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# The Combined Effects of Exogenous and Endogenous Variability on the Spatial Distribution of Ant Communities in a Forested Ecosystem (Hymenoptera: Formicidae)

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**ABSTRACT** Spatial patterns observed in ecosystems have traditionally been attributed to exogenous processes. Recently, ecologists have found that endogenous processes also have the potential to create spatial patterns. Yet, relatively few studies have attempted to examine the combined effects of exogenous and endogenous processes on the distribution of organisms across spatial and temporal scales. Here we aim to do this, by investigating whether spatial patterns of under-story tree species at a large spatial scale (18 ha) influences the spatial patterns of ground foraging ant species at a much smaller spatial scale (20 m by 20 m). At the regional scale, exogenous processes (under-story tree community) had a strong effect on the spatial patterns in the ground-foraging ant community. We found significantly more *Camponotus noveboracensis*, *Formica subsericae*, and *Lasius alienus* species in black cherry (*Prunus serotina* Ehrh.) habitats. In witch-hazel (*Hamamelis virginiana* L.) habitats, we similarly found significantly more *Myrmica americana*, *Formica fusca*, and *Formica subsericae*. At smaller spatial scales, we observed the emergence of mosaic ant patches changing rapidly in space and time. Our study reveals that spatial patterns are the result of both exogenous and endogenous forces, operating at distinct scales.

**KEY WORDS** self-organization, spatial patterns, ant mosaics

It has been widely recognized that ecosystems frequently exhibit signatures of spatial self-organization (Solé and Bascompte 2006). An important feature of such organization is the extent to which simple local interactions scale up to form large-scale macroscopic patterns across ecosystems, which is to say, the degree to which large-scale patterns depend only on locally available information (Pascual et al. 2002, Couzin and Frank 2003). On the one hand it is common to observe regular spatial patterns that reflect the heterogeneity of the underlying environment (Van de Koppel et al. 2008), an “exogenous” determination of pattern. However, the idea of spatial self-organization is that local interactions can lead to nonrandom regional distributions of organisms in the absence of underlying habitat variation (Vandermeer et al. 2008), an “endogenous” determination of pattern. We are thus faced with two forces, endogenous and exogenous, and the disarticulation of the two represents a major agenda for research aimed at understanding spatial pattern.

Much of the empirical work describing regular pattern formation has focused on vegetation communities (Gratzer et al. 2004), particularly in understanding patterns arising from underlying environmental conditions, referred to here as exogenous. Exogenous pattern forming processes may derive from a host of

habitat factors, such as those arising from disturbances or topographic variations. Recently there has been great interest in the possibility of endogenous pattern formation, arising from either physiological processes or local population interactions (Perfecto and Vandermeer 2008, Allen 2010). Thus, for example, the combination of local expansion of a prey item and the density-dependent attack of a predator, yields clusters of prey and predator, even in a uniform environment, imitating the famous Turing effect (Alonso and McKane 2002). Regular pattern formations from self-organizing processes have been described in animal populations (Maron and Harrison 1997, Vandermeer et al. 2008); terrestrial plants (Klausmeier 1999, Rietkerk and Van de Koppel et al. 2008); and in marine ecosystems (Wootton, Van de Koppel et al. 2008), suggesting that the formation of regular spatial patterns is a general phenomenon, with important implications for the structure and functioning of ecosystems (Kefi et al. 2007). For instance, recent work in a Mexican coffee agroforestry system (Perfecto and Vandermeer 2008) has shown that self-organized spatial patterns emerge as a result of both endogenous and exogenous forces. In a 45-ha homogenous plot, consisting of coffee and shade trees, researchers found that the aggressive arboreal ant *Azteca instabilis* (Vandermeer et al. 2008) formed clusters of nests, because of the establishment of local satellite colonies,

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but were subsequently controlled from further expansion by a predatory parasitoid fly that attacked the ants. In this specific case, the combined process of local satellite expansion by the ants and the density-dependent effect of the parasitoid fly gave rise to the formation of spatial pattern in the system.

It is clear that some spatial patterns are the result of underlying habitat variables (exogenous), although others clearly show a signal of self-organization independent of any underlying habitat spatial variation (endogenous). It is also the case that both endogenous and exogenous forces will frequently act simultaneously. Yet, combining the complex interactions between exogenous and endogenous factors in determining the distribution of organisms in ecosystems is not straightforward (Bolker 2003).

Here, we report on spatial pattern formation of several species of ground-foraging ants in an eastern North American deciduous forest. The forest is considered to be a transitional forest with oak and hickory trees dominating in the overstory, whereas the under-story is primarily composed of red maple (*Acer rubrum* L.), black cherry (*Prunus serotina* Ehrh.), and witch hazel (*Hamamelis virginiana* L.) that form patches apparently based on recent historical trends, especially the control of fires with the invasion of white settlers in the late 19th century. Red maple and black cherry were apparently much rarer previously because of Native American agricultural practices, including controlled fire regimes enabling oaks and hickories to dominate (Jedicka et al. 2004). Low tolerance to light levels by oak and hickory seedlings enable the more shade-tolerant under-story tree species to replace the forest in the future (Allen 2009).

The ground beneath this forest formation is home to a variety of woodland ant species (Talbot 1975). Microhabitat differences for these various species suggest that spatial patterns of the ants may follow whatever spatial patterns are evident in the microhabitats. And in this particular case it is reasonable to hypothesize that at least part of the salient microhabitats are created by the discarded leaves. Thus, it could be that the organizing processes that create the spatial patterns of the three dominant under-story trees, also create the spatial pattern of the microhabitats in which the ants live. Recent work (Allen 2010) at the E.S. George Reserve has shown that witch-hazel forms spatial patterns as the result of dispersal limitation and seed predation. As seeds are being dispersed locally, tree clumps form and reach a critical density size (i.e., predation attack limits the growth of the clump) that allows other species, such as red maple and black cherry trees, to colonize the unoccupied space. Thus, a combination of dispersal limitation and predation leads to the formation of endogenous spatial patterns of under-story-trees.

Thus, the unique combinations of historical processes, exogenous, and endogenous factors make this an ideal study system to compare the relative importance of endogenous versus exogenous origins of spatial pattern. That is, does the presumably self-organized (endogenous) spatial pattern of the trees

translate into an exogenous habitat pattern to which the ants respond? Or, are there signals of endogenous spatial pattern formation, above and beyond the evident patch structure of the trees? This study seeks to determine if 1) there is any signal in the ground foraging ant community that can be associated with the patches of different dominant tree species (evidence of exogenous effects), and 2) whether there are any evident patterns that are not associated with either the patches of dominant trees or underlying habitat variables (evidence of endogenous effects). From theoretical studies we expect that the evident competitive interactions among ground foraging ant species will be one of the major forces that generate spatial pattern (Vandermeer and Yitbarek 2011). In pursuit of these goals we measured 1) population changes of ants over time and their extension in space, and 2) implicit competitive interactions between ant species.

### Materials and Methods

**Study Area.** The study site is located at the ES George Reserve, a 525-ha preserve administered by the University of Michigan in Livingston County, MI (latitude 42.5 and longitude -83.9). The reserve is characterized by a rugged moraine and basin topography that receives an average annual precipitation of 76.2 cm and average temperatures ranging between -5°C in January and 22°C in July.

The study was conducted in a oak-hickory woodland in the northeastern part of the E. S. George Reserve, where an 18-ha permanent plot has been monitored for the past decade. The woodland is a transitional forest composed of oak-hickory trees more or less uniformly distributed in the over-story. The under-story is dominated by saplings of *Hamamelis virginiana* (witch hazel), *Acer rubrum* (red maple), and *Prunus serotina* (black cherry), which are expected to replace the oak-hickory forest in  $\approx 100$  yr (Voss 1985). All trees >10-cm girth at breast height have been identified and georeferenced within the 18-ha study plot. The spatial distribution of the under-story species is clearly nonrandom (Fig. 1), whereas the over-story of oaks and hickories (not shown) are either random or uniform, thus contributing nothing to the obvious patchwork created by the other three dominant species in the sub canopy.

**Field Surveys.** In total, six rectangular plots (40 m by 20 m) were established along the borderlines of patches of dominant under-story tree species: Red Maple-Witch Hazel, Red Maple-Black Cherry, and Black Cherry-Witch Hazel (Fig. 1). Each of the six plots straddled a border of the tree species patches, such that a 20-m by 20-m plot was located in an effective monoculture of tree leaves. These 40-m by 20-m plots are referred to as "combination plots." Using standard tuna baiting methods (Agosti et al. 2000), baits were placed at 2-m intervals to observe the presence and absence of foraging ants totaling 100 tuna baits per plot (10 by 10 baits in each 20-by 20-m plot). Ants were sampled and identified to morpho-species in the field and processed in the laboratory for iden-

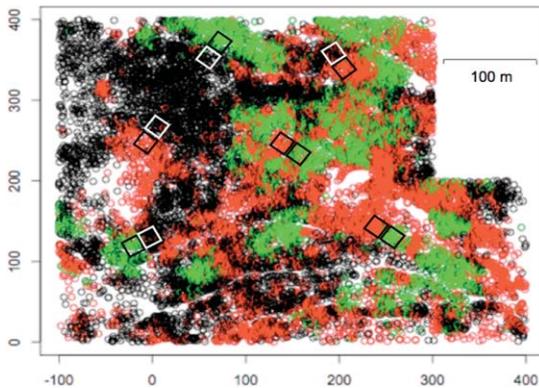


Fig. 1. Distribution of the six combination plots (40 by 20 m) in an 18-ha forest plot in Southeastern Michigan. Individual trees in the plot are coded as black = black cherry trees; red = red maple trees; green = witch-hazel trees.

tification to species. Ant sampling occurred at two different time intervals, once during the spring (May 2009) and once in late summer (August 2009) to assess any evident seasonal changes. Each sampling was done twice,  $\approx 1$  h apart, enabling an approximate assessment of possible competitive replacements at bait sites.

**Statistical Analysis.** We used a Monte Carlo simulation methodology to compare the frequencies of bait occupancies among plots for individual ant species. To detect any differences in bait occupancy, we divided each of the combination plots within the forest stands into four subparcels, demarcating each combination plot at the 10 m, 20 m, 30 m, and 40 m x-coordinates, such that two 10-m by 20-m plots were located in monocultures and two 10-m by 20-m plots were located near the border of the two monocultures (see Fig. 3a). For our analysis, we compared frequencies of bait occupancies within the 0- to 10-m and 30- to 40-m regions to minimize confounding overlapping influences from the two habitat types, because ant foragers may extend into the region between the forest stands (10–30 m). For each individual ant species occurring in the two subparcels (0–10 m, 30–40 m), we pooled together all of our observations (number of bait occupancies for that species) and repeatedly drew two samples ( $n = 10,000$  pairs). Each time, we computed the statistic ( $d$ ), the difference between the means from the two samples, which gives us a simulated null distribution from which we computed the  $P$  value. The  $P$  value was a count of the number of times the simulated difference was greater or equal to the observed difference, divided by the total number of repeated samples ( $n = 10,000$ ). We report the  $P$  values generated from the Monte Carlo simulation for the months of May and August samples pooled together.

**Neighborhood Analysis.** We used a nearest neighbor statistical approach to quantitatively assess the endogenous mosaic spatial patterns that emerge within the individual forest stands. To assess the mosaic spatial patterns created by individual species, we imposed a grid (8 by 8 squares) at the center of each

of the 20- by 20-m forest stands (we excluded the outer rows and columns to avoid edge effects). We then counted how many conspecific neighbors surrounded the Moore neighborhood (the eight squares surrounding a given square on the grid) of each of the individual species and subsequently computed the average cell occupancy for each species. We then computed the expected average cell occupancy for each of the individual species by counting the number of species occupying the grid as a whole, divided by the total number of possible cells that could be occupied ( $n = 64$ ), giving the probability that any cell is occupied for each species. This calculation then allowed us to compute the expected average number of cells by multiplying the occupancy probability times the eight cells in the surrounding Moore neighborhood. We ran a simple  $t$ -test to compare the differences between the conspecific average and the expected average for each of the species.

## Results

**Species Composition.** Results of the combination plots for the spatial patterns of individual ant species in the black-cherry-red-maple, witch-hazel-black-cherry, and witch-hazel-red-maple plots for each baiting period (2 hr apart), and for each season (spring and summer) are summarized in Figs. 2 and 3. We encountered 10 different species in total belonging to three subfamilies (Formicinae, Myrmicinae, Dolichoderinae), almost all of which were distributed quite unevenly among the sampling locations. Only one species, *Aphenogaster rudis*, was found in all plot types (Covert 2005).

The black-cherry-red-maple combination plots were predominately occupied by *A. rudis*, *Prenolepis imparis*, *Myrmica americana*, *Camponotus noveboracensis*, *Formica fusca*, *Lasius alienus*, *Camponotus chromaiodus*, and *Formica subsericae* species (Fig. 3A). Three species, *C. noveboracensis*, *Formica fusca*, and *Lasius alienus* were exclusively found in the black cherry plots (considering only the black cherry-red maple pairs). Within the individual red-maple plots, two species, *C. chromaiodus* and *F. subsericae*, were exclusively found within the individual red-maple plots.

The black cherry-witch-hazel combination plots contained all 10 species (Fig. 2b). *M. americana*, *F. fusca*, *F. subsericae*, and *C. noveboracensis* were exclusively present in the witch-hazel plots. *Aphenogaster tennessee* and *C. noveboracensis* were exclusively found in the individual black-cherry plots.

The witch-hazel-red maple combination plots were primarily occupied by *A. rudis*, *Camponotus pennsylvanicus*, *L. alienus*, *Prenolepis imparis*, *F. fusca*, *C. chromaiodus*, and *C. noveboracensis* species (Fig. 3c). Within the individual red maple plots, *F. fusca* and *C. chromaiodus* were found exclusively, whereas in individual witch-hazel plots only *C. noveboracensis* was found exclusively albeit in both cases with low abundances.

Monte Carlo estimates of  $p$  in the black-cherry-red-maple plots revealed significant differences in oc-

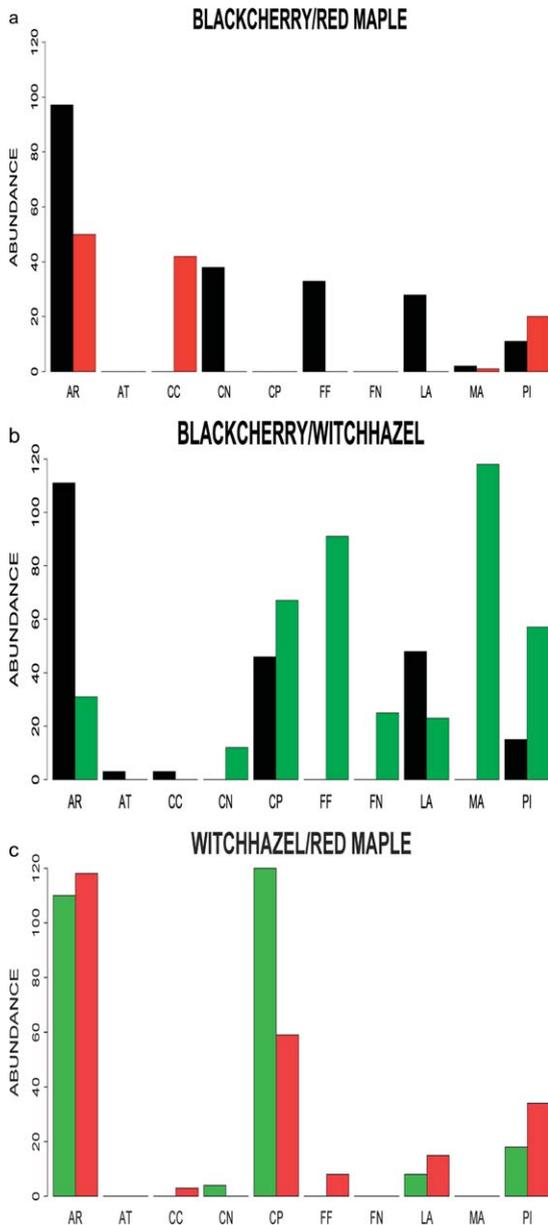


Fig. 2. Total ant abundance found in a) Black cherry-red maple. b) Black cherry-Witch-hazel. c) Witch-hazel-red maple combination plots. Species codes are AR = *Aphenogaster rudis*, AT = *Aphenogaster tennessee*, CC = *Camponotus chromaiodus*, CN = *Camponotus noveboracensis*, CP = *Camponotus pennsylvanicus*, FF = *Formica fusca*, FS = *Formica subsericea*, LA = *Lasius alienus*, MA = *Myrmica americana*, PI = *Prenolepis imparis*.

cupation of baits by *L. alienus* (preference for black cherry,  $P = 0.02$ ); *F. subsericea* (preference for red maple,  $P = 0.0004$ ); and *C. noveboracensis* (preference for black cherry,  $P = 0.0002$ ) species. For the witch-hazel-black cherry plots, analyses showed significant differences of bait occupancy by *M. americana* (preference for witch hazel,  $P = 0.0002$ ); *F. fusca* (preference for witch hazel,  $P = 0.00005$ ); and *F. subsericea* (preference for witch hazel,  $P = 0.0009$ ) species. In the witch-hazel-red-maple plots, bait occupancy of any species was not found to be significant ( $P > 0.05$ ). Thus, all significant differences were associated with comparisons with black cherry stands.

**Mosaic Spatial Patterns.** Results of the neighborhood analysis provide a quantitative assessment of the mosaic spatial patterns of individual ant species encountered in the forest stands for each of the baiting periods and seasonal periods. Results of the statistical analysis of individual ant species are highlighted in Table 1. We report the  $P$  values related to significant clustering for individual ant species encountered in each of the habitat patches after 1- and 2-h baiting periods. ( $P < 0.05$ , Table 1).

In the black cherry-red maple forest stands, mosaic spatial patterns were formed by *A. rudis*, *C. chromaiodus*, *F. fusca*, and *L. alienus* species. *A. rudis* and *F. fusca* exclusively formed mosaic spatial patterns after 2 h of baiting period, whereas the mosaic patches formed by *C. chromaiodus* and *L. alienus* quickly disappeared after 1 h.

In the witch-hazel-black-cherry forest stands, mosaic spatial patterns were formed by *A. rudis*, *C. pennsylvanicus*, *F. fusca*, *P. imparis*, *M. americana*, and *L. alienus*. Both the *A. rudis* and *M. americana* species formed fixed mosaic spatial patterns after 2 h. However, for *C. pennsylvanicus*, *P. imparis*, and *L. alienus* species we did not detect a clear temporal pattern within each of the forest stands.

In the witch-hazel-red maple forest stands, mosaic spatial patterns were formed by *A. rudis*, *C. pennsylvanicus*, and *P. imparis*. A clear temporal mosaic pattern emerges after 2 h for *C. pennsylvanicus*. However, mosaic patterns formed for *A. rudis* and *P. imparis* did not show a clear temporal preference.

## Discussion

Our results demonstrate that the presence of under-story ants follows, to some extent, the spatial patterns of under-story tree species. Some forest ant species tend to co-occur in both habitat patches, whereas other species only occurred in single habitat patches. In general, we found that the specific arrangements of the combination plots in large part determined the ant associations found within each of the forest stands. Although most of the species were found in all of the forest stands, abundances (i.e., number of baits occupied) varied considerably. In the black cherry-witch-hazel combinations plots we found that the number of baits occupied remained low as compared with some of the same species found in the black cherry-red maple plots where we observed increasing trends of bait occupancy. In particular, we found high abundance levels for *F. fusca* and *M. americana* species in the black cherry-red maple as compared with the other forest stand combinations. Meanwhile, we found high abundance levels for *A. rudis* and *C. pennsylvanicus* species in the witch-hazel-red maple forest

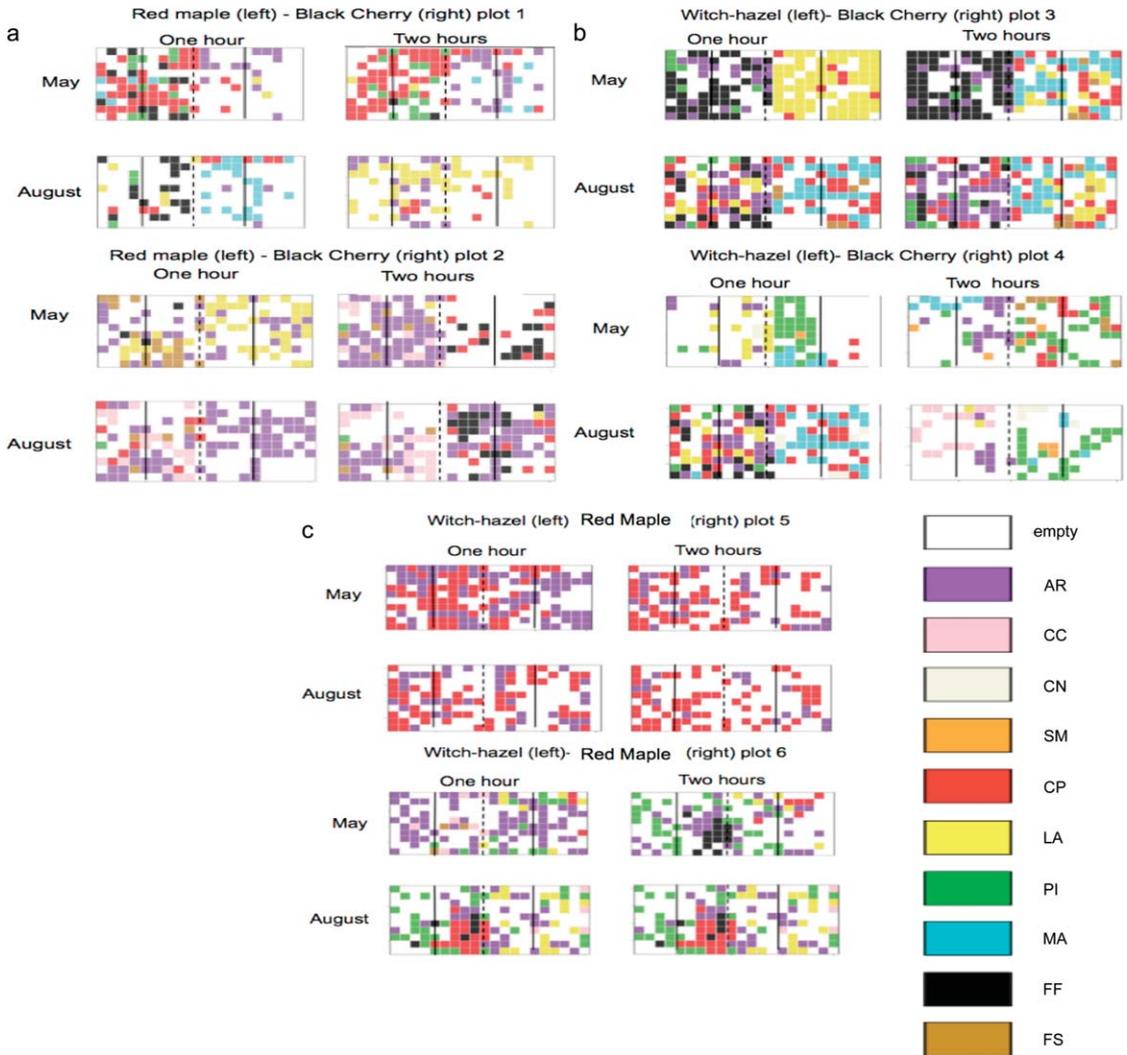


Fig. 3. Distribution of the ant species in the 20 by 40 m in all three combination plots, with each plot divided into 10-by 20-m subplots, two of which are in one habitat type the other two in the other habitat type. a. The two red maple-black cherry plots (Species codes as explained in Fig. 2). b. The two witch-hazel-black cherry plots (symbols as in a). c. The two witch-hazel-red maple plots (symbols as in a).

stands. This observation suggests that the combinatorial arrangement of the forest stands has important implications for ant habitat preferences.

For some of the ant associations within the individual forest stands, our results suggest that exogenous forces are important in determining ant preferences. In the case of the black cherry-red maple plots, we found that *C. noveboracensis*, *F. fusca*, and *L. alienus* occurred only in black cherry plots, while *C. chromiodes* and *F. subsericae* species occurred in red maple plots. One explanation for these species occurrences in the black cherry plots can be explained by the sheer abundances of extra-floral nectaries resources. *C. noveboracensis* and *L. alienus* species have been widely reported to forage on foliage for the consumption of honeydew, plant juices, and insects

(Covert 2005). Similarly, *F. fusca* species consume nectar from extra-floral nectaries as well as arthropod prey found on black cherry trees (Ayre and Hitchen 1968). In one study, Tilman (1978) found that *F. obscuripes* were attracted by extra-floral nectaries on black cherry trees, which are in turn protected by the ants from defoliation by tent caterpillars. In this case, the evolutionary timing of bud outbreaks by black cherry trees is believed to coincide with the defoliation by tent caterpillars. In the black cherry-witch-hazel plots, we observed relatively large abundances of *M. americana* and *F. fusca*, and lower abundances of *F. subsericae* and *C. noveboracensis* that only occurred in the witch-hazel plots. Witch-hazel patches most likely have greater soil-moisture levels because of the increased surrounding leaf litter and lower light avail-

**Table 1.** List of ant species found to have a non-random clustered spatial pattern after either 1 h or 2 h or both. Significant *P* values are highlighted in black (*P* < 0.05)

Species	Habitat	Time: 1 h	Time: 2 h	Season
<i>Aphenogaster rudis</i>	RM-BC	0.71	0.003	May
"	RM-BC	0.7	0.03	May
"	RM-BC	0.14	0.001	Aug.
"	RM-BC	0.28	0.007	May
"	WH-BC	0.35	0.02	Aug.
"	WH-BC	0	0.01	Aug.
"	WH-BC	0.92	0.009	Aug.
"	WH-RM	0.26	0.005	May
"	WH-RM	0.005	0.66	Aug.
"	WH-RM	0.004	0.03	Aug.
<i>Camponotus chromaiodus</i>	RM-BC	0.04	0.14	Aug.
<i>Camponotus pennsylvanica</i>	WH-BC	0.008	0.36	May
"	WH-BC	0.91	0.009	Aug.
"	WH-BC	0	0.01	Aug.
"	WH-RM	0.23	0.007	Aug.
"	WH-RM	0.15	0.0005	May
"	WH-RM	0	0.001	Aug.
<i>Formica fusca</i>	RM-BC	0	0.02	Aug.
"	WH-BC	0.0007	0.35	May
<i>Prenolepis imparis</i>	WH-BC	0.01	0.5	May
"	WH-BC	0.14	0.03	Aug.
"	WH-RM	0	0.02	May
"	WH-RM	0.02	0.01	May
<i>Myrmica americana</i>	WH-BC	0	0.02	May
"	WH-BC	0.16	0.02	Aug.
"	WH-BC	0	0.01	Aug.
"	WH-BC	0.03	0.5	Aug.
<i>Lasius alienus</i>	RM-BC	0.006	0	May
"	WH-BC	0.96	0.01	May

ability, providing a clearly distinct ground-level habitat background. *M. americana* is known to have a wider range of tolerance to extreme temperature changes (Talbot 1946). During the duration of the study, the forest reserve received most of its precipitation during the month of June, whereas the warmest period was recorded in the month of August. Therefore, *M. americana* individuals could have been physiologically adapted to maintain foraging activity at high temperature levels.

At the finer spatial scale, we observed the formation of mosaic ant patches. Here, the formation of mosaic patches appears to be driven primarily by endogenous forces. For instance, we found that *F. fusca*, *A. rudis*, and *P. imparis* dominated in one individual witch-hazel plot during the month of June. However, in the month of August a shifting pattern took place when *A. rudis* expanded out territorially by replacing *F. fusca*. This shift can be explained by the fact that *F. fusca* have restricted seasonal foraging patterns as compared with *A. rudis*, because they are found to forage throughout the summer period and are therefore physiologically adapted to cope with environmental stress (Fellers 1989).

In contrast, in one black cherry plot *C. noveboracensis* dominated the plot during the month of June, but this dominance waned in the month of August with the territorial take-over of *A. rudis* ( $t = 1$  h) and *P. imparis* ( $t = 2$  h). This observed difference between *A. rudis* and *P. imparis* corresponds with the temporal separation hypothesis whereby ant species forage during different parts of the day because of microclimatic

conditions. For instance, the foraging activities of *P. imparis* are primarily limited by high temperature levels, for which foraging typically takes during the cooler parts of the day (Fellers 1989).

Although temporal separation is considered to be the primary driver in forming mosaic ant patches at finer spatial scales, another contributing factor to the mosaic patterns can be explained by the fact that subdominant ants tend to avoid dominant ants during periods of competitive interactions. In a classic study Fellers (1989) investigated the daily and seasonal foraging activities of woodland ant species. Although the majority of subdominant ant species in the study overlapped with the foraging activities of dominant ant species, some ant species displayed seasonal separation. For instance, the subdominant *A. rudis* and *Myrmica* species were primarily active from late spring to early fall, whereas the dominant *P. imparis* species were found to be active in the fall and early spring. However, during competitive contests where overlap does occur, subdominant ants can use alternative competitive strategies to avoid dominant ants. It's well-known that evolutionary trade-offs exist between ants in which some species are strong "discoverers" whereas other species are strong "dominators" as they seek available food resources (Fellers 1987, Davidson 1998, Vandermeer & Yitbarek 2011). Thus, the particular balance of discovery and dominance of this collection of species might be an additional contributing factor that determines the way in which competition can indirectly drive the formation of mosaic patchworks.

Our study suggests that self-organization operates at different spatial and temporal scales in this forest ecosystem. At a larger scale (the level of the 18-ha plot), we found that certain ant species only occurred in single habitats, whereas other ant species co-occurred in multiple habitats. We believe that ant associations with tree patches are likely the result of exogenous factors, such as the availability of extra-floral nectary and soil moisture conditions. However, more studies are needed to elucidate the direct relationship between ant associations and exogenous factors. Future studies should include topographical variation and light availability as contributing factors to the observed spatial patterns. At finer spatial scales (100 by 100 m), we observed temporal separation among ant species that resulted in the formation of mosaic patches. Temporal shifts in ant occupancy within habitat patches can be attributed to physiological conditions. Although our study showed temporal differences on a daily basis (1 h and 2 h) and within the summer season (May and August), more studies are needed to assess whether the observed transient mosaics maintain themselves.

In summary, our study suggests that both exogenous and endogenous forces are involved in the creation of spatial patterns in these woodland ants. It is particularly interesting that the exogenous forces responsible for some of the pattern are themselves partially determined by biological self-organizing processes (the expansion of tree species from particular nuclei), sug-

gesting the possibility that a cascade of spatial pattern organizing processes is operative.

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