest, autumn olive thicket, and old field.



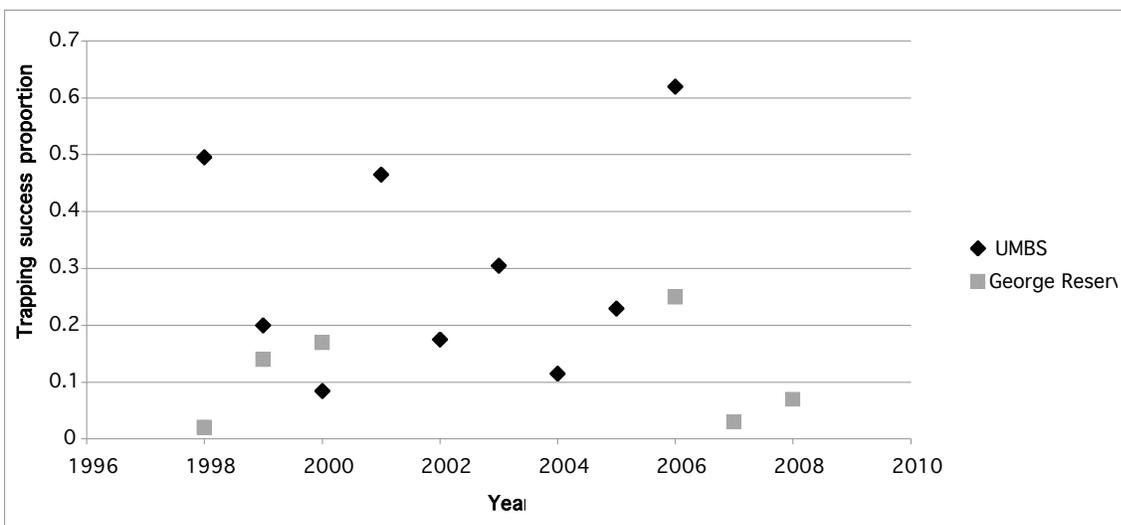
We found no correlation between food availability and the presence of mice (fig. 3).

Fig. 3. The average number of acorns and hickory nuts in sites where mice were captured vs. sites where mice were not captured (includes standard error bars).



The University of Michigan Biological Station has had, on average, a much higher trapping rate than the E.S. George Reserve (fig. 4).

Fig. 4. Trapping success at the University of Michigan Biological Station (Pellston, MI) and the George S. Reserve from 1998 to 2008.



DISCUSSION

We had a moderately high trapping success rate of *P. leucopus*, at seven percent. The highest trapping success ever observed in the ES George Reserve is 25%. Our results were consistent with the literature in that we caught all of the individuals but one in forested habitat or habitat characterized as “autumn olive” which provided ample cover for the animals. It would be interesting to see if autumn olive has increased populations of *P. leucopus* because it is possible that autumn olive would convert previously undesirable meadow habitat into suitable habitat.

Because food resources seem to be quite abundant this year it is surprising that our trapping success was not higher. It seems that *P. leucopus* is not food limited at the present time, given that we did not find a difference in food availability in the areas where we caught *P. leucopus* as compared to areas where we did not catch them. It is possible that there is a lag in the population abundance as related to food resources. Perhaps more individuals will reproduce successfully because of the high availability of resources and next spring trapping success will be much higher. Our data suggest that this is a possibility as four out of the five females captured were in a reproductive state. It is also possible that we did not find a correlation between food availability and *P. leucopus* capture because predator avoidance is a much stronger factor in habitat selection. If there is competition not only for food resources, but suitable habitat as a resource, then perhaps *P. leucopus* is limited by the amount of habitat which provides refuge from predators. This idea is supported by the fact that most captures occurred in forested or “autumn olive” habitat, where abundant cover is provided for foraging animals.

Though it has been suggested that there is a correlation between trapping success at the University of Michigan Biological Station in Pellston, MI, and success at the ES George Reserve (Phil Myers, pers. comm.) we were not able to observe this relationship. Because several years of data from the field ecology course are missing and the UMBS data was available only through 2006, it is possible that any pattern is simply lost due to lack of data. It would make sense that if *P. leucopus* populations fluctuate yearly due to temperature variations, patterns might be conserved across the state of Michigan. This effect is generally known as the Moran effect, where two populations with the same density-dependent structure are brought into synchrony by a correlated density-independent factor (Hudson and Cattordi 1999). Generally weather is the synchrony inducing factor, however, if populations are more influenced by masting events than weather, and masting events are not synchronous between UMBS and the George Reserve, it should follow that the population fluctuations of *P. leucopus* are not correlated between sites.

Many factors influence the population sizes and distributions of small mammals. *P. leucopus* in the ES George reserve seems to be distributed mainly according to habitat type. The population of *P. leucopus* may fluctuate with food availability, according to yearly variations in seasonal temperatures, or most likely, due to a combination of several factors. We did not observe enough individuals to make conclusions about the impact of botfly infections on *P. leucopus* populations. Through consistent trapping and data collection (see Appendix A) from year to year, a more complete picture of the population dynamics of *P. leucopus* in the ES George reserve could be developed.

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Appendix A

Data Collection Table

Trap Number	Species	Sex	Age (Adult/Juvenile)	Weight (g)	Parasites

THE DISTRIBUTION OF ADULT SALAMANDERS ON THE E.S. GEORGE RESERVE

HANNAH FOSTER

ABSTRACT

Recent declines in amphibian populations worldwide have led to an interest in the distribution and movement within amphibian communities. In this study, I attempt to gain a better understanding of adult salamander dispersal and migration in the E.S. George Reserve by observing their distribution with regards to local breeding ponds. Using 100-200m transects, I recorded the presence or absence of adult salamanders, soil moisture, distance from nearest pond, and other potential factors under any apparently suitable shelter within one meter of the transects. Due to a limited sample size, I was unable to come to any certain conclusions. However, there may be a positive correlation between salamander body length and distance from pond in addition to a weak correlation between soil moisture under shelter and salamander presence.

INTRODUCTION

Understanding the movement and distribution of organisms is critical in the area of conservation biology. Patterns in movement and distribution can affect the spread of disease and invasive species, the impact of land use, and responses to global climate change (Semlitsch, 2008), which are often the leading causes of species declines and extinctions.

Recent declines in amphibian populations and species diversity worldwide have resulted in a greater interest in the distribution, migration, and dispersal of amphibian populations. Most research heretofore has been on the aquatic phase of amphibian development, measuring density-dependence, predation and the link between the timing of hydroperiod in breeding ponds and reproductive success (Taylor, 2005). However, many scientists now believe that the success of individual populations is more dependent on postmetamorphic vital rates than on premetamorphic success (Taylor, 2005).

The movement of postmetamorphic amphibians generally consists of migration, the annual movement of adult amphibians to and from breeding ponds, and dispersal, the movement of juvenile amphibians to a pond other than their natal pond (Semlitsch, 2008). Although scientists know that, generally speaking, amphibians require terrestrial habitat that extends around 290m from their breeding ponds, little is known about their distribution within that area (Rittenhouse, 2007).

In this study, I seek to gain a better understanding of the spatial distribution of salamanders in the E.S. George Reserve, and therefore, also be able to gain some idea about their movement to and from the ponds. I hypothesized that I would find that the highest density of salamanders would be within 100m of their breeding ponds. In addition, I thought that the soil moisture in salamander refuges would be somewhat

higher than the soil moisture in areas without salamanders, and that refuges would not be completely rotten to the point of disintegration.

METHODS

In order to ascertain an idea of salamander distribution in the E.S. George Reserve, I began by setting up 100m transects running from the edge of a breeding pond into the surrounding woods. Beginning at the water's edge, I overturned any object within one meter of the transect on either side that would make an appropriate refuge for any of the five salamander species in the reserve. These objects included logs, branches, and bark. I took note of the object and its quality (not rotten, rotting, rotten, and disintegrating), the distance from the pond, the soil moisture underneath the object, and the presence or absence of salamanders. If a salamander was present, I recorded the species, in addition to its length. After very marginal success at finding salamanders within a 100-meter radius of the ponds, I increased the transects to 200m in length.

The experiment was completed entirely between 8:00 and 16:30 on Oct. 12, 2008 in the E.S. George Reserve in Michigan. I set up transects at three different ponds on the reserve: two 100-meter transects at Crescent Pond, one 100-meter transect and one 200-meter transect at West Woods Big Pond, and two 200-meter transects at Southwest Woods Pond.

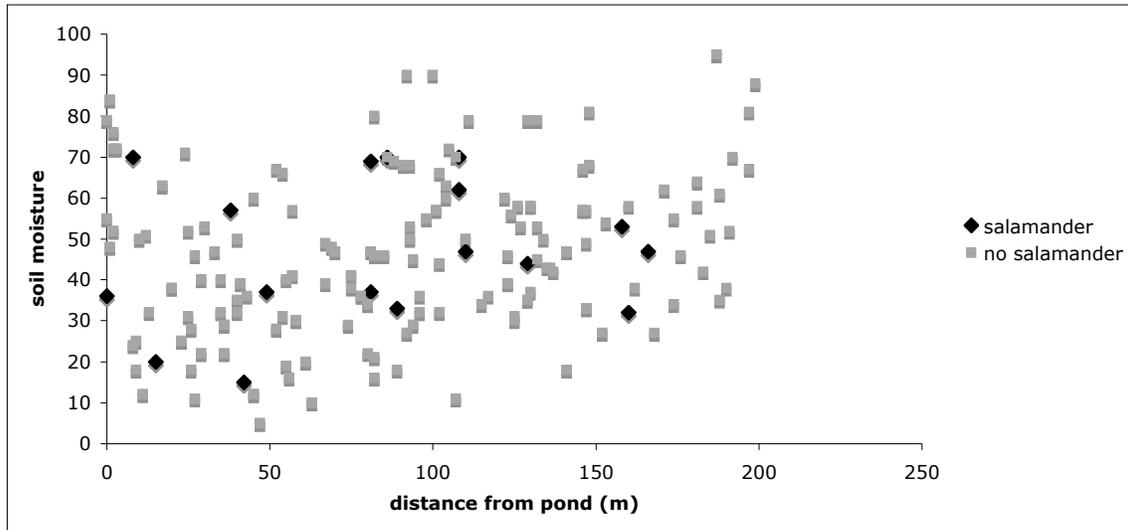
In analyzing the data, I used a linear regression to determine the significance of salamander length and distance from pond. Additionally, I used an unpaired t-test to compare soil moisture at sites with salamanders and soil moisture at sites without salamanders.

RESULTS

18 salamanders of four different species were found during this study, including thirteen *Ambystoma laterale*, two *Notophthalmus viridescens*, two *Hemidactylium scutatum*, and one *Ambystoma maculatum*. The greatest density of salamanders was found at Southwest Woods Pond with an average density of .015 salamanders/m², compared with .0065 salamanders/m² at West Woods Big Pond and .005 salamanders/m² at Crescent Pond. The greatest diversity was also found at the Southwest Woods Pond, with four different salamander species. Only two species were found at the other ponds.

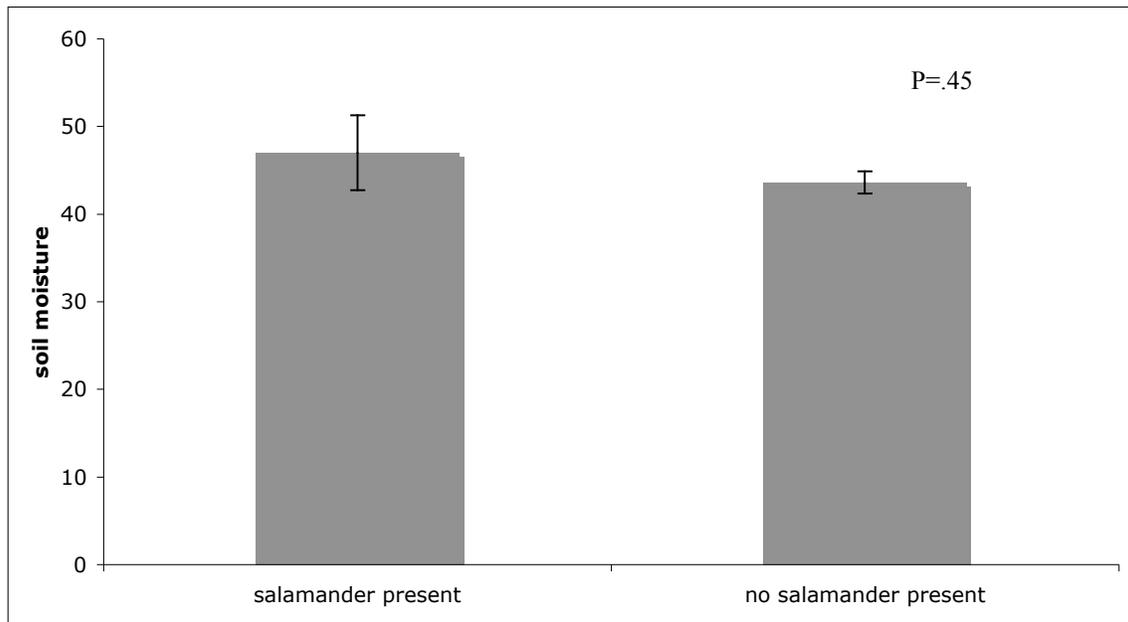
Soil moisture remained relatively constant as the distance from the ponds increased, increasing by only .072/m at sites without salamanders, and .052/m at sites with salamanders (fig. 1).

Fig. 1. The distance (m) from breeding pond and the soil moisture for sites with and without salamanders.



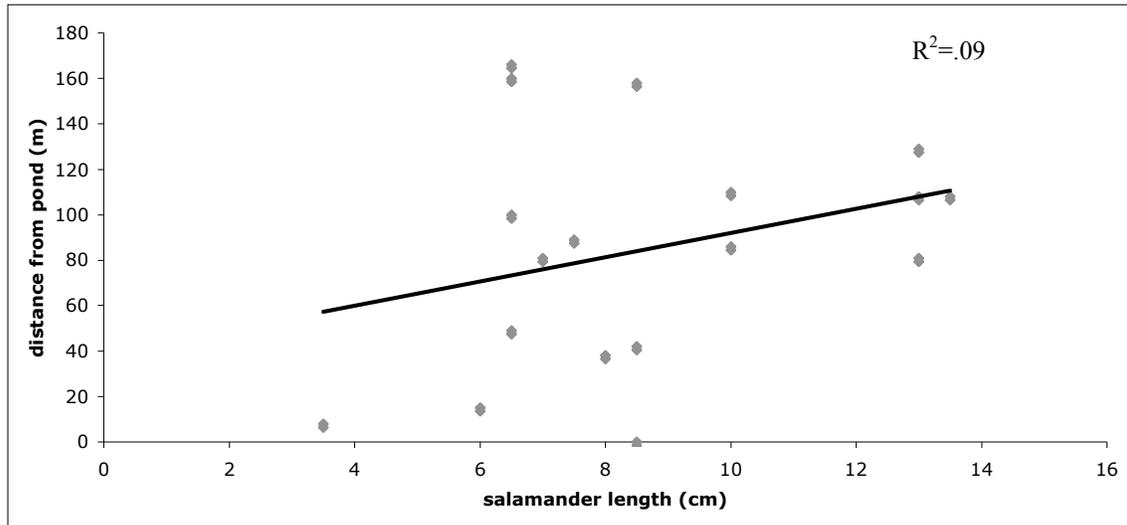
The average soil moisture for sites with salamanders was 7.8% greater than the average soil moisture of sites without salamanders (fig. 2).

Fig. 2. Average soil moisture at sites where salamanders were found compared to sites where no salamanders were found.



Salamander length increased with distance from the pond. On average, with every centimeter added to salamander body length, the distance from pond increased by 5.36m (fig. 3).

Fig. 3. The correlation between salamander length (cm) and distance from pond (m).



DISCUSSION

Due to the close proximity of all the ponds in the reserve, it was impossible to determine where individual salamanders came from, and therefore, the distance they traveled from their breeding and natal ponds. However, one salamander gives us a hint as to the distance it may have traveled: the larval form of *N. viridescens* was not found in the Southwest Woods Pond from 2005-2007, but one *N. viridescens* nymph was found along the edge of the pond during this study. Barring the event that this species has colonized the Southwest Woods Pond in the last year, we can make some deductions based on its location. The two nearest wetlands to the Southwest Woods Pond are the Southwest Woods Swamp and Fishhook Marsh, and larval *N. viridescens* have been found in both. From the Southwest Woods Swamp, the *N. viridescens* would have had to travel at the very least, around 180m, and from Fishhook Marsh, at least 240m. Either of these distances would support the known radius of 290m from breeding ponds that is needed by amphibians.

Salamanders may have a preference for sites with slightly above average soil moisture, which would support my hypothesis. These results were not statistically significant, but an increased sample size might make a stronger correlation. Very little is known about the preferred soil moisture of salamanders, so further study could be very useful in determining the type of habitat and refuges required for adult salamanders.

The strongest correlation I found in this study was between salamander length and distance from the pond. Although my results were not statistically significant, the trend is fairly strong and is supported by other studies, which found that newly metamorphosed amphibians tend to travel less than half the distance traveled by adult salamanders. This is most likely due to increased predation on younger animals, as well as increased susceptibility to desiccation due to their small body size (Semlitsch, 2008).

The fact that salamanders appeared to be clumped around the Southwest Woods Pond could either be an indicator of preferred habitat in that area or of a preference for living in close proximity. Our results are supported by other studies showing that

amphibians often exhibit a clumped distribution (Redmond, 1991). However, other studies have shown that there is a definite limit to the number of amphibians that can live in close proximity (Patrick, D.A., 2008), so clearly more research is needed to determine exactly where that balance is. A detailed analysis of soil pH, pond and topographical characteristics, available resources and soil moisture may prove helpful in understanding this clumped distribution.

Although, due to the brief nature of this study, it was impossible to come to any certain conclusions about salamander movement and distribution, many of my findings, however weak the trends, are supported by previous studies. With further study, these results may be useful in determining the amount of land and quality or type of land and resources that are needed to support a viable salamander population. This knowledge will help as conservationists worldwide work to preserve remaining small and fragile amphibian populations.

ACKNOWLEDGEMENTS

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RE-EXAMINATION OF HELMINTH PARASITES IN THE GEORGE RESERVE
WHITE-TAILED DEER (*Odocoileus virginianus borealis*)

TAMATHA PATTERSON

ABSTRACT

The helminth parasite load of deer on the George Reserve, Michigan, was re-examined 49 years after the first evaluation to determine if there had been a change in the incidence of infected deer and in the prevalence of any species of parasites. The study found a significantly higher proportion of deer with parasitic infection and a significantly higher proportion of deer with multiple infections. The deer lungworm, a *Trichostrongylus* sp., the most prevalent parasite in the deer in 1959, increased significantly by 2008, while others did not show detectable differences.

INTRODUCTION

The E.S. George Reserve white-tailed deer herd is one of the most studied, privately held populations and has been considered one of the most important wildlife resources in Michigan (Jenkins, 1964). In addition to population growth and management studies, research areas include deer social behavior, food preferences and habitat selection, and gender-based resource partitioning (McCullough, 1977, 1983, 1985; McCullough et al., 1989; Coblenz, 1970; O'Roke, 1948; Jenkins, 1964). Few, however, have considered host-parasite relationships in this population as a component of herd management. In 1941, a study on the effects of lungworms in deer was completed (Goble, 1941). In 1959, a parasite survey found 6 helminth parasites among 47 individuals on the George Reserve (Swanson, 1959). Similar studies of free-ranging white-tailed deer found 13 species of nematodes in 5 individuals from Kentucky, 12 nematode species in 6 deer from St. Vincent Island, Florida, and 9 species in 5 deer from Maryland and 8 species in 5 deer from Virginia (Davidson, 1985, 1987, 1983). These studies, however, did not consider the prevalence of parasite over time. The isolation of the George Reserve herd also restricted the parasite population and provided such an opportunity to investigate the host-parasite relationship through time. This study re-evaluated the intestinal parasite load of white-tailed deer on the George Reserve and compared the results with the historic evaluation. Due to the unique history of the herd, the prevalence of parasites was expected to have increased over the past 49 years; but as a result of natural selection, deer are expected to carry low parasitic burdens.

History of the E.S. George Reserve Deer Herd

In March of 1929, Colonel Edwin S. George purchased two bucks and four does, presumed pregnant, from Cleveland Cliffs Iron Co in Grand Island, Michigan, and released the group onto his private game reserve. He purchased and enclosed the approximately 1146 acres of abandoned farmland, forest, and wetlands in 1927. The reserve was donated to the University of Michigan in 1930. By the fall of 1933, deer grazing had notably damaged the reserve's

vegetation and on December 9, 1933, the first herd census recorded 162 deer (Hickie, 1937). Later, a reconstructed population size calculated a herd size of 222 deer in 1933 (McCullough, 1979). From 1934 to 1938, management strategies were experimental and the population fluctuated dramatically. From 1938 to 1942, the management strategy aimed to maintain the over-winter herd at 50-60 individuals and the fluctuations in size decreased. From 1942 to 1963, the herd was generally maintained between 50 and 120 individuals. Overall, between 1933 and 1963, 1229 deer were removed from the reserve during culling drives (Jenkins, 1964). Some early escapees of the culls, 24 deer were documented to have jumped the fence during the census drives from 1933 to 1963, are believed to be foundation animals of the area's wild population (Jenkins, 1964). In 1963, the 7.5 foot fence was replaced with an 11.5 foot fence which effectively isolated the herd. From 1966 to 1974, the herd was the subject of a population growth experiment. Deer were heavily culled to reduce the number to an estimated 10 animals and no harvests occurred during the following 5 years. In 1980, 220 deer were censused (McCullough, 1982). Based on McCullough's research, the carry capacity of George reserve was estimated at 174 deer (McCullough, 1979) and until the mid-1990's, annual harvests of 40-50 animals were maintaining this level (McCullough, 1979). From 1997 to 2000, no harvests were allowed due to university liability issues. In 2000, a contractor was hired to remove 101 deer and again no harvests were allowed until 2005. A private contractor now manages the herd and culls to maintain approximately 120 deer (Malcolm, 2008).

METHODS

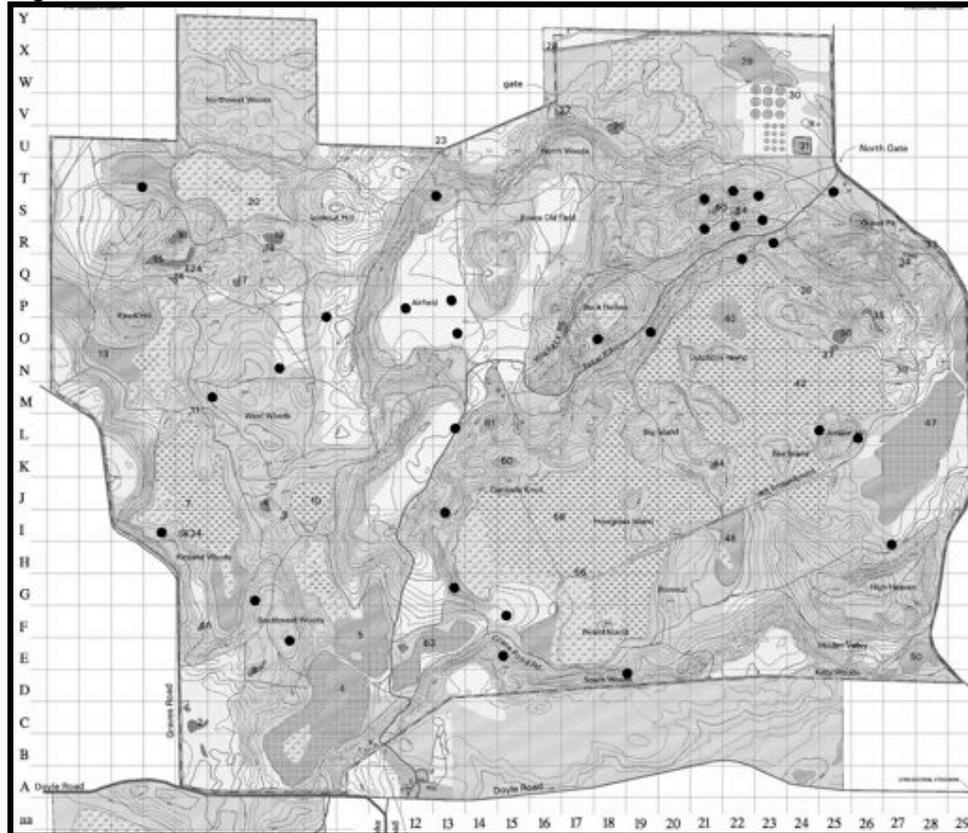
The Swanson study collected deer viscera during the December culling events of 1958-59. The organs were frozen and stored until they could be examined. The organs were then thawed and dissected in search for adult stage parasites. Adult nematodes were preserved in 70% isopropyl alcohol and cestodes and trematodes were fixed in a mixture of alcohol, formalin and acetic acid. The parasites were stained with Semichon's acetic carmine, mounted and identified microscopically.

For this study, deer feces were randomly collected on Saturdays and Sundays from September 20 to October 12, 2008, between 9am and 2pm. Deer trails and openings were visually scanned for fresh deer pellets at locations throughout the reserve (figure 1). This method does allow for the possibility of re-collecting feces from the same individual. As a result, the pattern and timing of collection was considered. Deer on the reserve are known to live alone or in small groups of same sex individuals such as a doe and her fawn. The female territories have a 60% overlap and males have a 44% overlap during this time of the year (McCullough, 1989). Thus, samples were collected in an area only during a single day's search. A similar method of intensive spring pellet surveys has been used to estimate population size as well (Jenkins, 1964). The condition of each was assessed. Those with little to no moisture, apparent decomposition, and contaminated with arthropods or worms were not sampled. For those that were still moist, firm, and free of arthropods, about 2 grams (4-5 fecal pellets) from the top and center were collected and preserved in sterile test tubes containing 1.5ml of 10% formalin and stored at room temperature (Foreyt, 1986).

In the laboratory, the standard floatation method was employed (Pratt, 1992). A commercially available sodium nitrate solution (Fecasol, Vetoquinol USA, Inc, Buena, NJ 08310) was used.

The slides were scanned at 100X and ova were measured and identified to genus at 400X (Foreyt, 2001, Olsen 1962). The number of ova per parasite for each deer was quantified based on standard veterinary practices (Pratt, 1992). Data was compared statistically to the historic infection rates by genus with binomial comparative contingency tables based on the chi-square distribution (Zar, 1999).

Figure 1: Locations of fecal collections



RESULTS

In his 1959 study, Swanson identified six species of parasite and found 34.0% (16/47) of the reserve deer were infected with at least one parasite and 17.0% (8/47) were infected with multiple parasites. By parasite species, infection rates were 2.1% (1/47) with *Trichuris ovis* (Trichuroidea, Trichuridae); 2.1% (1/47) with *Moniezia expansa* (Cyclophyllidea, Anoplocephalidae); 6.4% (3/47) with *Zygodontia schultzei* (Digenea); 12.8% infected with *Nematodirus filicollis* (Trichostrongyloidea, Heligmosomatidae); 19.1% (9/47) with *Oesophagostomum venulosum* (Strongyloidea, Trichonematidae); and 32.1% (17/53) infected with *Leptostromylus alpanae* (Trichostrongyloidea, Dictyocaulidae) (Swanson, 1959) (table 1).

This study found that 83.9% (26/31) of reserve deer were infected with at least one parasite and 41.9% (13/31) were infected with multiple parasites. By parasite species, infection rates were 3.2% (1/31) with *Trichuris* sp. (Trichuroidea); 70% (22/31) with *Trichostrongylus* sp. (Trichostrongyloidea); 16.1% (5/31) with *Strongyloides* sp. (Strongyloidea); 3.2% (1/31) with

Ascarid sp. (Ascaridoidea); 12.9% (4/31) with *Capillaria* sp. (Trichuroidea); 9.8% (3/31) with *Eimeria* sp. (Sarcostomastigophora) (table 1). The parasitic burden for all infected deer was determined to be <1 per low power field (lpf).

Table 1: Number and percent(%) of parasitized deer in 1959 and 2008 and comparative p-values (Bold indicates statistical significance)

	1959(Swanson)	2008(Patterson)	p-value
Number of samples	47	31	
Number infected (%)	16(34.0)	26 (83.9)	p<0.001
Number with multiple infections (%)	8(17.0)	13(41.9)	p<0.001
Number infected with <i>Trichuris</i> sp. (%)	1(2.1)	1(3.2)	p>0.50
Number infected with <i>Trichostrongylus</i> sp. (%)	17/53(32.1)	22(70.0)	p<0.005
Number infected with <i>Nematodirus</i> sp. (%)	6(12.8)	0(0)	p>0.10
Number infected with <i>Strongyloides</i> sp. (%)	9(19.1)	5(16.1)	p>0.95
Number infected with <i>Moniezia</i> sp. (%)	1(2.1)	0(0)	p>0.50
Number infected with <i>Trematoda</i> sp. (%)	3(6.4)	0(0)	p>0.25
Number infected with <i>Ascarid</i> sp. (%)	0(0)	1(3.2)	p>0.50
Number infected with <i>Capillaria</i> sp. (%)	0(0)	4(12.9)	p>0.50
Number infected with <i>Eimeria</i> sp. (%)*	--	3(9.8)	--

**Eimeria* is a parasitic protozoan (Sarcostomastigophora; Apicomplexa) and was not included in the analysis

DISCUSSION

The prevalence of parasites in the George Reserve herd increased significantly and substantially over the past 49 years. The founder effect, bottlenecking and isolation decrease the genetic diversity of a species and reduce its resistance to disease. The Reserve deer have been affected by all of these (O'Roke, 1948; McCullough, 1982b, 1983, 1984). Further, deer are species in which their numbers are primarily determined by density dependent relationships (McCullough, 1979; Keyser, 2005). The deer population can rebound quickly and rapidly become overcrowded without intervention (Jenkins 1964, McCullough, 1979). Crowding is known to increase parasite prevalence in deer as a result of chronic exposure (Van Cleaver, 1937). Even as early as 1941, there was some evidence that the herd was experiencing some of these consequences. The *L. alpanae* infection rate for the reserve deer was 55% and the rate within the state was 51% (Goble, 1941).

The helminth parasitic infection rate in deer is related to the lifecycle of the parasites. Roundworms, phylum Nematelminthes, have direct or indirect life cycles. Flatworms, phylum Platyhemintnes, require an intermediate host during its life cycle. Trematode flatworms utilize snails as intermediate hosts while other flatworms may use mites or other arthropods. Therefore, parasites like trichostrongylus sp. which has a direct life cycle in which the host injects the third stage larva with forage can propagate and infect the host organism more expeditiously than one with an indirect lifecycle (Olsen, 1962). Even as early as 1941, there was some evidence that the herd was experiencing some of these consequences. The *L. alpanae* infection rate for the reserve deer was 55% and the rate within the state was 51%

(Goble, 1941). The parasitic lifecycle is affected by climate and moisture as well. Generally cooler, dryer regions have fewer nematodes; while warmer, humid areas have a greater occurrence (Davidson, 1981). The George Reserve land cover is nearly 25% wetlands (Swanson, 1959, McCullough, 1979). Thus, the significant increase in the *trichostrongylus* sp. parasite in the herd is understandable. Interestingly, Swanson found a 32.1% infection rate for this parasite in 1959. The methods for recovering this species consisted of the evaluation of a single cubic inch of lung tissue. It is possible that the portion examined did not contain the parasite, despite being present in the animal.

Additionally, the parasitic burden in all infected deer was low. Young animals including fawns, are more susceptible to diseases than adults due to their naïve immune systems. The 1959 study found that yearling deer carried a notably higher parasitic burden than adult deer (Swanson, 1959). Over time, natural selection would favor deer with a proximate immune response that reacts to parasitic infection and reduces the burden in the absence of other selection pressures. Fawns that cannot thrive within the highly competitive herd will perish during their first winter.

This is the case on the reserve; hunting is the only traumatic mortality operating on the population (McCullough, 1984).

The difference between the methods of this study and the 1959 study introduced discrepancy and potential error into this analysis. The overall parasitism rate is unaffected, however. A parasite is either found and the animal is positive or none are found and the animal is considered negative. Additionally, comparisons were facilitated by comparing genus rather than species. This study methodology was not capable of identifying parasites to species, but only to genera. To accommodate comparisons, the 1959 study species parasites were regarded by their higher genus classification.

Management Implications

The George Reserve deer herd has been instrumental in developing deer management strategies. The herd has proved that a herd maintained below carry capacity can be equally productive to one maintained at higher densities. The difference is in the survivorship of the fawns (Jenkins, 1964). Lower densities also allow for more food resources per animal and increase body growth and size in individuals (McCullough, 1979). This study highlights additional benefits of this management strategy. The large herd has had a dramatic increase in parasitism as a result of chronic exposure and heavy intraspecific competition. At lower densities, the exposure risk to parasites will be reduced, food resources will better replenish, and the health of the deer will improve. For the hunters, the harvested animals will provide a greater return for their effort.

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DO TREMATODES AFFECT TADPOLE ABUNDANCE?

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ABSTRACT

Amphibians are known as an environmental quality indicator species and parasite-host interactions have been suggested as a measure of environmental change. This study utilized eleven experimental ponds and their resident populations of *Rana* frog species and trematode parasite, *Echinostomatoidea*, host snail species, *P. trivolvis*, to study the relationship between the resident tadpoles, snail species, and trematode parasite. The results indicate that there was a negative correlation between tadpole success and percent of infected snail hosts.

INTRODUCTION

Amphibians have been declining worldwide. There are 6,300 known amphibian species globally. In the last two decades, 168 of these have gone extinct and 32% of amphibians are listed as threatened or endangered. Further, 43% of amphibian populations are declining (Collins and Storer, 2003). The exact cause is still unknown, but it is highly likely that there are multiple factors influencing this phenomenon. Certainly habitat loss, fragmentation, and alterations are crucial components. Pollution and eutrophication have altered natural cycles and water chemistry to which amphibians are particularly sensitive. Introduced species and diseases, climate change, and exploitation are considerations as well. Cyrtid fungus, released from the African clawed frog in the Americas has been documented as decimating frog populations as it expands southward (Fellers et al. 2001 & Young et al. 2001).

A comprehensive understanding of the frog lifecycle and the effects of environmental variations is important to reverse the downward spiral of decline for these animals. Studies have shown that amphibians are especially sensitive to changes in their environment. Human alterations have shown to have a negative impact on amphibian species (Skelly et al, 2005). Amphibian-parasite interactions have revealed changing dynamics and have been suggested as a potential indicator of environmental conditions (Johnson and Chase, 2004 & Grenfell, 1995). Multiple factors are likely working synergistically in this regard. As notably environmentally sensitive species, amphibians act as the ‘canary in the coal mine’ of global health and knowledge of their biotic and abiotic interactions will be critical for the long term monitoring of global ecosystem health.

Tadpole success is reduced as a result of trematodiasis (Holland et al, 2006). Since *P. trivolvis* is known to carry the echinostome parasite of tadpoles, tadpole abundance should be inversely proportional to *P. trivolvis* abundance. To test this hypothesis, 11 experimental ponds were surveyed for *Rana clamitans*, green frog, and *Rana catesbeiana*, bull frog, tadpoles as well as for *P. trivolvis*.

MATERIALS AND METHODS

Study Organisms

Rana clamitans, Green Frog

The green frog is native species and is found in a wide variety of aquatic habitats including swamps, marshes, ponds, lakes, and streams. Green frogs breed in the late spring and eggs are laid on emergent vegetation. Tadpoles require from 3 to 22 months to begin metamorphosis into adults, which means that they are capable of hibernation and overwintering. Tadpoles were a focus of this study due to the role played in the life cycle of the trematode (Harding, 1997).

Rana catesbeiana, Bull Frog

The bull frog is another native species. Bull frogs prefer warm, shallow waters and are found living in close proximity to ponds, lakes, streams, and bogs. Females deposit thousands of eggs in calm, warm water to be fertilized by males. Metamorphosis is slow for bull frogs and can take between one and three years, necessitating hibernation and overwintering in higher latitudes. The bull frog tadpoles were a focus of this study due to the role played in the life cycle of the trematode.

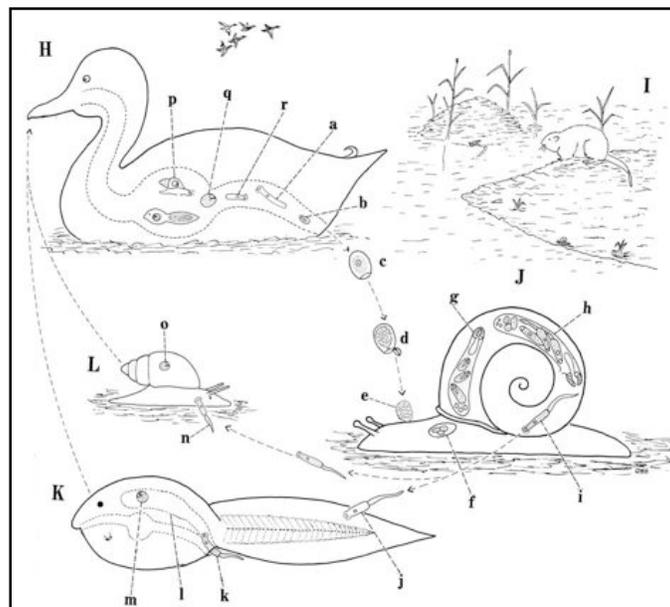
Planorbella trivolvis, Species of “Ram’s Horn” Freshwater Snail

Planorbella trivolvis is a species of freshwater, air breathing snail native to North America. It prefers habitats with floating vegetation. This species of snail plays host to a trematode species that can infect multiple tadpole species.

Echinostome trematodes

Echinostomida, an order of digenic trematodes, and suborder *Echinostomata*, and Superfamily *Echinostomatoidea*, utilize primarily *Planorbella trivolvis*, a species of ram’s horn aquatic snail, as its first intermediate host. The life cycle is indirect. The ova develop to a larval stage that infects *P. trivolvis*. A second intermediate host, typically tadpoles or silurid fish, is required. The cercaria, the free swimming form leaving the snail, infects the tadpole or fish by entering through the cloaca and migrating thru the ureters to encyst in the kidneys. The parasite will also infect other mollusks as secondary hosts through skin penetration. The definitive host, here a waterfowl or small mammal like the musk rat, is infected when it consumes the affected intermediate host. The organism grows to become a sexually reproductive adult in the ileum. (Davis, 2005)

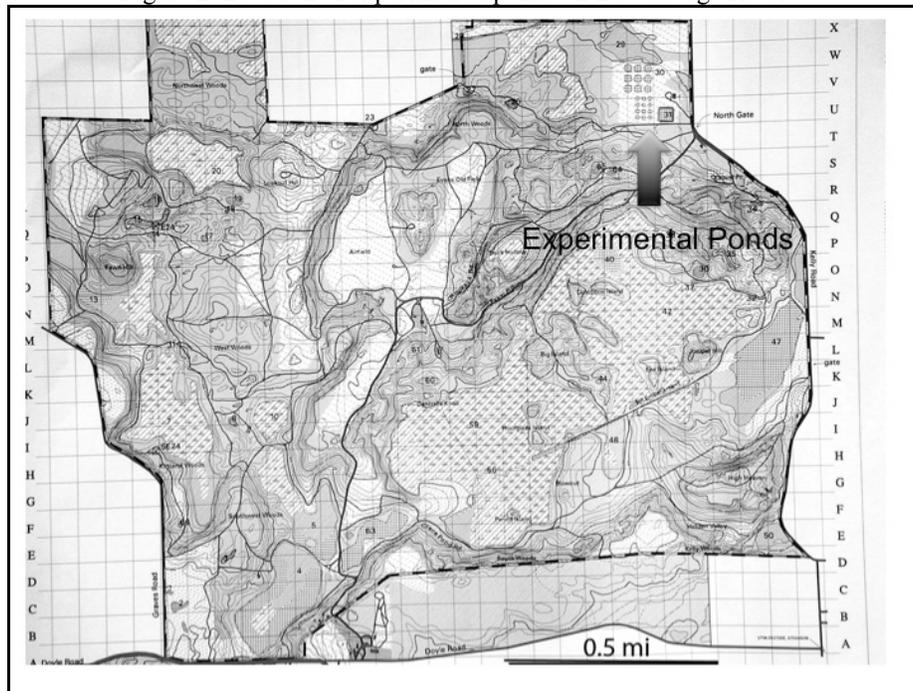
Figure 1: Life cycle of typical *Echinostomatoidea* species (Olsen, 1986)



Study Site and Sampling Methods

The 11 (12 minus the one pond over-run by an invasive Phragmites) experimental ponds at the E. S. George Reserve were utilized for this field problem. The ponds were constructed to be 15 meters in diameter and 1 meter deep.

Figure 2: Location of experimental ponds on E.S. George Reserve



The E.S. George Reserve, a University of Michigan property located approximately 25 miles northwest of Ann Arbor, Michigan, has 11 small, man-made experimental ponds that support a population of *Rana catesbeiana* (American bullfrog) and *Rana clamitans* (green frog) as well as populations of snails including *Planorbella trivolvis*, *Helisoma campanulata*, and *Phyla* species. Since the environmental variations are limited, these ponds make an ideal study system to evaluate the effects of trematode parasitism on tadpole success. Each pond was surveyed between 8am and 11am on an overcast day in which no breaks in the cloud cover was observed. Measurements included water temperature, pond depth, dissolved oxygen content, conductivity, percent vegetative cover, and vegetative species richness and abundance. Once the pond data were collected, two net-wielding group members at a time collected tadpole and snail specimens for ten-minute periods from each pond. All specimens captured were placed in cups and identified after the ten-minute period had expired, allowing for continuous data collection. Tadpole and snail abundance were noted for each pond and the snail specimens, *P. trivolvis*, were brought back to the lab to measure the percent of parasitism in the population as a whole.

To determine whether or not the snails were infected by *Echinostomata* or other parasites, the snails were placed in individual containers with approximately 60ml of de-chlorinated water and grouped by pond. Each snail was placed under heat lamps for a minimum of one hour to promote the exit of parasites from their hosts. The water from the snails' cups in which initial viewing yielded suspended particles were examined under a microscope to confirm the presence of trematode cercaria.

Statistical Analysis

The data was imported in SPSS 16 statistical package. Descriptive statistics were used to determine the generality of the pond metrics. Simple linear regression was employed to characterize the relationships between species.

RESULTS

The measured pond parameters--water temperature, dissolved oxygen, conductivity, and depth--showed little variation among the ponds (table 1). The vegetative parameters--total plant species and estimated percent cover--showed greater variation with some ponds having some unique species (table 1 & appendix A). The number of tadpoles and snails showed the greatest variation. Only 4 ponds contained *P. trivolvis*, 6 ponds contained *H. campanulata*, 5 ponds contained *Phya* sp. snails and only one pond contained both *P. trivolvis* and *H. campanulata*. *Phya* sp. snails were most often found with *H. campanulata* or alone. One pond did not contain any snails (table 2).

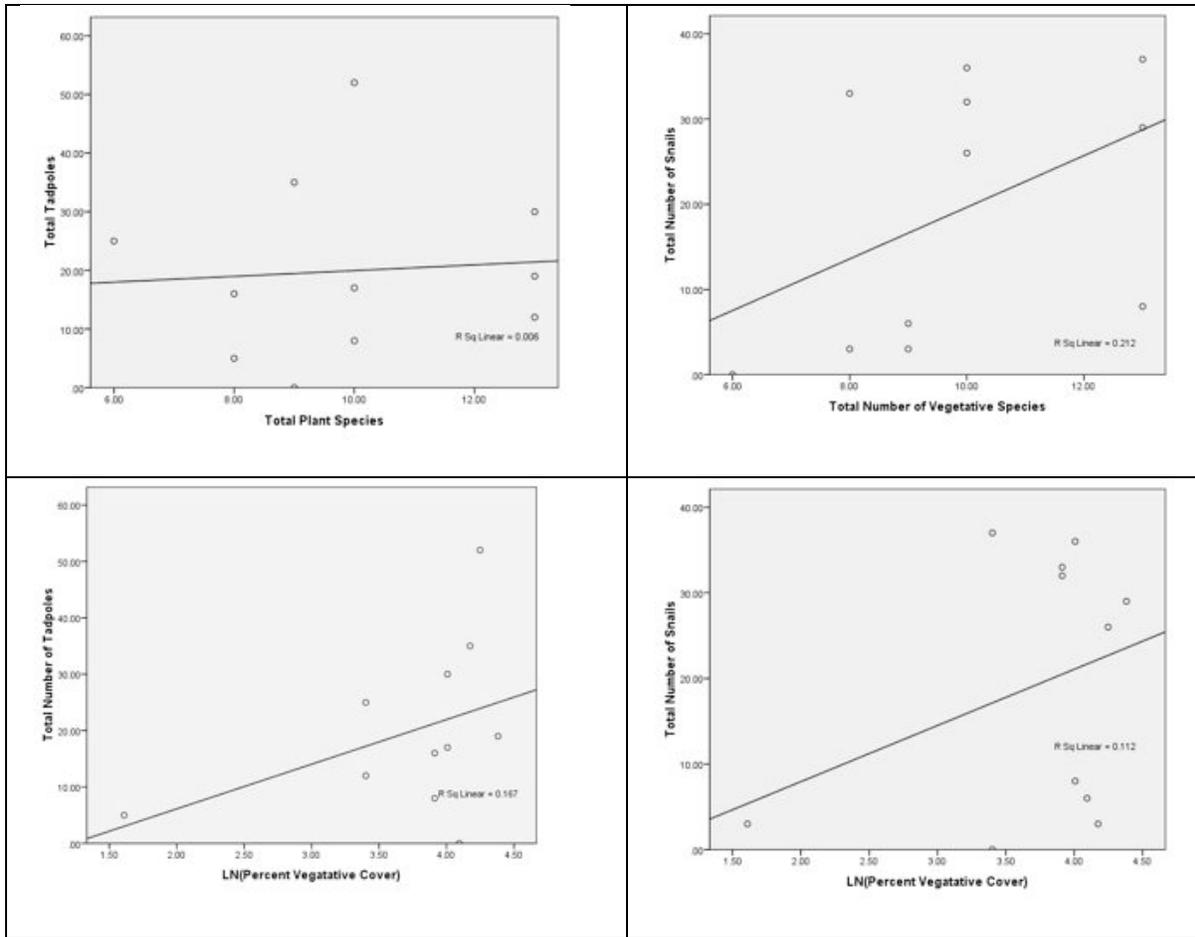
Table 1: Pond metrics						
	Water Temp.(C)	Dissolved O2 (mg/L)	Depth (cm.)	Conductivity (microS)	Cover (est.%)	Total Plant Species
Mean:	16.32	8.7	97.27	292.18	50	9.66
Standard Deviation:	0.66	0.18	9.62	21.25	21.21	2.3
Variance:	0.44	0.03	92.62	451.56	450	5.29

Table 2: Snails and trematode metrics						
	<i>P. trivolvis</i>	<i>H. campanulata</i>	<i>Phya</i> sp.	Total snails	trematode infection in <i>P. trivolvis</i>	% infected <i>P. trivolvis</i>
Mean:	9.64	8.64	1.09	19.36	5	17.66
Standard Deviation:	15.27	12.34	1.45	15.13	3.74	7.37
variance:	233.25	152.25	2.09	228.85	14	54.24

Regression analysis yielded little relationship between tadpole abundance and water temperature ($R^2=0.212$), dissolved oxygen ($R^2=0.054$), and conductivity ($R^2=0.116$). Tadpoles showed some preference for shallower ponds ($R=0.288$). Relationships were minimal between snail abundance and water temperature ($R^2=0.174$), dissolved oxygen ($R^2=0.054$), depth ($R^2=0.073$), and conductivity ($R^2=0.194$).

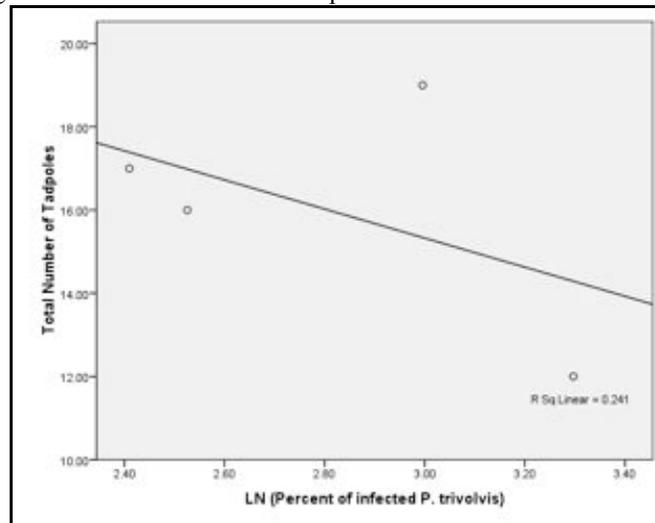
Tadpoles showed no preferences with vegetative species diversity ($R^2=0.006$), but some preference for cover ($R=0.167$). Snails showed more preference for species diversity ($R^2=0.212$) and a slight preference for cover ($R^2=0.112$) (figure 3).

Figure 3: graphs of relationships between tadpoles and vegetation (left) and snails and vegetation (right)



There was no direct correlation between total tadpole abundance and total snail abundance ($R^2=0.004$) nor between total tadpole abundance and *P. trivolvis* presence ($R^2=0.039$). There was a moderately declining relationship between total tadpole abundance and percent of infected *P. trivolvis* ($R^2=0.241$) (figure 4).

Figure 4: Correlation of total tadpoles & Percent infected *P. trivolvis*



DISCUSSION

Although our sample size was small, the results did provide some support for our hypothesis that tadpole abundance is negatively affected by the abundance of *P. trivolvis* snail, but the relationship is indirect. There is no preference or aversion to tadpole and snail co-existence in a given pond. This is important because any such condition may mask the relationship between the tadpoles and the trematode. In all four ponds containing *P. trivolvis*, trematode infection was detected. Tadpoles were averse to living with infected *P. trivolvis*--one of the studies strongest correlations.

The data seems to be influenced in part, by one pond which had little vegetative cover and abundant tadpoles. This pond was suspected of being previously treated with herbicide due to the observation of an abnormally formed, four-headed flower on one of the sparse cattails in the pond. The herbicide which may have additionally killed the snails and/or lack of aquatic plants which are a necessary food source for snails explains the absence of snails in this pond. Further, shallower ponds are more conducive for snails. Sunlight reaches a greater proportion of the bottom area and as result the shallower ponds are more productive and plant species diverse. Further investigations into snail plant preferences may yield some direct correlations that could be useful in predicting likelihoods of specific snail species presence in different ponds. More detailed environmental metrics like pH, nutrient (nitrogen, carbon, and phosphorous), and chemical (herbicide) levels may be useful to deciphering the variability in diversity.

Different methodologies may provide better correlations. Certainly, the efficiency of specimen collection changed in each pond with different co-investigators and a learning curve. A capture-mark-recapture methodology of estimating total snail and tadpole populations may have produced better population parameters. Additionally, potentially, two different species of trematode cercariae were observed to have emerged from the snails. One appeared to have a beige tint while the other was translucent. Preserving the cercariae and viewing them under a more powerful microscope, as well as staining, may have clarified this issue. Likewise, trematodiasis in tadpoles could have been evaluated if individuals were sacrificed and their kidneys could be dissected from the body and examined. A more in depth analysis could be achieved if an uninfected pond could be isolated and employed as a control pond, then tadpole mortality due to trematode infection verses other forms of mortality may be determined. All parameters could be monitored annually to document the changes in infection and effects on tadpole success.

Although not documented during data collection, three ponds had evidence of muskrat dwellings. In retrospect this would have been important to note since muskrats, in addition to waterfowl, act as definitive hosts for echinostomes, *Echinostoma revolutum* in particular. It is more likely that the muskrat transported the trematode into the ponds. Waterfowl, likely, do not find the small experimental ponds preferable to the larger nearby experimental pond or to the reserve's ample wetlands. Since the musk rats can access all of the ponds, each has potentially been exposed to the parasite. This study did not include this variable but further studies should include a comparison of muskrat residential ponds and non-residential ponds as well as muskrat trematode infection rates within the reserve.

These results illustrate several important points. First, parasites do indeed have some affect on amphibian success. Thus, any environmental change that benefits parasites harms amphibians and so forth up through the food chain. For example, increase nitrification results in increased primary production; this vegetative production may result in an increased snail population which increases the likeliness that a hatched trematode larva, miracidia, finds a suitable snail host. With more infected snails come more cercariae present in a pond available to infect and reduce the success of young amphibians. These detrimental affects could spread throughout the ecosystem. Secondly, there are obviously more factors involved in tadpole success than simply trematode infection. These factors should be sought and fully investigated in order to understand the dynamics and sensitivities of the environmental change.

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INVESTIGATION OF HISTORICAL AGRARIAN LAND USE WITHIN A TEMPERATE NORTHERN HARDWOOD FOREST

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ABSTRACT

Historical agrarian land use potentially caused notable long term effects to woodlots. Field investigation was conducted to observe evidence of historic livestock grazing and other agricultural practices at the E.S. George Reserve within an 18 ha temperate northern hardwood forest plot locally known as Big Woods Field. Investigators utilized metal detectors and visual observation to find historic barbed wire fencing and other artifacts such as an early 20th century shotgun shell. One observable barbed wire fence line was mapped out and georeferenced with an existing data set identifying all woody species within the Big Woods plot greater than 10 cm girth at breast height (GBH). Statistical comparisons were made to determine any difference in forest community species composition and GBH inside and outside of the fence line. The georeferenced fence line was overlain on historic plat maps of the area in an effort to correlate the fence location with any historic property boundaries.

INTRODUCTION

Disturbances affect the formation of landforms and the function of ecosystems. The greatest transformative disturbance of southeast Michigan in recent geologic history was the Wisconsinan Glaciation, which receded some 10,000 years ago (Barnes et al., 1998). As the glaciers receded, melt waters cut river valleys, wind and animals dispersed seeds helping the forest expand, and lightning sparked fires which have leveled sections of forest and rejuvenated others. Since glacial times, however, no natural force has shaped the landscape of southeast Michigan more than humankind. In order to understand current landforms and ecosystem community characteristics, knowledge of human activities within an area is as important as knowing the glacial history.

The E.S. George Reserve (ESGR), located in southwest Michigan, encompasses moraine and basin landforms on the edge of an interlobate moraine (Scheuller et al., 2008) and includes forest, wetland, and old field ecosystems. While it may be assumed that Native Americans historically used this area, no definitive evidence exists of Native American influence, and such disturbance is not within the purview of this paper considering more recent agrarian history. Prior to the purchase of the ESGR by Colonel Edwin S. George in 1927, the land encompassed approximately twelve farms. Agricultural practices included production of row crops, orchards, and raising livestock. Most agricultural practices declined since around 1900. No significant logging occurred in the wood lots, though they were used for pasture and firewood (Scheuller et

al. 2008). Dominant livestock was presumably sheep, though other livestock may have been reared. What was the effect of livestock browsing on today’s forest? One might postulate that historically browsed areas would have evidence of growth suppression, resulting in smaller (i.e. younger) individuals and/or fewer species.

With very limited knowledge of the extent of agriculture practices within forested portions of the ESGR, only existing physical evidence and historic aerial photography can provide direction for where to search. The Big Woods plot within the ESGR is a heavily researched woodlot, including a mapped inventory of every living woody plant with 10 cm or greater girth at breast height (1.37 m), tagged with a circular aluminum numbered disc, and plotted onto a grid system. Historic aerial photography review identified some patchy canopy cover within Big Woods, and subsequent field investigation resulted in the discovery of degraded barbed wire providing physical evidence of historic agrarian land use. Through broader field investigation utilizing metal detectors to find old barbed wire fencing, attempts were made to map historic barbed wire enclosures and extrapolate effects on current forest plant community composition.

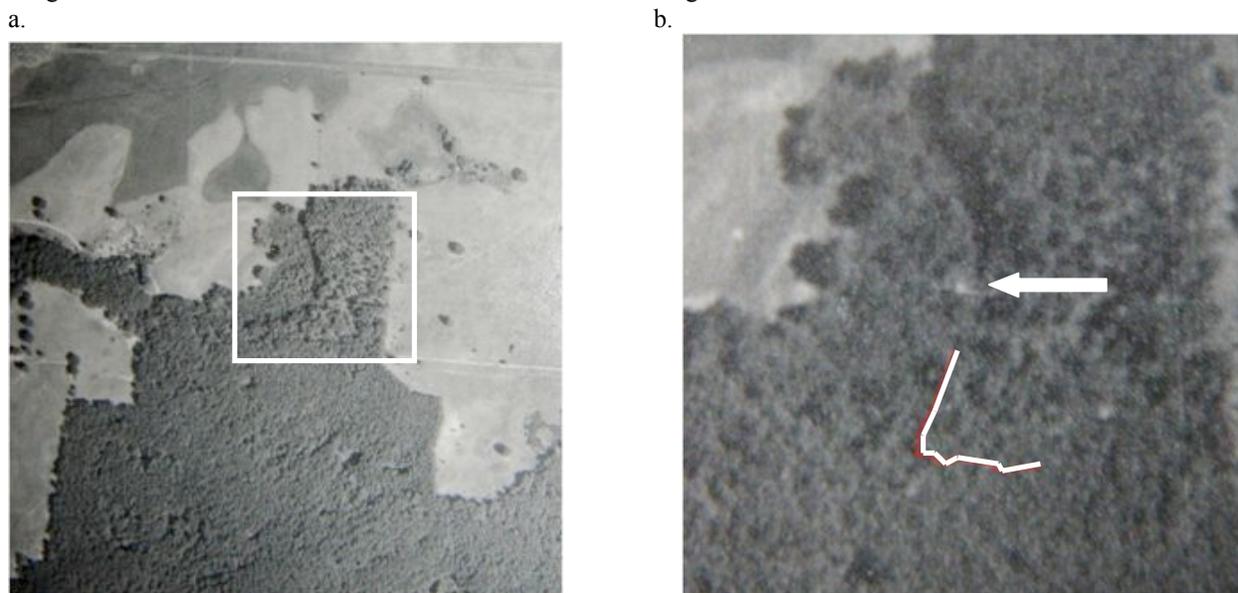
METHODS AND RESULTS

The study was conducted at the E.S. George Reserve, a 464 ha tract of forests, wetlands, and old fields, located within Livingston County, MI. This study area was located within an 18-hectare oak-hickory plot locally referred to as Big Woods (Figure 1).

Figure 1. 18 ha. Big Woods plot with individual hectares labeled with letters ranging from A to R. Each hectare represents a 100 meter by 100 meter plot. Hectares were outline and labeled from previous research at the ESGR. The vertical lines within this plot are generally oriented from the northwest to the southeast.

R	N	F	G	
Q	M	E	H	
P	A	D	I	L
O	B	C	J	K

Figure 2. 1940 aerial photographs (not to scale). a. depicts the initial area of investigation and the patchy tree cover. The northwest corner is a wooded swamp. b. the arrow indicates a white spot, an area of interest; the white line is the georeferenced barbed wire fence line determined from tree tag numbers.



In 2007, Professor John Vandermeer of the University of Michigan, Department of Ecology and Evolutionary Biology (EEB), observed a patchy tree cover pattern within the northwest corner of the Big Woods plot, encompassed within plot G (Fig. 2.a.). Upon field investigation, Vandermeer discovered several lengths of rusted, weathered barbed wire within plot G (Vandermeer, personal communication). In 2008, upon inspection of a separate 1940 aerial, a white spot within the vicinity of the patchy tree pattern provided an area of interest to be investigated (Fig. 2.b. arrow). On October 4, 2008, four groups of investigators searched for additional barbed wire and other signs of historic land use.

Group 1 searched within plot G at known locations of barbed wire, proceeding to carry out a systematic survey of plot G with a White's Prizm III metal detector. Investigators in Group 1 realized that the metal detector required setting adjustment to the highest sensitivity in order to detect the degraded barbed wire. The metal detector was maneuvered side to side just above the ground, and an approximate 8 inch hole was dug wherever a clear signal emerged. When barbed wire was found, the wire was flagged with orange flagging tape, and the distance and azimuth (utilizing a compass) to the nearest tagged oak (*Quercus*) was recorded. Tag numbers from identified oak trees were recorded to document the location of any potential historical findings. The barbed wire location measurements were later plotted with respect to the tree grid, and the fence line was georeferenced to the Big Woods plot and overlain on the 1940 aerial photograph (Fig. 2.b. white line). Two types of barbed wire were found: one was a traditional barbed wire with two twisted wires and intermittent 4-pointed barbs (Fig. 3.a.); the second was a twisted iron ribbon approximately 2.5 cm in width with one side sawtoothed (Fig. 3.b.).

Figure 3. Representative pictures of barbed wire found in plot G. a. is traditional barbed wire; b. is known as Allis Sawtooth – small tooth variety (Brauer, personal communication).



Various tree species within the vicinity of the fence line in plot G were compared using the Big Woods inventory data. The “inside” of the fence line was considered to be the area north of the existing road and northeast of the fence line. “Outside” of the fence line was considered to be the remaining area to the south and west. Several species had significant differences in GBH from one side of the fence line to the other (Table 1). Common shared species on both sides of the fence line include: red maple (*Acer rubrum*), serviceberry (*Amelanchier arborea*), pignut hickory (*Carya glabra*), shagbark hickory (*C. ovata*), witch-hazel (*Hamamelis virginiana*), black cherry (*Prunus serotina*), white oak (*Q. alba*), black oak (*Q. velutina*), and sassafras (*Sassafras albidum*).

Table 1. Comparison of Shared Species GBH Inside and Outside of Fence line. T-tests were used to compare significance (p=0.05). Cells highlighted in gray indicate species with significant difference of GBH inside and outside of the fence as well as the total average GBH comparison for all shared species.

	Total	<i>Acer rubrum</i>	<i>Amelanchier arborea</i>	<i>Carya glabra</i>	<i>Carya ovata</i>	<i>Hamamelis virginiana</i>	<i>Prunus serotina</i>	<i>Quercus alba</i>	<i>Quercus velutina</i>	<i>Sassafras albidum</i>
Mean CBH In	43.7	35.1	14.5	98.8	105.8	10	50.3	122.9	91.8	41.5
Mean CBH Out	30.3	17.6	13.3	101.8	127	11.2	27.3	95.5	122.4	27.5
t	5.19	68.594	0.661	-0.218	-0.344	-1.439	3.789	1.835	-2.867	2.24
P	0.000	0.000	0.514	0.829	0.789	0.155	0.000	0.079	0.005	0.02

Group 2 searched plots A, D, F, G, H, I, M, N, P, Q, and R through a meander search method, looking for evidence of historic land use and using a White’s Prizm II metal detector for buried metal. No systematic route was taken through the plots. The metal detector was calibrated to a low sensitivity setting using a U.S. quarter coin. The metal detector was maneuvered side to side just above the ground, and an approximate 8 to 12 inch hole was dug wherever a clear signal emerged. No barbed wire or other metal was found, but a stone (roughly 40 cm in diameter) with apparent tool markings was found in plot D; the nearest tagged oaks were recorded, but the finding was not georeferenced (Fig. 4.). Professor Catherine Badgely of EEB, a paleoecologist, reviewed pictures of the rock, and stated that it was likely not of Native American origin, but rather from European settlers.

Figure 4. Stone with cut groove around center.

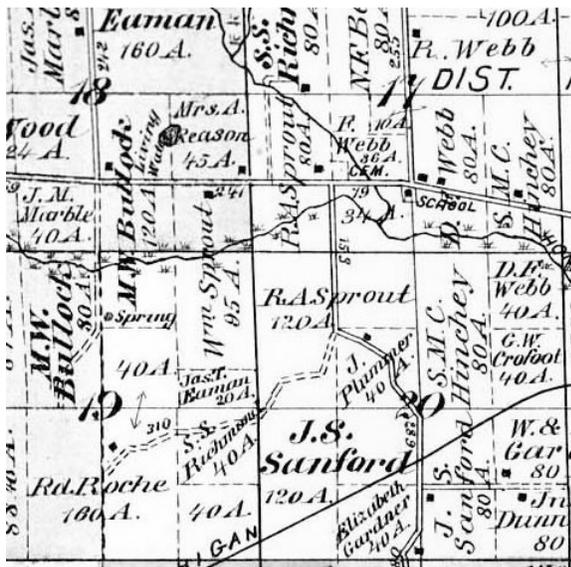


Group 3 searched plot M for a coil of barbed wire described by David Allen, PhD candidate in EEB, and for any other evidence using a White's Prizm III metal detector. The metal detector was calibrated to the highest sensitivity in order to detect the degraded barbed wire. The metal detector was maneuvered just above the ground, and an approximate 8 to 12 inch hole was dug wherever a clear signal emerged. The coil of barbed wire (similar to Fig. 3.a.) was located lying against a tree. The coil was approximately 1 m in diameter and the bundled portion was approximately 30 cm in circumference. The headstamp metal end of a 12 gauge shotgun shell and an unidentifiable piece of rusted metal were also found in the vicinity of the barbed wire coil (both items were removed from the site). Of particular note, the coil of barbed wire was partially buried (assumed to have sunk into the soil over years), and the subterranean portion of the coil had predominantly degraded into rust. Only small portions of the barbed wire could be identified, with the majority disintegrated into the soil. It was observed that the soil in where the barbed wire had formally been was so iron rich (in the form of rust), that the metal detector produced a clear signal. To test this reaction to rust rich soil, handfuls of the rust rich soil was transported meters away to an area that had previously produce no signal. When tested, the transported handfuls of rust rich soil produced clear signals from the metal detector. It is possible (for all groups) that false positives—clear signals without any metal—may not have been false but were rust rich soil from degraded iron.

Group 4 walked to the area corresponding to the white dot on the 1940 aerial photograph (Fig. 2.b). Metal detectors were not utilized; only visual inspection of the area occurred. The plant community was primarily oaks with bigtooth aspens (*Populus grandidentata*), the land sloping westward towards a swamp dominated by red maple (*Acer rubrum*). The area which appeared to correspond with the white spot on the aerial was a small peninsula extending into the swamp, the terminus of a low, gradually sloping ridge. No large trees existed on the peninsula, but no evidence of human disturbance was clearly visible. Walking along the swamp edge to the south, a wire gate was found suspended approximately 1 to 1.5 m off the ground by a black oak (*Q. velutina*) which had grown up in the middle of the gate (apparently laying on the ground when the oak was a sapling). No other evidence of human disturbance was found.

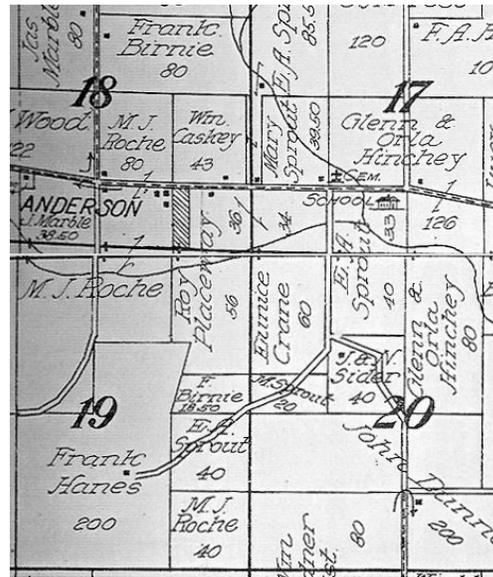
With the knowledge that the ESGR was historically broken into approximately twelve farms, historical plat maps of Putnam Township, Livingston County, MI years 1875 and 1915 were consulted (Fig. 5. and 6.). In an effort to discern if the plotted fence line as identified in the field corresponded to historic property boundaries, the georeferenced Big Woods plot with the fence line was overlain on both plat maps. In both maps, the north-south line of the fence roughly corresponds with a property boundary (Fig. 7. and 8.).

Figure 5. Portion of 1875 Plat Map of Putnam Township, Livingston County, MI. The dot below 19 is Col. George's home (still standing). not to scale



www.memoriallibrary.com

Figure 6. Portion of 1915 Plat Map of Putnam Township, Livingston County, MI. The dot below 19 is Col. George's home (still standing). not to scale



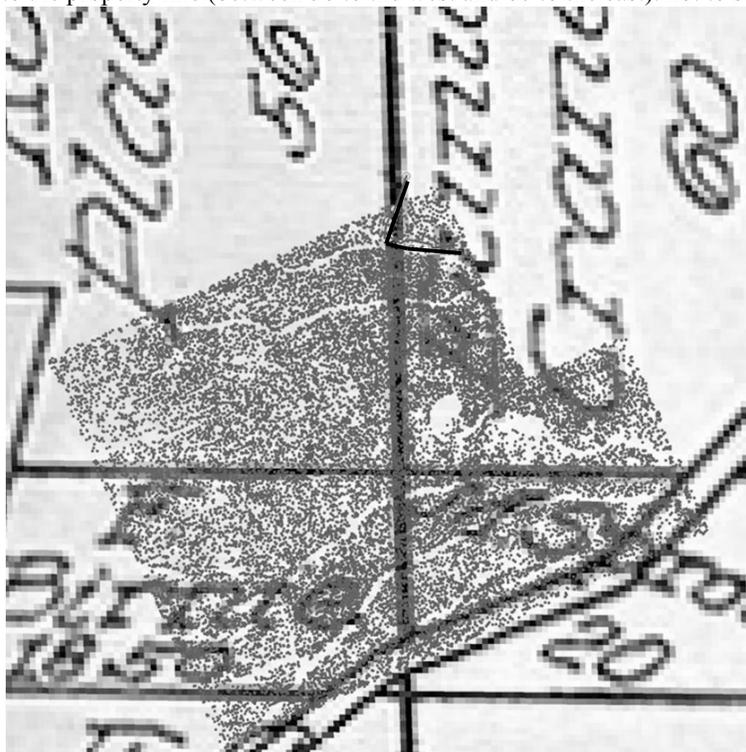
www.memoriallibrary.com

Figure 7. 1875 Plat Map with Big Woods plot with trees and the fence line. The north-south portion of the fence line corresponds to the property line (between 95 to the west and 120 to the east). not to scale



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Figure 8. 1915 Plat Map with Big Woods plot with trees and the fence line. The north-south portion of the fence line corresponds to the property line (between 56 to the west and 60 to the east). not to scale



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DISCUSSION

The discovery of degraded barbed wire within plot G of Big Woods indicates historic agrarian land use within woodlots at ESGR. As all agricultural practices ceased after the purchase of the reserve by Colonel George, it is reasonable to assume that the barbed wire pre-dates 1927. The condition of the barbed wire itself cannot provide sufficient information about its age or when it was placed, although the wire is significantly degraded and corroded leading one to believe it has weathered the elements for several decades. The sawtooth ribbon barbed wire and the headstamp of the shotgun shell, however, provided some dating information.

The Ellwood House Museum has thoroughly documented the history of barbed wire since barbed wire was first patented by Joseph Glidden of DeKalb, IL in 1874, and the bulk of barbed wire was manufactured in DeKalb through 1938 (Ellwood House Association, 2008). Knowing that barbed wire first patented in 1874, and all agricultural practices ceased in 1927 with the purchase of the reserve, the potential timeframe for the agricultural practices discussed herein spans no more than 53 years. The sawtooth ribbon narrows the timeframe by at least seven years, thanks to the consultation provided by Mr. Gerald L. Brauer, the Director of the Ellwood House Museum. Mr. Brauer identified the sawtooth ribbon wire from a picture, indicating that the wire is likely US Patent 244, 726 (July 26, 1881) by Thomas V. Allis of New York, NY. Barbed wire collectors refer to this type as the small tooth variety of “Allis Sawtooth” (personal communication). This information implies that the fence was either not built until sometime after July 26, 1881, or a section of the fence was repaired with Allis Sawtooth after 1881.

The headstamp of the 12 gauge shotgun shell provides an even narrower timeframe; however, it is critical to note that the headstamp was found in plot M, over 100 m away from the fence. The shotgun shell does not necessarily have any bearing on the fence line, though it should be noted that the shell was found approximately 7.6 m northeast of the previously referenced coil of barbed wire. The headstamp matches a variety of shotgun shell, Western Field, formerly produced by the Western Cartridge Company (Fig. 9). According to Mr. Curtis Steinhauer, a shotgun ammunition aficionado, the Western Cartridge Company only distributed ammunition from 1898 through 1932. In 1932, Western Cartridge Company acquired Winchester Repeating Arms Company and discontinued the Western Field line and other Western Cartridge Company brand names (Steinhauer, 2008). The shotgun shell indicates discharge of a 12 gauge shotgun as recently as 1898 within the area.

Figure 9. Western Field 12 Gauge Shotgun Shells box. Pictures show the top, bottom, and side of the ammunition box. The headstamp of the shell found in the field matches the headstamp on the side panel of the box. Headstamps varied with each variety of shell (Steinhauer, 2008).



http://www.antiquemystique.com/pages/7065_jpg.htm

In regards to the forest community of Big Woods plot G, significant differences do exist between the average GBH and species inside and outside of the fence line. For the purpose of this paper, it is assumed that livestock grazing occurred within this area until the reserve was purchased in 1927, allowing for 76 years without grazing conditions (GBH was measured in 2003). Only one species was found exclusively inside the fence: sugar maple (*Acer saccharum*). The following species were found exclusively outside the fence: American beech (*Fagus grandifolia*), American elm (*Ulmus americanus*), choke cherry (*Prunus virginiana*), flowering dogwood (*Cornus florida*), hop-hornbeam (*Ostrya virginiana*), and yellow birch (*Betula alleghaniensis*). Although live-stock browsing may have had influence on the additional species found inside and outside, the shared species also represent the dominant species on either side of the fence. One could postulate that fewer exclusive species were found within the fence because of grazing pressure preventing establishment. The comparison of GBH between the inside and the outside of the fence presents an interesting pattern, however.

The investigators assumed that “inside” the fence would have been an enclosure for the grazing animals and that this area would have smaller tree individuals and fewer species from grazing pressures. This grazing pressure would be expected to result in the average GBH of the trees within the enclosure to be smaller than those trees “outside.” Reviewing the shared species data with significant differences in GBH inside and outside of the fence (Table 1), the trend appears to be reversed with the exception of *Q. velutina*. *Acer rubrum*, *Prunus serotina*, *Sassafras albidum*, and the total average GBH of all shared species have larger GBH outside of the fence. One may be inclined to reconsider where the livestock grazed—perhaps the fence line was a livestock *exclosure*, not an *enclosure*. One possible explanation of why *Q. velutina* did not follow the same trend is that this species may have been avoided by livestock; the inner bark of *Q. velutina* is known to be very bitter and may not have been palatable considering the other options available (Barnes, 2004). If this species had been avoided by livestock, one would expect the GBH to be much more similar inside and outside of the fence; however, this is not the case. One possible explanation for more exclusive species outside of the fence, in the heavy grazing area, may be that grazing maintained a relatively open understory allowing for more species to colonize the relatively bare understory one livestock were removed. Further investigation is necessary to determine the limits of the fence line and the boundaries of a potential livestock exclosure.

The findings within this paper merely scratch the surface of investigating the extent of historical agrarian land use within the wood lots of the ESGR. Further study should include establishment of a systematic protocol for searching the remaining plots of Big Woods, as well as attempting to find the limits of the fence extending outside of plot G. Additional research into the use and calibration of the Prizm metal detectors is also recommended. Are the detectors truly sensitive enough to positively signal the presence of rust? If so, many findings may have been overlooked during this study. Although physical pieces of fence or other artifacts may not be present, a fence line could potentially be plotted out through flagging signal locations. Somewhat surprising, the University of Michigan has very little information about the agricultural practices and land owners prior to the purchase of the reserve by Colonel George. Interesting results could be gathered if a chain of title of the reserve properties was established. Ancestors of the former owners could be located through a simple internet search or through historical-genealogical projects such as the Livingston County MI History and Genealogy Project (<http://www.livgenmi.com>). Oral history or old written records could provide robust facts about historic land use, or potentially provide concrete direction for future investigations on the effect of historic agrarian land use on the E.S. George Reserve.

ACKNOWLEDGEMENTS

Special thanks to Professor John Vandermeer for sharing his personal metal detectors; to David Allen for his observation of the barbed wire coil during his exploits studying *Hamamelis virginiana*; and to Gerald L. Bauer, Director of the Ellwood House Museum for taking the time to correspond with us regarding the Allis Sawtooth barbed wire.

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APPENDIX A

Tag Numbers and Coordinates from Big Woods Plot – Individual Hectares ESGR 2008 (Oaks)

Stone Artifact (Plot D):

adjacent tag: 7010; Black Oak; x (coord) 147.8; y (coord) 174; 194.1cm GBH

Coil of Barbed Wire (Plot M):

adjacent tag: 5279; Black Oak; x (coord) 86.4; y (coord) 217; 112.9cm GBH

Headstamp 12 gauge Shotgun Shell; unidentifiable piece of rusted metal (Plot M):

adjacent tag: 5347; Black Oak; x (coord) 88.6; y (coord) 224.3; 140.6cm GBH

APPENDIX B

Transcript of Personal Communication via E-mail with Gerald J. Brauer, Director of the Ellwood House Museum, DeKalb, IL :

Date: Thu, 16 Oct 2008 12:10:00 -0500
From: ellwoodhouse@tbc.net
Subject: Re: Barbed Wire dating
To: pmw@umich.edu

Hi,

The wire appears to be US Patent 244,726 (July 26, 1881) by Thomas V. Allis of New York, NY. This is known to collectors as Allis Sawtooth (small tooth variety).

In regard to the age of your specimen it would be obviously after the patent date, but it is really impossible to say how much later.

Hope this helps,

Jerry

Gerald J. Brauer, Director
Ellwood House Museum

ISLAND BIOGEOGRAPHY THEORY APPLIED TO PITCHER-PLANT MOSQUITOES IN A
NORTHERN TEMPERATE BOG.
ASHLEY LARSEN

ABSTRACT

Island biogeography theory suggests island communities should be strongly influenced by size of the island and distance to the mainland. In this study I investigated whether the size component of island biogeography theory predicts the abundance of mosquito larva occupying pitcher plants in a northern temperate bog. Furthermore, I investigated which physical dimensions of the pitcher plant influence female oviposition preference, and whether oviposition preference is influenced by the presence of conspecific larva already occupying the cavity. I found that neither size of the plant nor volume of the liquid was directly related to mosquito larva abundance. However, ovipositing females appear significantly more likely to oviposit eggs in plants already containing conspecific larva. Further investigation is needed to determine whether this preference is due to abiotic factors such as structural stability or biotic factors such as habitat modification.

INTRODUCTION

Island biogeography theory states that the community composition of an island is determined by immigration and extinction, and thus strongly influenced by island size and distance to a source population (i.e. mainland; Simberloff & Abele 1976). Recently, island biogeography theory is falling out of favor because most ecological populations are found within matrices of high and low quality patches rather than distinct islands (Ricketts 2001). Metapopulation theory emphasizes the importance of between patch connectivity. While individual populations function independently and can go locally extinct due to stochastic factors, movement between local populations creates a source-sink dynamic enabling persistence. However, for certain systems, dispersal or physiological limitations restrict movement between patches and effectively isolate the population or community to discrete islands. In these cases, island biogeography theory may be a more useful model for understanding population and community dynamics.

One such island system can be observed in pitcher plants. Pitcher plants are carnivorous plants that have evolved a liquid filled cavity used for trapping prey. Most pitcher plants excrete dissolving enzymes that break down their prey, and many also have a mutualistic relationship with an invertebrate community that shred the captured prey and make nutrients available to the plant. In many species of pitcher plants, that community is dominated by mosquito larvae (Heard 1994).

Since mosquito larvae within a pitcher plant are completely isolated, these plants serve as discrete islands. Furthermore, because the ovipositing females can disperse a great distance, island size (i.e. volume of liquid) and not distance to a source population is expected to be important to oviposition behavior. However, complications arise because mosquitoes are multivoltine, and thus, pitcher plants may be occupied by an earlier oviposition event. Thus, I wanted to investigate what characteristics of pitcher plants determine the oviposition preference of female mosquitoes as evidenced by the abundance and distribution of larvae, and whether the presence of older larvae has an influence on the abundance of younger larvae.

METHODS

This study was carried out on October 12, 2008 in Hidden Lake Bog, located on the E.S. George Reserve, Michigan, USA. In this bog, pitcher plants of the species *Sarracenia purpurea* exist in a clumped distribution from the edge of the forest to open water, but are more commonly found in the open transition zone.

11 pitcher plant clumps were chosen as they were discovered. In each clump between one and three plants were chosen at random for a total of 22 individuals. Any plants with damaged or dry cavities were excluded from the study.

For each plant, measurements were taken of plant height, hood height, opening width. Plant height was defined as the exterior length from the highest part of the plant to the bottom of the cavity. Hood height was the distance from highest part of the plant to the opening of the cavity. Opening width was measured as the length of the cavity rim.

The cavity liquid of each plant was extracted and taken back to the laboratory. The volume, pH of the liquid was measured, and a clarity value (0-5) was assigned based on the amount of non-particulate and particulate matter present.

The contents of each plant were observed separately and the number of mosquito larvae was counted. Individuals were assigned to a size class; small, medium or large larvae. A fly larva was found in many plants, so its presence and abundance was also noted. The presence of other invertebrates was noted based on morphospecies as either present or absent.

RESULTS

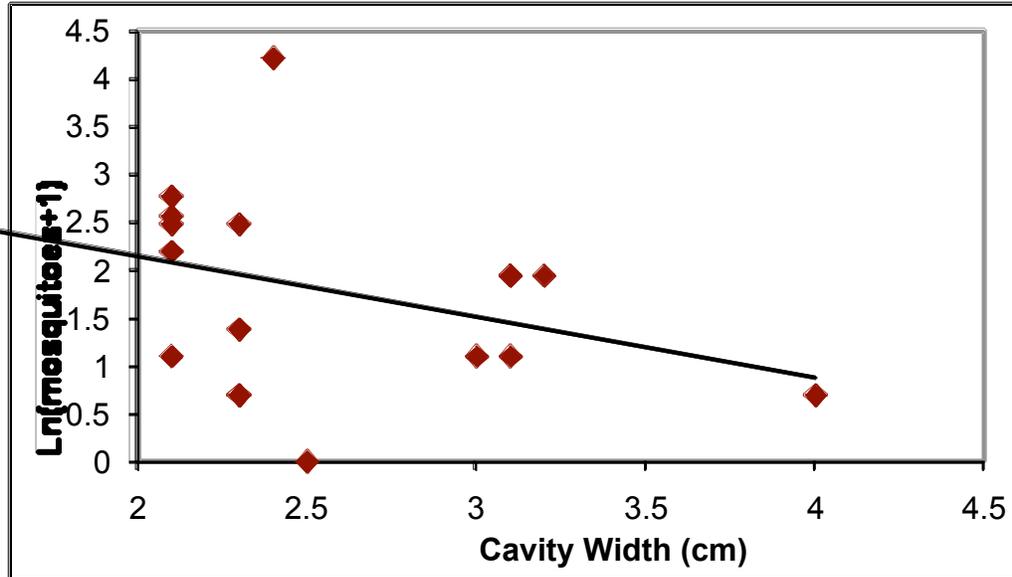
Mosquito larva was found in 21 of the 22 plants sampled. The abundance of mosquito larva per plant ranged from 0 to 67 individuals and averaged 10.86 ± 6.61 (mean \pm 2SE). There was no significant difference in the average number of individuals in each size class.

The number of mosquito larva was independent of plant height, cape height, and relative cape height. There was no relationship between liquid volume or clarity and the abundance of mosquito larvae.

There was a strong trend towards decreased abundance of mosquito larvae as width of the cavity increased, but this was not significant (Fig.1; $r^2=0.16$, $p=0.063$)

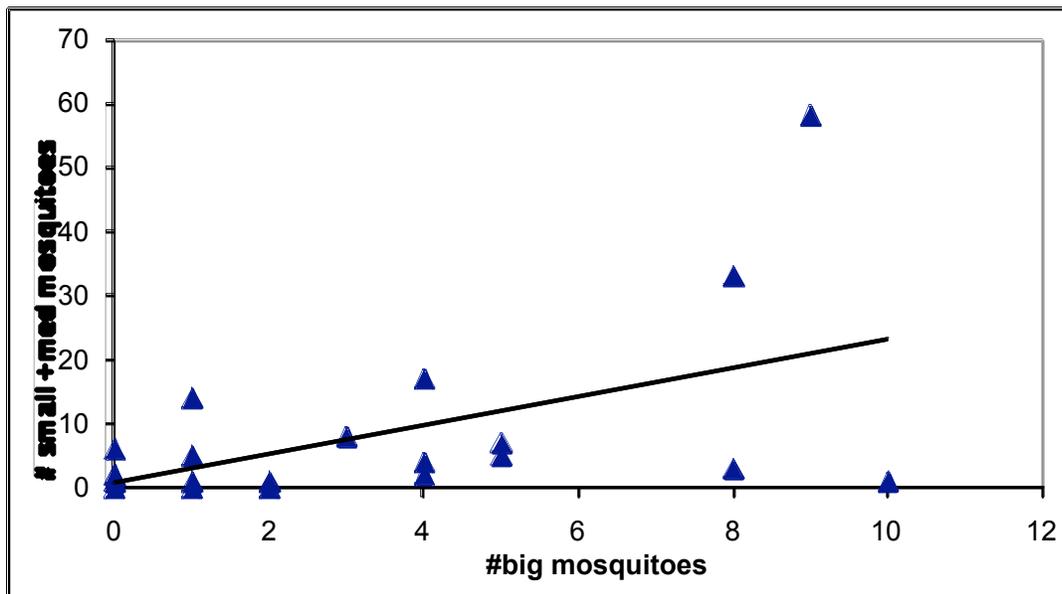
$$(y=-0.64x+3.42).$$

Figure 1. Mosquito larvae abundance decreases with increased cavity width ($y=-0.64x+3.42$, $r^2=0.16$, $p=0.063$)



There was a significant positive relationship between the number of large larva and the number of small and medium larva occupying a cavity (Fig. 2, $r^2=0.29$, $p<0.01$)

Figure 2. The number of small and medium sized mosquito larvae increases with increased abundance of large mosquito larvae ($y=2.25x+0.83$, $r^2=0.29$ $p<0.01$).



Fly larva was the second most abundant invertebrate found. When fly larva and mosquito larva were present together ($N=10$), the number of fly larva was inversely related to the number of mosquito larva, though this trend was not significant ($r^2=0.23$, $p=0.14$).

DISCUSSION

Island biogeography theory predicts that the community of an island should reflect the size and proximity of the island to the mainland based on probabilities of extinction and colonization. As applied to mosquito larva in this study, extinction is larval eclosing and

colonization is oviposition by the adult female. The focus of this study was on colonization/oviposition based on plant characteristics. Because adult mosquitoes are highly mobile, I expected size and volume of the pitcher plant to determine larva 'colonization'.

Surprisingly, I found that neither height nor volume predicted the abundance of mosquito larva. This indicates that other factors influence oviposition preference besides space resources. One such factor appears to be the size of the cavity opening. Smaller cavity openings may result in less risk of larva predation or possibly less risk of structural damage to the plant by flooding from excess rain water. In addition, a smaller cavity opening may reduce evaporation and desiccation during the summer months which would be fatal to larval survival (Heard 1994).

The positive correlation between abundance of large larva and smaller sized larva may indicate either abiotic or biotic processes. If space resources are not limited, ovipositing where larva already exists may be a result of selection of good nursery habitat by the female mosquito. This would indicate other variables that were not measured in this study such as distance to the open water or numbers of plants in a clump are important to oviposition preference. However, it is also possible that larger larvae modify the environment inside the pitcher by shredding captured prey and therefore release nutrients that benefit larval development. If this is situation, it would be advantageous for the female mosquito to select plants that were already occupied by conspecific larva.

Similar results were found by Heard (1994) who found that oviposition by the mosquito *Metriocnemus knabi* in pitcher plants was more common in plants already containing conspecifics. Heard (1994) notes that individual larva performance is suboptimal in plants containing a high abundance of conspecifics. However if other factors such as desiccation risk are considered, it still may be advantageous to chose already inhabited locations despite tradeoffs in larva performance.

More sampling is need to elucidate the relationship between fly larva and mosquito larva. It appears that the abundance of fly larva is inversely related to the abundance of mosquito larva. It is possible, but unlikely, that the two species compete for nutrients. Mosquito larva is highly mobile within the liquid medium and is not usually found on the bottom. The fly larva is has a worm-like morphology that is not conducive to swimming. Therefore, the height stratification in the water column would likely separate the two species spatially. Since some prey float and other sink (both based on prey morphology and level of decomposition), the spatial separation also may result in food partitioning as well. It was observed that the fly larva were concentrated in patches with high algal and particulate matter. Based on the data and this observation, it is more likely that the fly larva is related to algal or particulate contents of the plants rather than mosquito abundance. Again, a larger sample size of plants containing fly larva is needed to understand what influences its distribution in pitcher plants.

ACKNOWLEDGEMENTS

I thank John Vandermeer, Ivette Perfecto and Dave Allen for logistical help and experimental design.

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ARE ISLANDS REALLY HABITAT ISLANDS?

DAVID N. ALLEN, JOHN VANDERMEER, AND IVETTE PERFECTO

ABSTRACT

Here we present a method for determining if putative islands are truly functioning as habitat islands. We do so by assessing if the species distribution pattern across the islands conforms with the predictions of the theory of island biogeography. The putative islands in our study are a series of hummocks in a swamp in the ES George Reserve, Ann Arbor MI. We assess the tree fauna on each hummock and find that hummocks that are a distance from the forest that abuts the swamp have fewer tree species than subsets of the mainland of the same area as the island. These results suggest that the hummocks function as biological islands for trees.

INTRODUCTION

It is often the case that habitats occur in a patchwork, vaguely suggestive of “islands” of habitat type in a “sea” of some other habitat type, and bringing to mind modern theoretical formulations. But is this framework legitimate? That is, do we have reason to believe that the habitat patchwork so common in terrestrial systems do indeed accord with what has come to be understood about “real” islands. The equilibrium theory of Island Biogeography (MacArthur and Wilson, 1967) makes predictions about the number of species inhabiting an island based on that island’s size and distance from the mainland. It has been successful at explaining patterns of biodiversity on oceanic islands (Simberloff, 1976), some habitat island situations (Brown and Kordic-Brown, 1977), and most recently has provided a framework to think about biodiversity in fragmented landscapes (Harrison and Bruna, 1999). Here we suggest another application -- the predicted patterns of the theory could be used to infer if the extinction/recolonization process is operative in a given system. In other words for a given set of species in a given landscape, is a system of putative islands really one of biological islands. We use this application to determine if a system of island hummocks in a hardwood swamp function as biological islands from the point of view of the trees growing on them.

The equilibrium theory of island biogeography assumes that on a given island extinctions are inevitable and take place at a rate inversely proportional to the size of that island. These extinctions are countered by re-colonization of the island from the mainland, which happen at a rate inversely proportional to the distance from the mainland. This gives us two predictions 1) larger islands have more species 2) islands closer to the mainland have more species. If we take an ‘island’ to be nothing more than a sample of a particular size embedded in the mainland, recolonizations of the ‘island’ will happen at the greatest possible rate. This gives rise to a third prediction 3) islands should have fewer species than areas of equal size sampled on the mainland.

Here we test these three predictions in a system of eight terrestrial hummocks located in a swamp that abuts an Oak-Hickory forest. The tree flora on each island is evidently a subset of the tree flora of the nearby Oak-Hickory forest. If the above predictions are met for the pattern of tree diversity on the islands we can infer the island nature of the hummocks. On the other hand if the predictions are not met, these

hummocks are just extensions or samples of the nearby forest and the application of island thinking is illegitimate.

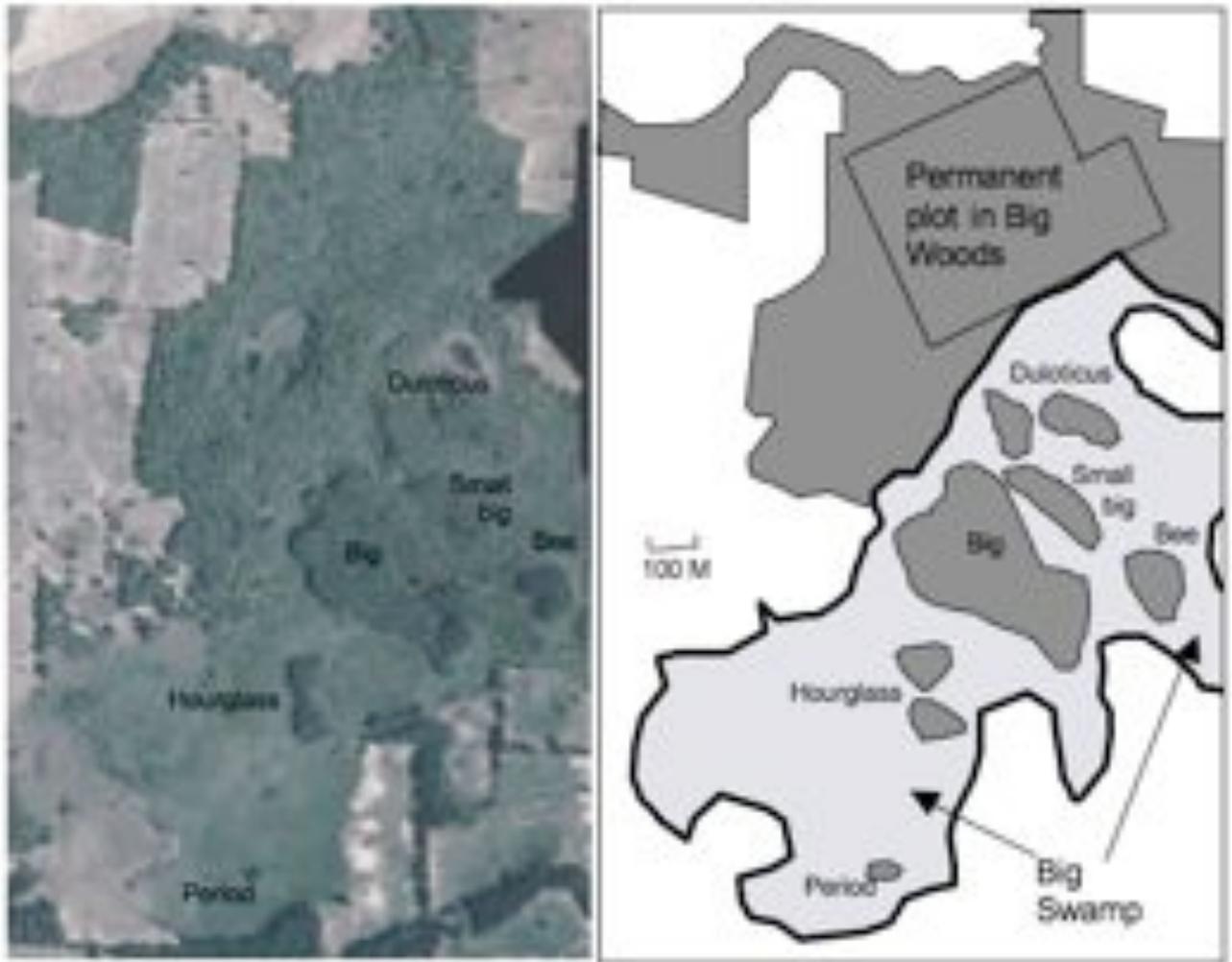
METHODS

The study site is part of the E. S. George Reserve, owned and operated by the University of Michigan consisting of a mosaic of forests, old fields and aquatic habitats. The terrestrial habitats have been strongly influenced by human activities, the old fields a consequence of row crops and pasture in the earlier parts of the twentieth century and the oak/hickory woodlots a likely consequence of fires resulting from Native American agriculture and hunting prior to European invasion.

The canopy of the forest is dominated by white oak (*Quercus alba*) and “black” oak, the later being a hybrid swarm of *Q. velutina*, *Q. rubra*, with occasional *Q. coccinea* (Wagner, personal communication, Voss, 1985), as well as pignut hickory (*Carya glabra*) and shagbark hickory (*Carya ovata*). The oak dominance has been interpreted as a consequence of Native American hunting and agriculture and their use of fire. Subsequent to the eliminating of fires with the expansion of White colonists, the subcanopy and understory have been taken over by red maple (*Acer rubrum*), black cherry (*Prunus velutina*) and witchhazel (*Hamamelus virginiana*), plus 15 other less common species. In an 18 ha permanent plot on the “mainland” all trees greater than 10 cm GBH (girth at breast height) have been marked, measured and mapped. This permanent plot will be referred to as the “mainland.” Further details on the site and census methodology can be found in Jedlica et al. (2004).

The hummocks are located in an extensive and diverse swampland, known locally as big swamp (Fig 1). The forest on each of these hummocks is similar to the mainland forest from casual observations. On each hummock two to four (depending on its length) transects were conducted across the short dimension of the island and all trees within 5m of each side of the transect and with a GBH >10cm were recorded. The transects were spaced evenly along the long axis of the island. Afterwards an observational sweep of the island was conducted to record any species that were missed in the transect samples. The transects provided information on the relative abundances of the species on the island, while the sweep gave the total diversity on the island.

Figure 1. A map of the eight islands studied and an aerial photograph of the area from 1940.



For each island size, 1000 random resamples of the Big Woods were taken twice, one time of the same area as the transects of the island and the other time the same area as the island as a whole. The relative abundances of species in the first samples were compared to the relative abundances in the transect data from the islands and the raw number of species in each of the second set of samples were compared with the number of species on each island from the island sweeps. The distance to the mainland was taken as the distance from the northern edge of each island to the northern edge of the swamp. The area to the south of the swamp has only recently been reforested after a long history of grazing and agriculture, while the area to the north has been more continuously forested (see fig 2) and considered to be the main source area.

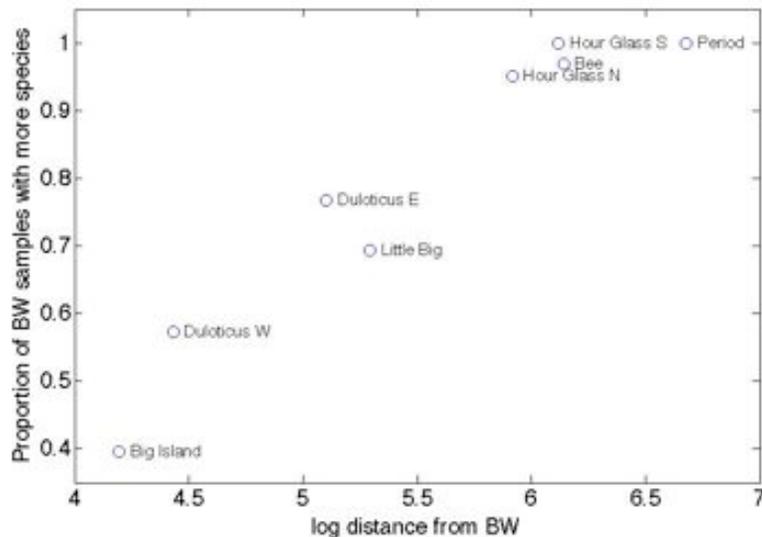
Figure 2. An aerial photograph of the area from 1940. Note that the area to the south of the swamp is largely deforested.



RESULTS

For four of the islands over 95% of the resamples of the same area as the island of the Big Woods had more species. These were the four islands furthest away from the mainland (Fig 3). Distance from the mainland significantly correlated ($p < .001$) with island have fewer species than samples of the same size of the mainland, but area of the island did not. Smaller islands had fewer species, but smaller islands were not any more or less likely to have fewer species than samples of their size of the Big Woods.

Figure 3. The significant relationship between island distance from the mainland and the proportion of big woods samples with more species.



DISCUSSION

These results suggest that the hummocks located at a distance greater than about 7 function biologically as islands, while the closer islands, even though they are not contiguous, are functioning biologically as extensions of the forest. Thus near-by islands are re-colonized at a rate not that much different than the mainland recolonizes local extensions within itself, while the further island recolonization rates are much lower resulting in the lower species numbers.

Since the long-term history of the area is well known, we are able to further tease out some of the island-like patterns. Specifically, since the oak overstory has been in existence for about 150 years or more, and the distinct assemblage of understory has much more recently been dispersing into the overall are (we estimate, from cores, about 30-40 years in process), we can separate the large trees from the small ones and redo the above analysis. These results show that the for more recent species the hummocks look even more like biological islands, but for the older species the relationship between distance and proportion of big woods samples with more of the old species decreases in effect and significations ($p=.065$). This may suggest that the island pattern may be a temporary phenomena until the more recent species is the forest have time to get to the further islands.

The procedure of looking for pattern as a signal of the island biogeography process could be useful way to assess the impact of habitat fragmentation in human-impacted systems. It maybe possible to use such a technique to assess matrix quality generally, or, if known, the effect of particular constructs of the matrix (row cropping versus pastures, for example).

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