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Island biogeography: the effect of area and isolation on forest composition

Nathan J. Meyer 1996

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<u>Commons Attribution-NonCommercial-NoDerivatives 4.0</u> <u>International License</u>. MEYER, NATHAN J. Saint Olaf College, 1500 Saint Olaf Ave. Northfield, MN 55057-1001, USA. Island biogeography: the effect of area and isolation on forest composition.

The purpose of this study was to describe the effects of stand area and degree of isolation from surrounding stands on the composition of fragmented continental forest stands that are surrounded by "oceans" of human development. Three stands were chosen in southeastern MN, near Saint Olaf College that maximized the difference in relative size and isolation, and minimized the difference in environmental factors (soil composition, drainage etc.). The woody plant/seedling, sapling, and mature tree compositions were sampled at nine random points within each stand. Any compositional differences were then compared with differences in area and distance from surrounding stands. Results suggested that there were compositional differences between the stands. However, these differences were not significantly attributable to either stand area or relative isolation. Possible sources of error are highlighted, and avenues for future research are discussed

Island Biogeography: The Effect of Area and Isolation on Forest Composition

By: Nate Meyer

Introduction:

In the late 1970's, the theory of island biogeography was often being applied by conservation biologists striving to preserve continental habitat fragments. Due to agricultural and industrial development, much of the original continental habitats have been destroyed. Consequently, restoration and preservation efforts must often be aimed toward isolated fragments of hospitable land that have been overlooked by developers. Theoretically these fragments, lying like islands in a "sea" of human development, are analogous to landbridge islands (Diamond 1972). Basically, the biologists were using the theory in an attempt to answer a question of size (Lewin 1984; Higgs and Usher 1980). Is the preservation/restoration of a few isolated large parks, or a larger number of less isolated small parks a more cost effective means of protecting diversity?

However, the analogy between continental land fragments and islands has been the subject of recent criticism (Doak and Mills 1994). Research (Case and Cody 1987, Weins 1995) has pointed out that land fragments include a wide range of factors differing from conventional island biogeography. The theory might be much more complex when applied to land fragments. While it is generally agreed that species diversity increases as a function of fragment area, there is debate concerning the comparative isolation of land fragments and true islands. Doak and Mills (1994) explain that the intent of the original authors of the

theory of island biogeography was not that land fragments and true islands are completely analogous. MacArthur and Wilson (1967) and MacArthur (1972) repeatedly described the isolated fragments of habitat as islands, but they were also careful to differentiate them from oceanic islands by saying that the later "are separated by a vacuum insofar as land birds or insects are concerned, whereas mainland islands are separated with other habitats filled with birds and insects (from MacArthur 1972:105)."

Yet, there is a possibility that the theory of island biogeography may still be appropriately applied to the vegetative makeup of a development-bound habitat fragment. Although the degree of isolation of animal species within such fragments is questionable, plant species are likely to be as constrained from emigration and immigration within such habitats as they would be on a water-bound island. Unlike animal motility, most plant populations must move gradually by the mechanisms of seed dispersion. Subsequently, it is almost impossible for plants to move through developed habitat. For instance, grasses invading an agricultural plot will inevitably be cut down to make way for the "cash" crop. Thus, a developed area essentially becomes a barrier, effectively halting population movement. As a result, plant populations must "jump" over developed areas, much like bodies of water, if they are to emigrate from isolated land fragments.

However, few studies have described isolated plant populations in terms of the theory of island biogeography. One experiment (Kadmon and Pullman 1993) suggests that the degree of isolation does play a role in the vegetative composition of islands in Clarks Hill Reservoir in Georgia. Yet, it is obvious that before the theory of island biogeography may be adequately applied to the vegetative composition of continental land fragments, more information concerning the effect that the relative isolation and habitat area exert on the vegetative composition of land fragments needs to be gathered. Basically, two questions need to be answered: a) how does the degree of isolation relate to the species composition of vegetation within land fragments, and b) what effect does the fragment area have on its vegetative composition?

This study provides a starting point for answering these questions. The aim of this study is to scrutinize isolated forest fragments in the largely agricultural setting of the Cannon Valley Watershed in Southeastern Minnesota according to theory of island biogeography. The composition of forests stands, isolated among a "sea" of farm fields are compared according to relative size and distance from surrounding stands. The null hypotheses tested were: a) that fragment area has no affect on vegetative species composition, and b) that relative isolation has no effect on vegetative species composition.

Materials and Methods:

Site Description:

Three isolated forest stands were selected within the Saint Olaf College area that maximized the difference in relative size and distance from other stands, and minimized the difference in environmental factors (soil composition, drainage etc.). Site 1 is located directly adjacent to the southern side of the

campus. Formally known as "Norway Valley," it contains about 9.754 hectares of trees. Both site 2 and site 3 lie North of site 1, directly adjacent to the southern side of Hwy. 23. Site 2, comprised of 4.83 hectares, is located on the eastern edge of the Shea/Ferris property. Site 3, comprised of .836 hectares is located along the southwestern edge of Hwy. 23--where the highway curves from a North/South to East/West direction. Site 1 and site 2 are separated by 2.27 km, while site 3 is separated from site 1 by 2.83km, and site 2 by .335km. The sites were sampled one week apart from each other during early to late October, 1995. Experimental Design:

Three transect lines were set in each stand along a North/South directional axis, and spaced throughout the stand to maximize the sample area. In order to minimize the effect of sampling upon the results (Curran, Hill, and Foody 1994), three points were spaced randomly along each transect line for a total of nine sample points in each stand--twenty-seven total sample points.

Standardized quadrats (Brower, Zar, and von Ende 1989) were then employed to sample woody plant and tree vegetation at each point. Seedlings (<0.5m) and woody plants were identified within 0.71m x 1.41m plots. Saplings (>0.5m and <13 DBH) were identified within 2.24 x 4.47m plots. Mature trees (13 and above DBH) were sampled according to the point-quarter method developed by Cottam and Curtis (1956). The diameter of each mature tree was also measured

The sample data was used to construct stand tables for each test area, giving the densities of woody plants, and tree species within each site. In

addition, importance values were computed for all mature tree species. An ANOVA test was used to compare the variance from the mean of mature tree diameters between both site and individual species. The variance from the mean between sites of both seedling and sapling densities was also compared using ANOVA. All statistical tests were computed using the *Statview 7-users* program (Macintosh version).

In order to quantify species diversity, the numbers of seedlings, saplings, and mature trees sampled of each individual species within each site were totaled. With these numbers, the *Morisita 1.2* program (designed by Dr. Ferris for the Macintosh) was used to compute both Shannon and Simpson diversity index values for each site. Differences between the Simpson values were also compared for statistical significance.

Finally, the results of the data were compared to the null hypotheses, and conclusions were drawn.

Results:

	Comparison of the mean VA test showed significan		r mature trees at each site 006) between sites.
Site	Mean Diameter	Std. Dev.	Std. Error
1	42.006	22.151	3.692
2	30.861	16.126	2.688
3	25.622	13.92	2.32

An ANOVA test showed a highly significant (p=.0006) difference between the mean diameter of mature trees sampled at each site (Table 1). Moreover,

there was a positive correlation between site area and tree diameter. The mean diameter tended to increase as site area increased. The total coverage values for each site support this trend (Table 2). Over eleven times more area was covered by mature trees in site 1 than site 2, and nearly two times more area in site 2 than site 3. This trend is attributable to the differences between the composition of mature trees at each site. An ANOVA test also showed a significant (p=.0001) difference between the mean tree diameters of each species sampled (Table 3). Essentially, some of the trees that were sampled within the three sites grow larger than others. Furthermore, the importance values of the larger trees tended to increase as site area increased. Both the first (Norway spruce), third (basswood), and fourth (sugar maple) largest tree species that were sampled had high importance values at site 1. In fact, over 50% of the mature tree species sampled at site 1 were ranked in upper five largest species. On the other hand, both site 2 and site 3 each contained two of the larger trees; but, the fifth largest tree (boxelder) had by far the highest importance value (above 1) in each stand.

Table 2: A compa	arison of the total co	verage values (in square meters) for the
three sites.		
**************************************	Site	Total Coverage
	1	.351
	2	.031
	3	.016

Table 3: The results of an ANOVA test showing significant (p=.0001) difference between the mean tree diameters (cm²) of mature tree species sampled at the three sites. The trees are placed in order of descending mean diameter, and the importance values for each species at the tree sites have been added.

Species	Mean Diameter	Std. Dev.	Std. Error	Impo	ortance Va Site	alue	urbinnessaut
Norway				1	2	3	
spruce	66.822	16.625	5.542	.511	0	0	
Cottonwood	59.975	15.151	7.575	0	.667	0	
Basswood	52.7	20.605	8.412	.981	.261	0	
Sugar Maple	34.759	16.615	3.542	.941	0	.422	
Boxelder	26.664	11.836	1.784	0	1.323	1.71	
Prickly Ash	25.367	3.194	1.844	0	.285	0	
American elm	23.033	9.254	5.343	.3	0	0	
Slippery elm	20.7	6.255	1.615	0	.375	.871	
Ironwood	17.45	5.303	3.75	.161	0	. 0	

However, there was no significant difference between the mean diameters of individual tree species represented in the samples from two sites (Table 4). Regardless of stand area, the trees grew equally well in each site in which they were sampled. In fact, in the case of both basswood and sugar maple trees, the mean diameter of the sample was higher in the smaller sites.

Species	Sample sites	Mean Diameter	Std. Dev.	Std. Error	p-value
Slippery	site 2	22.2	6.419	2.871	.6541
elm	site 3	20.5	6.916	2.187	
Boxelder	site 2	26.059	10,465	2.231	.8548
	site 3	25.432	12.08	2.575	
Basswood	site 1	49.9	26.004	13.002	6889
	site 2	58.3	.424	.3	
Sugar mapl	e site 1	33.733	14.193	3.345	.552
	site 2	39.375	27.5	13.75	

Site 2 exhibited the highest mean densities of both trees and seedlings, while site 1 had the highest mean density of saplings. However, there was little difference between the densities of the mature tree stands at each of the sites (Table 5). In fact, the difference between mature tree densities only ranged from .004-.0044. The seedling and sapling densities from each of the three sites were also very similar (Table 6). Mean sapling densities showed a slightly higher range of difference (.011-.1)than either of the other density classes, and mean seedling densities ranged from .778-1.444. Furthermore, ANOVA tests showed no significant differences between the mean densities of seedlings and saplings that were sampled at the three sites.

Table 5: Summery of the total densities of mature trees (individuals/m²) sampled at each of the three sites. The density value represents the summation of the total densities of each tree species sampled within the site.

Site	Density	
1	.02	
2	.0244	
3	.024	

Table 6: Results of ANOVA tests of differences between mean plot densities (individuals/m²) of a) saplings and b) seedlings that were sampled at each site.

Saplings	\$			
Site	Mean Density	Std. Dev.	Std. Error	p-value
1	.511	.395	.132	.8185
2 .	.422	.192	.064	
3	.411	.457	.152	
Seedling	gs			
Site	Mean Density	Std. Dev.	Std. Error	p-value
1 .	1.778	1.641	.547	.3582
2	3.222	1.922	.641	
3	2,444	2.603	.868	

Finally, a total of eight species were sampled within the mature tree, seedling, and sapling plots at site 1 (Table 7). There were also eight species in the total sample from site 2 (Table 8), and six species in the total sample of site 3 (Table 9).

Table 7: A list of species sampled within the plots at site 1. Values represent the total number of individuals within each maturity class that were sampled within the site.

Species	Number	Totals		
•	Tree	Sapling	Seedling	
Norway spruce	9	0	0	9
Sugar maple	18	11	4	33
Ironwood	2	2	0	4
American elm	3	0	0	3
Basswood	4	1	0	5
Elderberry	0	26	3	29
Slippery elm	1	0	0	1
European buckthorn	0	3	9	12

Table 8: A list of species sampled within the plots at site 2. Values represent the total number of individuals within each maturity class that were sampled within the site.

Species	Number	Total			
· ·	Tree	Sapling	Seedling		
Boxelder	22	10	0	32	
Slippery elm	5	2	0	7	
Basswood	2	0	0	2	
Prickly ash	3	1	0	4	
Cottonwood	4	0	0	4	
European buckthorn	0	20	23	43	
Elderberry	0	1	1	2	
Gooseberry	0	0	5	5	

Table 9: A list of species sampled within the plots at site 3. Values represent the total number of individuals within each maturity class that were sampled within the site

Species	Number	Total		
•	Tree	Sapling	Seedling	
Sugar maple	4	13	5	22
Slippery elm	10	10	0	20
Boxelder	22	6	0	28
Elderberry	0	8	2	10
European buckthorn	0	0	14	14
Gooseberry	0	0	1	1

Both site 2 and site 3 had one mature tree species represented within their respective samples that was also represented in the sample from site 1. Site 2 and site 3 had two mature tree species represented in both samples. However, no species was represented in the mature tree samples of all three sites. Sugar maple saplings were represented in the sapling samples of both site 1 and site 3, and the European buckthorn was represented in the sapling samples of site 1 and site 2. Both elderberry and slippery elm saplings were represented in the samples of all three sites. Likewise, both elderberry and European buckthorn

were represented in the seedling samples of all three sites. Seedling samples from site 1 and site 3 each contained sugar maple seedlings, and gooseberry seedlings were contained in the samples from site 2 and site 3. In addition, both the Shannon and Simpson diversity indices showed little differentiation between the species diversities of the three plots (Table 10). The difference in Shannon values ranged from .06-.09, and the difference between Simpson values ranged from .05-.08. Furthermore, the difference between diversity values from site 2 and site 3 was the only comparison deemed significant (p=.05).

indices. The or	nery of the results from both Shanno ly significant difference between Si and site 3 (p=.05).	
Site	Shannon value	Simpson value
1	1.65	.76
2	°1:56	.71
.3	1:59	79

Discussion:

There are obvious compositional differences between the stands that were sampled at the three sites. Site 1 was composed predominately by sugar maple, basswood, and Norway spruce. On the other hand, both site 2 and site 3 were composed mainly of boxelder trees. In addition, there was a significant difference between the mean diameter and total coverage of the mature trees sampled in each stand. This difference is attributable to significant differences between the mean diameters of the tree species within each of the samples. Essentially, site

1 was composed on average of naturally larger trees than site 2, which contained more naturally large trees than site 3.

However, it is unlikely that these compositional differences are related to stand area. First of all, there was no significant difference between the mean diameters of identical species that were sampled at two of the sites. Each of the four tree species that were represented in the samples of two sites had attained nearly the same mean diameter in both instances. Hence, tree growth was not suppressed within the smaller sites.

Instead, the differences in stand composition between the sites seems to be attributed to the respective ages of the stand. In a study of the geological characteristics of the Saint Olaf Campus, Edward W. Schmidt (1945) points out that site 1, except for the planting of Norway spruce, has remained relatively undisturbed since the inception of the college. However, the stands on both site 2 and site 3 have only recently been allowed to regrow (Dr. Kathy Shea *personal communication*). Subsequently, this difference in age is directly related to the successional stages of each of the three sites.

The large, shade tolerant trees, such as Norway spruce, sugar maple, and basswood, that had the highest importance values at site 1 coincide with later successional stages (Huston and Smith 1987). On the other hand, the smaller, and less shade tolerant boxelder species that predominate the compositions of site 2 and site 3 intimate an early stage of succession. It is also noteworthy to point out that the similar stage of succession evident at site 2 and site 3 may be the reason that the comparison of their diversity values was significant.

Furthermore, the compositions of the stands in this study correlate with Bray's (1956) conclusion that forests in southeastern MN--formerly known as the Big Woods ecosystem--conform to the tolerance model of succession.

Recognition of the fact that the three sites described within this study are representative of different stages in the tolerance model of succession may help to explain the extreme similarity between the diversity of species sampled at each site. Krebs (1994) points out that stands in the later stages of tolerance succession will be composed primarily of shade tolerant species, which indirectly inhibit the growth of more intolerant species by decreasing the amount of light reaching the forest floor. By virtue of this fact, shade intolerant species will be pressed toward extinction as succession progresses unless a disturbance in the canopy allows light to reach the floor of the site. Therefore, if site 1 has experienced few episodes of disturbance, the diversity of species in the stand may be depressed by the predominance of shade tolerant species. Moreover, it is possible that the diversity of site 2 and site 3 may decrease as the stand ages, and more shade tolerant species reach maturity. Essentially, this means that differences in the successional stages of the stands have an effect on their diversity that may preclude a significant measure of differences resulting from site area and isolation. In the future, it may be interesting to follow-up with an identical study of these sites. For instance, evidence of the maturation of shade tolerant species is visible for site 3 in the large number of sugar maple seedlings and saplings that were sampled in the plots. As site 2 and site 3 reach later stages of succession, differences in diversity between the sites, resulting from

stand area and degree of isolation, will probably be more evident. In addition, through future studies, it would be possible to note the effects of stand area and isolation on the rate of succession.

It is also possible that the average longevity of the woody vegetation sampled in this study contributes significantly to the lack of difference between the diversities of the sites. In a study conducted by Simberloff and Wilson (1970), it took over 720 days, and numerous generations for the species diversity of insects to reach a state of equilibrium. Yet, the longevity of insects is much shorter than the longevity of trees. As a result, it may take years for a stand of trees to reach its equalibrial species diversity. Obviously, this means that the time scale of this study is not long enough to accurately describe the diversities of the test stands. While it is possible that the diversity of site 1 has reached a state of equilibrium, the diversity of site 2 and site 3 is most likely still fluctuating because of the young age of the sites. In order to negate this error, this study should be repeated for a number of years. Concurrently, it may also be advantageous in the future to center sampling efforts on herbaceous plants because of their short lifespans. This would lead to more accurate samples of diversity in a shorter period of time.

The size of the samples at each site are also a source of possible error. While nine plots may have been a large enough sample to accurately illustrate the diversity of the stand in site 3--.836 hectares, it is doubtful that this number of plots depicts the diversity of the stand in site 1--9.745 hectares, which is nearly ten times as large. It is probable that species resident in the larger stands were

not represented in the plots because a large portion of the stand was not included within the transects. Therefore, future studies should be conducted with higher sample sizes that decrease the chance of misrepresenting the diversity of larger stands.

In addition, the relatively small number of sample plots at each site may not have been large enough to significantly describe any differences between the seedling, sapling, and mature tree densities at the three sites. Like measurements of diversity, the densities were also very similar for each of the plots. However, in this case, error is unlikely because the p-values from ANOVA tests of the difference between the densities at each site were extremely high. Due to this fact, the chance that the density values would be significantly changed by the addition of more sample plots is very small. Thus, it is safe to conclude that stand area, and the degree of isolation do not affect the densities of seedlings, saplings, or mature trees.

Finally, there was no trend relating the diversity of seedling, sapling, and mature tree samples with the relative isolation of the test sites. The occurrence of a species in the samples of two or more sites appeared to be entirely random. This supports the study conducted by Kadmon and Pullman (1993), which concluded that inter-island distances had no statistically significant effect on composition. However, the low sample size in this study most likely makes the conclusion questionable. It is probable that the relative isolation of three sites did not provide a statistically viable sample of inter-stand distances. The range of distances may not have been high enough to show differences. Furthermore,

other stands, which were not tested, lay at intermediate points between the test sites. Thus, the similarity between the samples of the more distant sites could be attributed to the fact that the gap between stands may not be as large as this study reported. In order to correct these problems, future studies need to sample more plots, and correctly account for the degree of isolation by sampling any intermediate sites as well.

In conclusion, the results of this study showed a significant difference between the stand compositions of three study sites. However, these differences were not related to the relative area or degree of isolation of the stands. As a result, both of the null hypotheses are accepted. Yet, numerous sources of error within the experimental design of this study may possibly make these conclusions insignificant. For this reason, the effect of stand area and degree of isolation on the vegetative composition of continental habitat fragments needs to be the subject of further study. Moreover, in order to diminish the possibility of error, future studies need to be centered on stands of similar age, and successional stage. In addition, more sites need to be sampled (including any intermediate stands), and more plots within each site need to be sampled. Also, the timescale of these studies needs to be lengthened to include numerous generations of the subjects being sampled. Due to the necessary length of these studies, future studies may be more effectively geared toward smaller herbaceous plants within each site, and studies centered on woody vegetation may be narrowed to test the effect of either area or isolation, not both.

Essentially, this study provides a "snapshot" of a single instant within a much larger process. Although the theory of island biogeography does not seem to apply within this instant, the conclusions of this study do not entirely rule out the possibility that it plays a role in the larger process. At this point, it is not safe to assert whether the theory can be applied by conservation biologists to questions concerning the preservation of isolated continental stands of vegetation. Yet, this study highlighted a number of solutions that will allow the extension of this "snapshot" into a description of the role of the theory of island biogeography in the larger process of vegetative development. By following these criteria, it is probable that the question can be adequately answered.

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