



When are habitat patches really islands?

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ABSTRACT

Here we present a method for determining whether habitat patches are truly functioning as habitat islands. We do so by assessing if the species distribution pattern across the islands, when compared to a mainland pattern, conforms to 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, Pinckney, MI. We assess the tree flora on each hummock and find that hummocks that are at a distance from the mainland forest have fewer tree species than subsets of the mainland having the same area as the island. The four hummocks greater than 350 m from the mainland had significantly fewer species than mainland samples of the same size, while those less than 200 m away were not statistically different. These results suggest that at least some of the hummocks function as biological islands for trees.

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1. Introduction

It is often the case that habitats occur in a patchwork, vaguely suggestive of “islands” of suitable habitat in a “sea” of unsuitable habitat, and bringing to mind modern theoretical formulations, such as island biogeography. 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 and Abele, 1976), some habitat island situations (Brown and Kordic-Brown, 1977), and most recently has provided a framework to think about biodiversity in fragmented landscapes (Simberloff and Abele, 1976). Here we suggest another application—that the predicted patterns of the theory could be used to infer whether the extinction/recolonization process is operative in a given system. This would allow one to determine if, for a given set of species in a given landscape, is a system of putative islands really one of biological islands. A similar conceptual framework was put forth by Bond et al. (1988), but here we combine it with a modern resampling based statistical approach. We use this application to determine if a particular system of island hummocks in a hardwood swamp in southern Michigan function as biological islands with regards to 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 recolonization of the island from the mainland, which happens at a rate inversely proportional to the distance from the mainland. The best way to test if putative islands are biological ones would be to directly measure these extinction and colonization rates, but for long lived organisms these processes take place over a time scale too large to easily measure. The theory of island biogeography provides predictions based on these assumptions of extinction/colonization species turnover that allow us to infer this turnover without directly measuring it. There predictions are: (1) larger islands have more species and (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 extinction/recolonization turnover and thus 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. We are additionally interested to see how these patterns differ if we look at trees of different successional stages within the forest.

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2. 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 the fires escaped therefrom. Subsequent to fire exclusion with European colonization, the subcanopy and understory have been taken over by red maple (*Acer rubrum*), black cherry (*Prunus serotina*) and witchhazel (*Hamamelus virginiana*), plus 15 other less common species, with very few *Quercus* in the subcanopy. This shift in species composition of some northeastern North American forests since European colonization, marked by a decrease in the number of *Quercus* and increase *Acer rubrum*, is well described (Abrams, 1998; Zhang et al., 2000; Heitzman, 2003; McDonalds et al., 2003). In an 18 ha permanent plot on the “mainland” all trees greater than 3.18 cm DBH (less than 10 cm 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 Jedlick et al. (2004). See Appendix for a list of species in the Big Woods plot (Table 1).

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, with the tree flora on each a subset of the Big Wood tree flora (see Appendix). On each hummock two to four (depending on its length) 5 m belt transects were conducted across the short dimension of the island and all trees with DBH >3.18 cm were recorded. We ignored any individuals that grew right along the

Table 1

Description of the putative islands.

Island name	Area (m ²)	Distance (m)	Species number
Big Island	80,571	66	20
Little Big Island	15,003	199	14
Bee Island	12,780	464	12
Hourglass North	6,665	371	10
Hourglass South	5,560	454	8
Period	1,575	769	4
Duloticus East	10,558	84	14
Duloticus West	7,224	164	12

swamp-island border, as these were mostly swamp trees not colonists from the Big Woods. 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 species number on the island. These data were collected in 2007 and 2008 and pooled to get a more complete accounting for the species number of each island.

To resample the transects randomly selected 100 individuals from the transect(s) on a given island and then 100 individuals from a randomly place ‘transect’ on the Big Woods mainland of the same size as the island transect(s). We repeated this process 1000 times to difference in number of species for each island samples compared to similar samples of the mainland. This difference was compared to the distance between the island and mainland and the area of each island. 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 continuously forested at least since 1940 (see Fig. 1) and considered to be the main source area. The areas were estimated when we conducted the transects in October 2008. The size of the islands is variable expanding in dry times, during the driest Duloticus east and west and Hourglass South and North each form single islands.

This resampling was then redone separately with two subgroups of species. The first, called the ‘old’ species, included

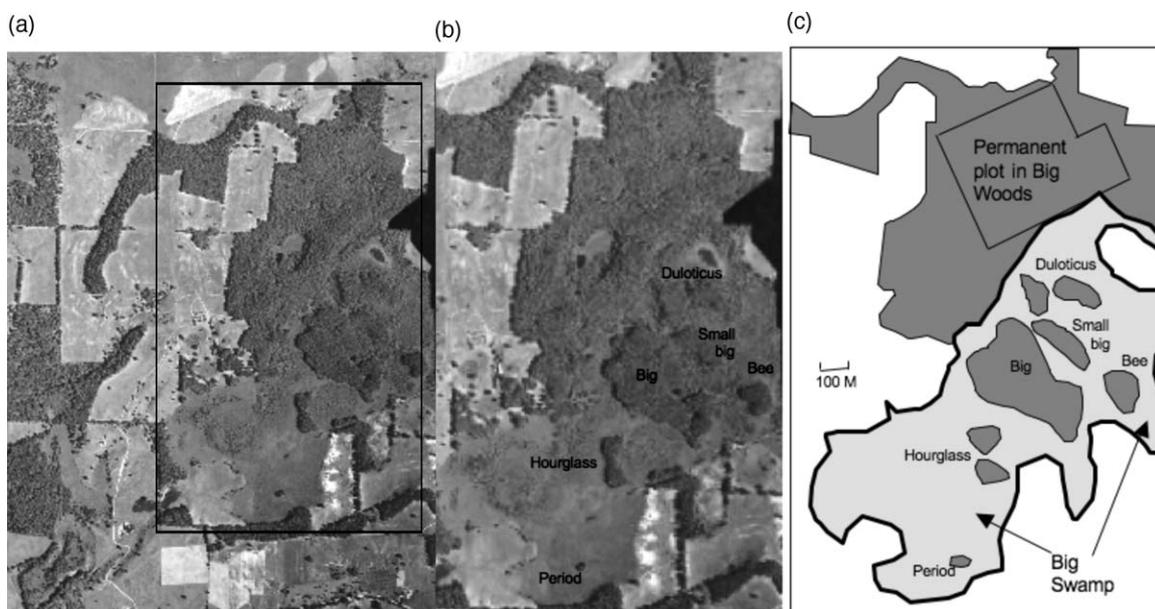


Fig. 1. (a) An aerial photograph of the study region from 1940. The area to the north of the swamp is heavily forested, while that to the south is largely grazing land. (b) A close up from this photograph highlighting the islands in the swamp and the forested area to the north. (c) A cartoon representation of the photograph in (b).

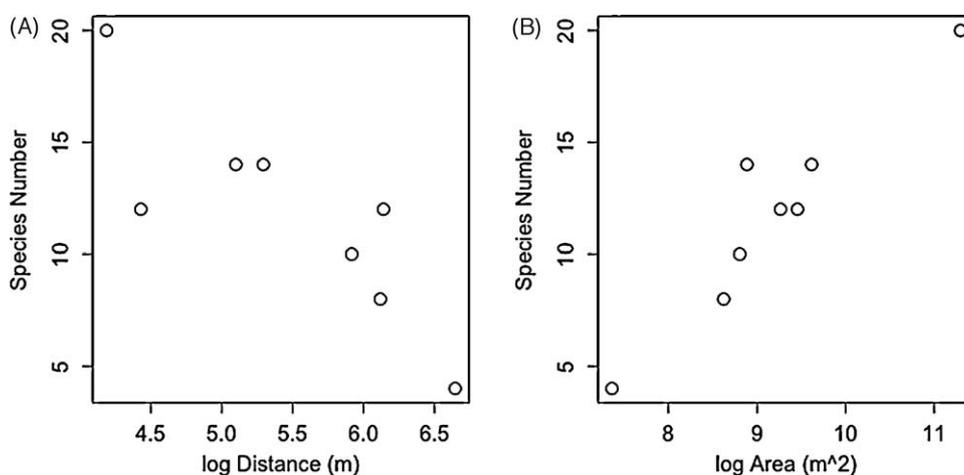


Fig. 2. The total number of species on each island versus that islands size and distance to the mainland.

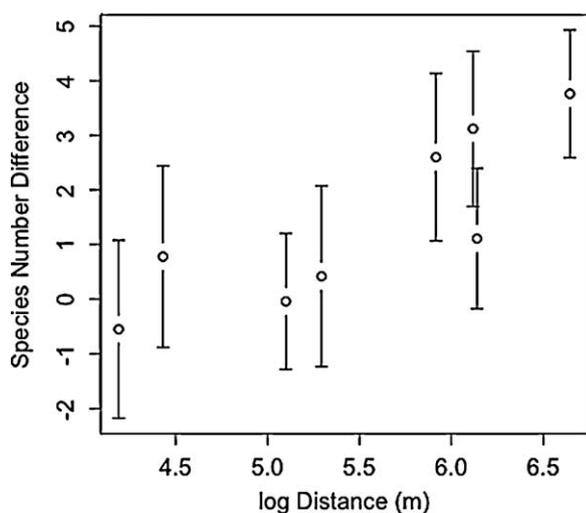


Fig. 3. The relationship between island distance from the mainland and the number of species in the Big Woods sample minus the number in the island transects resamples. Bars indicate the standard error.

the five ‘canopy’ species which have formed canopy of the Big Woods forest currently and before European colonization: *Q. alba*, *Q. velutina*, *Q. rubra*, *C. glabra*, *C. ovata* and *C. cordiformis*. The second group, called the ‘young’ species included all others, which maybe

have been present in the Big Woods before European colonization but have most likely greatly increased their numbers (Abrams, 1998; Zhang et al., 2000; Heitzman, 2003; McDonalds et al., 2003). This will allow us to examine the temporal scale of island colonization.

3. Results

Our results confirm the prediction of the theory of island biogeography; larger island had more species and islands closer to the mainland had more species (Fig. 2). In addition resamples of the transects of the four islands closest to the mainland, all less than 250 m away, did not have a significantly different number of species than Big Woods samples of the same size (Fig. 3). On the other hand, Big Woods resamples had significantly more species than resamples of the transects of the four islands farther than 250 m away from the mainland (Fig. 3). The Big Woods samples had between, on average, one to three and a half more species than the island samples.

This difference in species number was solely driven by the difference in the number of ‘young’ species. The Big Woods resamples had significantly more ‘young’ species than the island resamples for the four farthest islands (Fig. 4). While, for all islands, no matter their distance from the mainland, there was no statistical difference between the number of ‘old’ species in the island resamples and in the Big Woods resamples (Fig. 4).

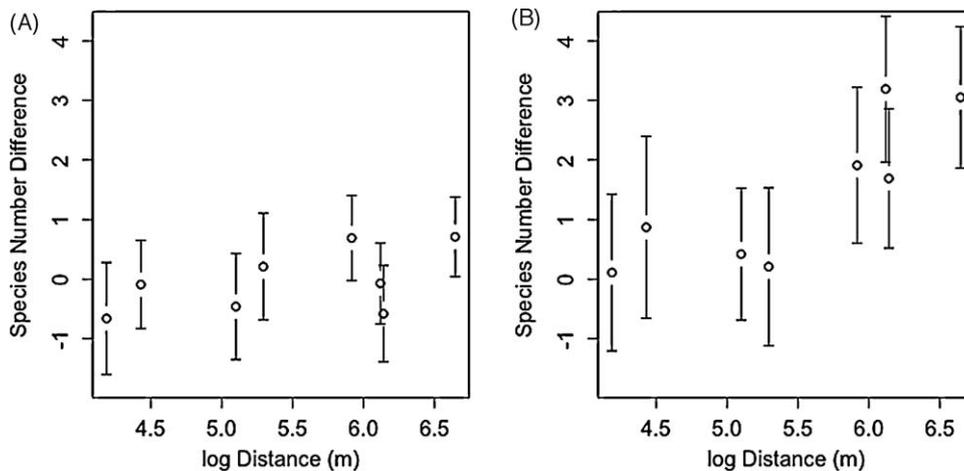


Fig. 4. The relationship between island distance from the mainland and the number of species in the Big Woods sample minus the number in the island transects resamples broken up by species type. Bars indicate the standard error. (a) For ‘young’ species, see Section 2 for description, and (b) for ‘old’ species.

4. Discussion

These results suggest that the hummocks located at a distance greater than about 250 m function biologically as islands, while the closer islands, even though they are not contiguous, are functioning biologically as extensions of the forest. Thus nearby islands are re-colonized at a rate not that much different than the mainland recolonizes local extensions within itself, while the furthest 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 150 years or more, and the distinct assemblage of understory has much more recently been dispersing into the overall area (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 for the more recent species the hummocks look even more like biological islands, but for the older species the relationship between distance and proportion is only marginally significant. This may suggest that the island pattern may be a temporary phenomenon until the more recent species in the forest have time to colonize the farther islands.

This could also be explained by a stepping-stone model in which the furthest islands are colonized from other islands not the mainland. This process could take many decades to complete, in which case species which have a long history on the mainland have had time to 'step' out to the furthest island, while those whose numbers have increased only recently have not had time.

The procedure of looking for pattern as a signal of the island biogeographic process could be a useful way to assess the impact of habitat fragmentation in human-impacted systems. It could be used to determine if a system of fragmented habitat function as biological islands, and more specifically for which segment of the biota they do. It may be 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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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.foreco.2009.07.060](https://doi.org/10.1016/j.foreco.2009.07.060).

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