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ISLAND BIOGEOGRAPHY: EFFECT OF GEOGRAPHICAL ISOLATION ON SPECIES COMPOSITION[1]

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Abstract. Island biogeography theory attempts to explain and predict among-island variation in species richness. However, two islands with the same number of species may still differ from each other considerably in their species composition. In this study we test the hypothesis that among-island variation in species composition is predictable and can be related to the corresponding differences in distance to the mainland. We focus on woody plants inhabiting islands in the Clarks Hill Lake, a reservoir completed in 1954 on the Savannah River, between Georgia and South Carolina, USA. Two groups of islands were sampled: islands that were logged prior to the filling of the reservoir and islands that were not logged. Each island was surveyed for the presence of all tree and shrub species, and its distance from the mainland was determined. In both groups of islands, the degree to which two islands are similar in their species composition was negatively and significantly correlated with their difference in distance to the mainland. Species richness, however, was correlated with distance to the mainland only on logged islands. We conclude that geographic isolation may affect species composition on islands, and that such an effect may occur even in the absence of a corresponding effect on species richness.

Key words: colonization; island biogeography; isolation effects; logging; similarity indices; species composition; woody plants.

INTRODUCTION

Theoretical and empirical studies of island biogeography traditionally have focused on explaining variation in species richness among islands (Preston 1962, MacArthur and Wilson 1963, 1967, Diamond and Mayr 1976, Wilcox 1978, Dueser and Brown 1980, Heaney 1984, Hobbs 1988, Heatwole 1991). Yet, two islands that have the same species richness may differ considerably in species composition, ranging from complete similarity (all species are common to both islands) to complete dissimilarity (no species in common). Understanding the ecological and geographical factors that are responsible for such a variation is important to the development of a more comprehensive theory of island biogeography.

In this study we demonstrate that differences among islands in the degree of isolation may lead to related differences in species composition. We focus on woody plant species (trees and shrubs) inhabiting islands in the Clarks Hill Lake, a reservoir completed in 1954 on the Savannah River, between Georgia and South Carolina. Several properties of this island system make it particularly suitable for testing the effect of isolation on species composition. First, the vegetation on the mainland surrounding the reservoir is relatively homogeneous, so that all islands can reasonably be assumed to receive colonizers from the same species pool. Second, the large number of islands available makes it possible to select islands that are relatively similar in physiography, edaphic conditions, and area, but differ from each other substantially in the degree of isolation. Third, some of the islands were logged prior to the filling of the reservoir, and it has previously been found that such islands differ considerably from unlogged islands in the effect of isolation on species richness (R. Kadmon and H. R. Pulliam, *unpublished data*). Most importantly, on logged islands, species richness is negatively correlated with distance to the mainland ($r = -0.94$, $P < .002$), while on unlogged islands species richness is independent of distance to the mainland ($r = 0.14$, $P > .1$). The presence of logged vs. unlogged islands in the same system allowed us to test the effect of isolation on species composition under two contrasting situations: in the presence of a strong distance effect on species richness (unlogged islands), and in the absence of such an effect (logged islands).

THEORETICAL CONSIDERATIONS

Predictable patterns of among-island variation in species composition may be produced by a variety of factors. For example, differences among islands in habitat conditions may lead to related differences in species composition if the colonizing species differ from each other in their habitat requirements. Similarly, differences among islands in distance to the mainland may cause related differences in species composition if the potential colonizers differ from each other in their dispersal ability. Island area may also be important in

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TABLE 1. Indices used to quantify between-island similarity in species composition. S_{ij} = number of species common to islands i and j; S_i = number of species present on island i but absent on island j, S_j = number of species present on island j but absent on island i, S = number of species present on at least one of the studied islands but absent on islands i and j.

Index name	Index equation
Jaccard	$J = S_{ij}/(S_{ij} + S_i + S_j)$
Dice	$D = 2S_{ij}/(2S_{ij} + S_i + S_j)$
Simple Matching	$SM = (S_{ij} + S)/S_{ij} + S_i + S_j + S)$
Sokal and Sneath similarity measure I	$SS = 2(S_{ij} + S)/(2S_{ij} + S_i + S_j + 2S)$

determining species composition if the colonizing species differ from each other in their "minimum area" requirements. In all of these cases, some property of the island (the available habitat conditions, the degree of isolation, or the area of the island) restricts its actual species composition to some subset of the available species pool. The important point is that this subset of species is not a random sample of the potential colonizers but, rather, a result of some constraints imposed by the properties of the island.

Consider a system of M islands that receive colonizers from a common species pool of N species inhabiting the mainland. Each species has some probability of reaching each of the islands depending on its dispersal ability, its abundance on the mainland, and the distance of the relevant island from the mainland. If the potential colonizers differ from each other in dispersal ability or abundance on the mainland, islands at different distances from the mainland can be expected to be colonized by different subsets of species, and, consequently, similarity between islands in species composition should be positively correlated with their similarity in the degree of isolation. Here we provide evidence supporting this prediction.

METHODS

The island system

Based on information from air photographs (USDA 1942, 1955), we sampled seven islands in which all mature trees were logged prior to the filling of the lake, and five islands that were not logged. We hypothesized that logged islands had fewer woody plant species than unlogged islands at the time of their disconnection from the mainland. In selecting the islands for each group, we attempted to maximize among-island differences in the degree of isolation, but to minimize differences in other respects. Distances between the islands selected and the mainland ranged from 20 to 816 m (average: 268 m), island area ranged from 0.28 to 0.84 ha (average: 0.59 ha), the maximum elevation of islands ranged from 1 to 3 m (average: 1.4 m), and distances among the selected islands ranged from 0.5 to 13 km (average: 4.7 km). Differences between the two island groups in all attributes were not significant, except that logged islands had fewer species than unlogged islands (average $\pm$ 1 SD = 28.0 $\pm$ 4.2 and 33.2 $\pm$ 1.3 species on logged and unlogged islands, respectively; R. Kadmon and H. R. Pulliam, *unpublished data*).

Sampling of the vegetation

The islands selected for the study were sampled for the presence of tree and shrub species during April–May 1991. Each island was surveyed by walking along concentric belts 5 m wide, starting from the shore of the island and progressing towards its interior. All tree and shrub species were recorded, including saplings and seedlings.

Data analysis

An index expressing the degree to which two islands, i and j, are similar in their degree of isolation was quantified as DIS = $|D_i - D_j|$, where D_i and D_j are distances from the mainland of islands i and j, respectively. Distances were measured on topographic maps (USGS 1971). Note that DIS is a measure of dissimilarity: its value is zero if $D_i = D_j$, and it increases with increasing difference between D_i and D_j.

Between-island similarity in species composition was calculated using four different measures of similarity (Table 1). By using several alternative indices we attempted to reduce the likelihood that our results would be dependent upon the specific properties of the index being used. The four indices—Jaccard (J), Dice (D), Simple Matching (SM), and Sokal and Sneath (SS)—differ from each other in respect to two main properties (Janson and Vegelius 1981, Hubalek 1982): (1) whether only joint presences (as in J and D) or also joint absences (as in SM and SS) occur in the numerator, and (2) whether matches are double-weighted (as in D and SS) or not (as in J and SM).

In analyzing the data we distinguished between islands that were logged and islands that were not logged prior to isolation. Using the four similarity indices listed in Table 1, four species-similarity matrices were constructed for each group of islands. A fifth matrix was constructed for the DIS values. The elements in each of the species-similarity matrices were then tested for their association with the corresponding elements in the DIS matrix using Mantel's randomization test (Manly 1991). This test measures the association between the elements of two matrices by a suitable statistic and determines the significance of this by comparison with the distribution of the statistic found by randomly reallocating the order of the elements in one of the matrices. The Pearson correlation coefficient was used as the test statistic because there was no evidence for nonlinearity in the data. Each test was based on 5000 random permutations that were performed using a FORTRAN program available in Manly (1991). Significance levels were based on one-tailed tests.

Additional Mantel tests were performed to analyze the relationships between each of the species similarity

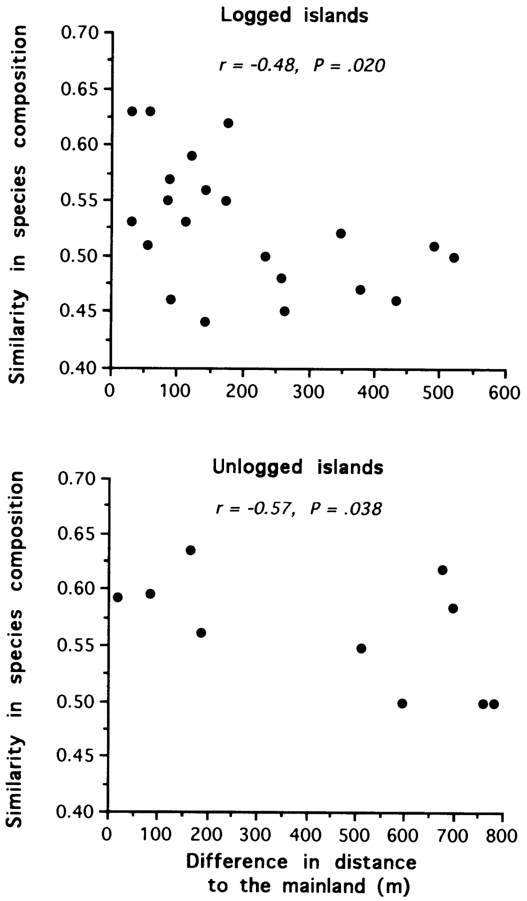

FIG. 1. Between-island similarity in woody species composition expressed by the Jaccard index and plotted against the corresponding between-island difference in distance to the closest mainland.

indices and (1) similarity in island area, (2) similarity in island elevation, and (3) inter-island distance. Similarities between islands in area and elevation were quantified using the same approach that was used to quantify similarity in distance to the closest mainland, except using area and elevation in place of distance. Distances between islands, island elevations, and island areas were measured on topographic maps (USGS 1971). Island areas were quantified using a Tectronix 4054 computer with a digitizing tablet.

RESULTS

Sixty-four tree and shrub species were recorded in the study. Of these, 10 species were found on every island: *Pinus taeda, Ulmus alata, Quercus alba, Quercus falcata, Quercus nigra, Juniperus virginiana, Liquidambar styraciflua, Myrica cerifera, Vaccinium corymbosum,* and *Prunus serotina.* On most of the islands *Pinus taeda* and *Ulmus alata* were the dominant tree species. Among the shrubs, *Myrica cerifera, Crataegus flava,* and *Vaccinium corymbosum* were the most abundant species.

The Jaccard index was significantly and negatively correlated with degree of isolation, DIS, in both the logged and the unlogged islands (Fig. 1). Similar results were obtained for the Dice index (data are not shown). In both island groups, the correlation coefficients obtained for the Jaccard and Dice indices were almost identical (logged islands: $r = -0.48$, $P = .020$ and $r = -0.47$, $P = .021$, respectively; unlogged islands: $r = -0.57$, $P = .038$ and $r = -0.57$, $P = .038$, respectively). These results are consistent with our prediction and indicate that the distance of a particular island from the mainland is important in determining its species composition.

Different results were obtained for the Simple Matching index of similarity (Fig. 2). This index was significantly and negatively correlated with DIS in the case of the unlogged islands ($r = -0.59$, $P = .038$), but it was uncorrelated with DIS in the case of the logged islands ($r = -0.16$, $P = .223$). The corresponding correlation coefficients obtained for the Sokal and Sneath

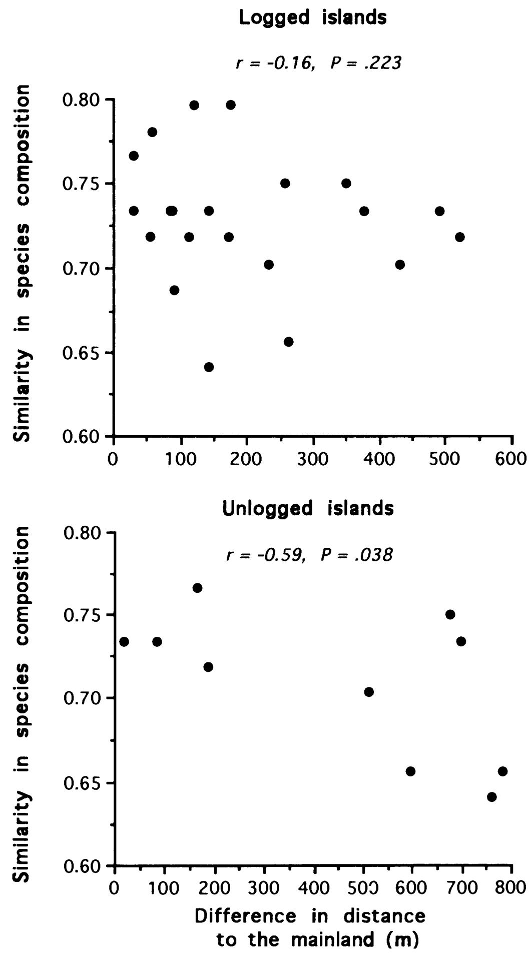

FIG. 2. Between-island similarity in woody species composition expressed by the Simple Matching index of similarity and plotted against the corresponding between-island difference in distance to the closest mainland.

TABLE 2. Correlations of four alternative indices of species similarity (see Table 1) with two measures of island similarity and with inter-island distance.

Index of species similarity	Logged islands		Unlogged islands	
	r	*P*	*r*	*P*
Island area similarity				
Jaccard	0.13	.298	−0.21	.735
Dice	0.14	.291	−0.20	.735
Simple Matching	0.26	.234	−0.11	.628
Sokal and Sneath	0.24	.247	−0.10	.614
Island elevation similarity				
Jaccard	−0.01	.561	−0.19	.781
Dice	−0.03	.572	−0.19	.781
Simple Matching	0.04	.489	−0.19	.780
Sokal and Sneath	0.04	.532	−0.18	.787
Inter-island distance				
Jaccard	0.18	.256	0.39	.136
Dice	0.18	.256	0.39	.136
Simple Matching	0.10	.297	0.34	.171
Sokal and Sneath	0.10	.299	0.33	.169

index were very similar (unlogged islands: $r = -0.60$, $P = .037$; logged islands: $r = -0.15$, $P = .214$). Thus, including joint absences as a component that contributes to "similarity" did not affect the correlation between species similarity and isolation similarity in the case of the unlogged islands, but it reduced the correlation coefficients to nonsignificant levels in the case of the logged islands.

All other factors that were tested for their correlation with species similarity revealed nonsignificant results (Table 2).

DISCUSSION

The results of this study demonstrate that species composition of woody plants inhabiting islands in the Clarks Hill Reservoir is affected by distance to the mainland. Particularly interesting is the fact that such an effect was obtained for the unlogged islands. These islands did not show any correlation between distance from the mainland and species richness (R. Kadmon and H. R. Pulliam, *unpublished data*) but they did show a distance effect on species composition (Figs. 1 and 2). This finding demonstrates that a failure to detect distance effect on species richness does not mean that distance is unimportant in determining patterns of island occupancy.

Previous studies have recommended the use of several alternative indices of similarity when analyzing ecological or biogeographical data (Goodall 1978, Janson and Vegelius 1981). In this study we used similarity indices that differ from each other in two basic properties (Hubalek 1982): the weighting of matches vs. nonmatches, and the sensitivity to joint absences (Table 1). The correlation coefficients obtained for similarity indices in which matches are double-weighted (D [Dice] and SS [Sokal and Sneath]) were very similar to those obtained for indices in which matches and nonmatches receive equal weighting (J [Jaccard] and SM [Simple matching]). This result is not surprising because J and D as well as SM and SS are related monotonically. More interesting is the fact that including joint absences as a component that contributes to the value of the similarity index did not increase (and in the case of the logged islands even reduced) the correlation between species similarity and isolation similarity. Assuming that isolation affects species composition by *preventing* some of the potential colonizers (i.e., those with limited dispersal ability) from colonizing islands at relatively large distances from the mainland, we expected that including information on joint absences in the similarity indices would increase their correlation with the distance–similarity index. The fact that indices containing information on joint absences did not give higher correlation coefficients than corresponding indices based on presence data alone suggests that other factors rather than isolation (e.g., post-isolation extinction events) were important in causing among-island variation in species absence.

Because no previous study has attempted to test for relationships between isolation similarity and species similarity, evaluating the extent to which our results can be generalized to other insular systems is difficult. However, there is some evidence that the distance between islands may be important in determining their similarity in species composition. Power (1975) analyzed patterns of bird species distribution among the Galapagos islands and found that avifaunal similarity is negatively correlated with inter-island distance. Between-island similarities in area and elevation were not correlated with avifaunal similarity (Power 1975). In the system studied by us none of these factors was correlated with species similarity (Table 2). However, in interpreting these results it should be remembered that islands were a priori selected in such a way that among-island variation in area and elevation would be small. The nonsignificant correlations obtained between species similarity and inter-island distance are more interesting because the range of variation in inter-island distance was relatively high (0.5–13 km). Thus, although distances between islands in the system studied by us are much greater than distances between individual islands and the mainland (averages: 4.7 km vs. 268 m, respectively), two islands that are isolated from each other, but have a similar distance to the closest mainland, are more likely to have species in common, than are two islands that are close to each other but differ in their distance to the closest mainland. This result is consistent with the assumption that islands at different distances from the mainland receive colonizers from a similar species pool.

Isolation effects on species richness are well documented in the ecological literature (MacArthur and Wilson 1967, Case 1975, Brown 1978, Wilcox 1978, Dueser and Brown 1980, Scanlan 1981, Heaney 1984, van Dorp and Opdam 1987, Soulé et al. 1988). This study demonstrates that isolation may be important in determining patterns of species composition, and that such an effect can be found even in the absence of a corresponding effect on species richness. Taking these findings into account, as well as identifying other factors that may account for biogeographic patterns of species composition, is important for further development of island biogeography theory.

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