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INTERSPECIFIC INTERACTION AND SIMILARITY
IN SPECIES COMPOSITION

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Biogeographers and ecologists have studied the similarity of species lists from different geographic units for more than 75 years (Jaccard 1908). The idea that factors affecting species distributions will also affect similarity has motivated studies seeking to make inferences about biological phenomena from patterns of similarity. In particular, the Galápagos Islands have been the subject of attempts to investigate the importance of interspecific interactions, especially competition, in determining species distributions (Power 1975; Connor and Simberloff 1978; Simberloff 1978). These attempts have been based on intuitive ideas about the effects of such interactions on similarity, but these ideas have never been rigorously developed. Our primary purpose here is to investigate this theoretical relationship. We begin by addressing the question of what, if any, effects interspecific interactions can have on similarity. Then we ask whether the results of Power (1975) and Connor and Simberloff (1978) suggest that interspecific interactions have had these effects in the Galápagos Islands.

EFFECTS OF INTERSPECIFIC INTERACTIONS ON SIMILARITY

We examine expected values of similarity, treating the distribution of species among islands as an occupancy matrix with R rows representing species and C columns representing islands. Matrix entries $m(i, j)$ equal one if species i is present on island j , and zero if it is absent. For islands j and k ($j \neq k$), similarity is $S(j, k)$, and

$$S(j, k) = \sum_{i=1}^R m(i, j) m(i, k). \quad (1)$$

The expected value of $S(j, k)$ can be written in terms of expected values and

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covariances of the matrix elements

$$E[S(j, k)] = \sum_{i=1}^R E[m(i, j) m(i, k)]$$

$$E[S(j, k)] = \sum_{i=1}^R \{E[m(i, j)] E[m(i, k)] + \text{cov}[m(i, j), m(i, k)]\}. \tag{2}$$

Since the $m(i, j)$ take only the values 0 and 1, $E[m(i, j)] = P[m(i, j) = 1]$, which is the unconditional probability that species i occurs on island j . We define $p(i, j)$ as $P[m(i, j) = 1]$, and equation (2) becomes

$$E[S(j, k)] = \sum_{i=1}^R \{p(i, j) p(i, k) + \text{cov}[m(i, j), m(i, k)]\}. \tag{3}$$

We now consider the implications of this result. Expected similarity is a function of both the $p(i, j)$ and the covariances in equation (3). We call these covariances the intraspecific interisland covariances. Everything affecting the probability that species i occurs on island j will, by definition, affect $p(i, j)$. This includes, for example, any mutualistic abilities, the probability of encountering mutualists, competitive ability, and the probability of encountering a competitor, as well as the more commonly considered factors such as island size and colonizing ability. Thus, one way in which interspecific interactions affect similarity is through their effects on the $p(i, j)$.

The covariances in equation (3) can be written in terms of conditional and unconditional probabilities of occurrence:

$$\text{cov}[m(i, j), m(i, k)] = \{P[m(i, j) = 1 | m(i, k) = 1] - p(i, j)\} p(i, k). \tag{4}$$

These covariances will be nonzero if and only if conspecific populations on different islands are interdependent, that is, if $P[m(i, j) = 1 | m(i, k) = 1] \neq p(i, j)$. Thus, any biological processes that create or modify intraspecific interisland dependence will affect similarity via the intraspecific interisland covariances.

Two types of biological phenomena may affect similarity through these covariances. The first of these is interisland colonization. For example, if species 1 is present on island 1, it probably has been there for some time and has been a potential source of species-1 colonists for island 2. Thus, species 1 is more likely to be found on island 2 when it is present on island 1 than when it is absent from island 1. In other words,

$$P[m(1, 2) = 1 | m(1, 1) = 1] > P[m(1, 2) = 1 | m(1, 1) = 0], \tag{5}$$

and we know that $\text{cov}[m(1, 1), m(1, 2)] > 0$. Hence, interisland colonization tends to increase expected similarity.

This argument is formalized in the analysis of the path diagram in figure 1. The purpose of this analysis is to establish that when interisland colonization is possible, $m(1, 1)$ and $m(1, 2)$ are positively correlated and hence have a positive covariance. Although this result is intuitive and could be offered without support,

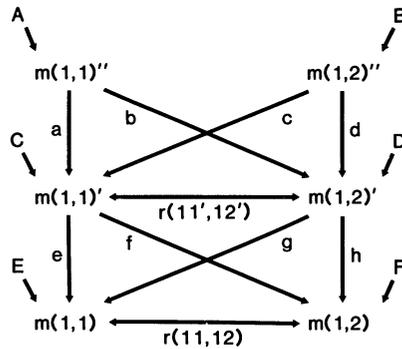


FIG. 1.—A path diagram showing the development of a positive intraspecific interisland correlation from the effects of interisland colonization. See the text for details.

the following analysis serves as a necessary precursor to the analysis of the consequences of interspecific interactions.

In figure 1, the correlation between $m(1, 1)$ and $m(1, 2)$ is given by $r(11, 12)$. All double-headed arrows in path diagrams indicate correlation; single-headed arrows indicate effects of the variable at the tail of the arrow on the variable at the head. The variables $m(1, 1)$, $m(1, 2)$ indicate the status of species 1 in the present (or when the data were collected). Variables $m(1, 1)'$, $m(1, 2)'$ indicate presence at some earlier time, and $m(1, 1)''$, $m(1, 2)''$ at an initial time before any interisland effects that could generate an intraspecific interisland correlation. In figure 1 this assumption is indicated by the determination of $m(1, 1)''$, $m(1, 2)''$ from uncorrelated causes A and B . As a result of these initial conditions, no paths connect $m(1, 1)''$ and $m(1, 2)''$. All other causes not relevant to this analysis but contributing to the values of the matrix elements shown are summarized in the variables C , D , E , and F . These variables are not correlated with anything in the diagram except the variables they help determine.

First, we seek an expression for $r(11', 12')$, the correlation of $m(1, 1)'$ and $m(1, 2)'$. Following the rules of path analysis (Li 1975), we see that two paths connect these variables. Their correlation is the sum of the values of these paths,

$$r(11', 12') = a b + c d. \quad (6)$$

The effects of persistence on $m(1, 1)'$ and $m(1, 2)'$ are given by a and d , and the effects of interisland colonization by b and c . The positive effects of interisland colonization were explained in the example leading to equation (5). Possible persistence also has a positive effect, since a species known to have occurred on an island in the past will still be on that island if it persists or colonizes. If it were absent in the past, the only way it could occur would be through colonization. Since the effects a , b , c , and d are all positive, $r(11', 12')$ must also be positive.

The present intraspecific interisland correlation $r(11, 12)$ is the sum of three paths connecting $m(1, 1)$ and $m(1, 2)$:

$$r(11, 12) = e f + g h + e h r(11', 12'). \quad (7)$$

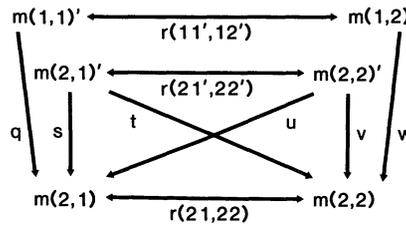


FIG. 2.—A path diagram showing the development of a positive intraspecific interisland correlation from the combination of interisland colonization and interspecific interactions. Only necessary variables and arrows are included. See the text for details.

The first two of these paths are analogous to the paths in equation (6), and they are positive for the same reasons. The third path represents the contribution of the combination of the positive effects of persistence (*e*, *h*) with past intraspecific interisland correlation [*r*(11', 12')]. As we have shown, this past correlation is positive; thus, *r*(11, 12) > 0. We conclude that interisland colonization generates positive intraspecific interisland covariances.

Now we ask if a second factor, interspecific interaction, also affects similarity by affecting these covariances. Figure 2 is a path diagram showing only the variables and arrows included in the paths connecting *m*(2, 1) and *m*(2, 2), the variables indicating the status of species 2 on islands 1 and 2. Here our interest is in *r*(21, 22), the correlation between these two variables. Four paths connect *m*(2, 1) and *m*(2, 2), resulting in

$$r(21, 22) = s t + u v + s v r(21', 22') + q w r(11', 12'). \tag{8}$$

The first two paths in equation (8) represent the interacting effects of persistence (*s*, *v*) and interisland colonization (*t*, *u*). The third and fourth paths represent the effects of persistence (*s*, *v*), of past intraspecific interisland correlations, *r*(21', 22'), *r*(11', 12'), and of interspecific interactions *q* and *w*, the effects of species 1 on species 2. As we show, any of these four paths may be zero or positive depending on the assumptions made about the effects they represent.

First, assume that we are interested in *r*(21, 22) at some "initial" time before any interisland colonization. No past interisland colonization means that *t* = 0, *u* = 0, and, by analogy with equation (6), *r*(11', 12') = 0 and *r*(21', 22') = 0. Thus, the absence of interisland colonization results in *r*(21, 22) = 0. Note that this result does not depend on the values of *q* and *w* and is thus independent of any effects of interspecific interactions.

Next assume that interisland colonization by both species takes place but that species do not interact; that is, *q* = 0 and *w* = 0. This assumption reduces equation (8) to one analogous to equation (7), repeating our earlier result that in the absence of interspecific interactions, intraspecific interisland covariances will be positive.

Finally, assume that species 1 and 2 compete such that if species 1 were present on an island in the past, species 2 would be less likely (than its unconditional probability) to be found there in the present. Past competition affects the present

probability of occurrence because such competition would reduce the probability of persistence to the present for species 2. Thus, competition leads to negative effects of $m(1, 1')$ on $m(2, 1)$ and of $m(1, 2')$ on $m(2, 2)$ (effects q and w in fig. 2). Also assume that this competition has been unimportant in the past, such that $r(11', 12')$ and $r(21', 22')$ can be taken as positive as a result of the effects of past interisland colonization. Under the assumption that q and w are both negative because of competition, the product $q w r(11', 12')$ must be positive. Hence, all four paths in equation (8) are positive, and $r(21, 22) > 0$.

Consideration of the path including interspecific interactions, $q w r(11', 12')$, leads to an important, and counterintuitive, conclusion. We have assumed that q and w represent competitive effects; thus, both were negative, and the path containing their product was positive. The positivity of this product, however, requires only that q and w have the same sign. Thus, all types of interspecific interactions have positive effects on intraspecific interisland correlations as long as the interactions have the same qualitative effects (positive or negative) on both islands. Examples include mutualism and competition, both of which have positive effects on these correlations except for unlikely cases such as mutualists on one island that compete on another.

We conclude that interisland colonization creates, and species interactions of all types reinforce, positive intraspecific interisland covariances; and, therefore, these phenomena increase expected similarity beyond their effects on the $p(i, j)$. An understanding of the qualifying phrase, "beyond their effects on the $p(i, j)$," is vital to clarifying the issues involved in analyses of similarity. Recall that in our analysis we first concluded that anything affecting the $p(i, j)$ would affect expected similarity through the first term in equation (3). For example, high values of the $p(i, j)$ result in high expected similarity. Since many factors may contribute to similarity in this way, high (or low) similarities, per se, do not support the importance of particular phenomena such as interisland colonization and interspecific interactions.

Suppose the values of the $p(i, j)$ are fixed, even though we do not know which factors have combined to determine them. With the $p(i, j)$ fixed, consider two alternative cases.

1. Interisland colonization and interspecific interactions have had no effects on species distributions, that is, no effects on the $p(i, j)$. In this case, intraspecific interisland covariances are zero, and

$$E[S(j, k)] = \sum_{i=1}^R p(i, j)^* p(i, k)^*, \quad (9)$$

where the $p(i, j)^*$ are the fixed values of the $p(i, j)$.

2. Interisland colonization and interspecific interactions have both contributed to determining the values of the $p(i, j)$. Here, the intraspecific interisland covariances are positive, and

$$E[S(j, k)] = \sum_{i=1}^R p(i, j)^* p(i, k)^* + \sum_{i=1}^R \text{cov}[m(i, j), m(i, k)]. \quad (10)$$

If the $p(i, j)^*$ are equal in cases 1 and 2, expected similarity is greater in case 2 because interisland colonization and interspecific interactions have introduced positive intraspecific interisland covariances.

This restatement of our earlier result is intended to emphasize the point that interisland colonization and interspecific interactions can affect expected similarity in two ways: through their effects on the $p(i, j)$ and through their effects on the intraspecific interisland covariances. The direction of their effects via the $p(i, j)$, of course, need not be positive even though they have positive effects via the intraspecific interisland covariances.

This last point explains why the result that competition tends to increase similarity (given interisland colonization) appears to be counterintuitive, whereas the same conclusion for interactions such as mutualisms does not. It seems reasonable that mutualisms would increase the probability of persistence for a species, which, in terms of our model, would result in higher values of the $p(i, j)$ for mutualists and tend to increase expected similarity. Thus, it is easy to accept the idea that mutualisms may also increase expected similarity via the intraspecific interisland covariances.

For competition, however, our intuitive expectation is that competing species would be less likely to persist and therefore have lower values of $p(i, j)$. This situation would result in a lower contribution to expected similarity via the $p(i, j)$ than would be the case if competition were somehow eliminated. At the same time, however, competition tends to increase similarity through the intraspecific interisland covariances. Thus, the total effect of competition could be either positive or negative, even though beyond its effects on the $p(i, j)$, competition can have only positive effects on similarity.

INFERENCES FROM THE GALÁPAGOS BIRD FAUNA

Power's (1975) Analysis

Power (1975) believed that interspecific competition should reduce similarity and that this effect should be greatest among congeners. He examined an index of similarity [a function of our $S(j, k)$] for all pairs of islands in the Galápagos. He calculated the index separately for three groups: bird species lacking congeners, and species in the genera *Geospiza* and *Camarhynchus*. As expected under his competition hypothesis, the index of similarity was greatest for noncongeners. Power concluded that this reflected "repulsed" distributions among congeners, presumably resulting from competition.

Power's approach, however, does not control for the effects of the $p(i, j)$ on similarity; and the pattern of similarities he observed is most simply explained by differences in the $p(i, j)$ for the bird species studied. The more islands occupied by a species, the higher its estimated $p(i, j)$. The species lacking congeners and the species of *Geospiza* and *Camarhynchus* occupy averages of 10.6, 8.5, and 5.6 islands, respectively (Harris 1973). The rank correlation of these values with the average indexes of similarity for these groups reported by Power is perfect. Thus, the pattern of similarities is consistent with differences in the numbers of islands

occupied by species in the different groups or, in terms of equation (3), predictable from the $p(i, j)$. Since many phenomena affect the numbers of islands occupied, the observed pattern of similarities does not provide evidence for the importance of interspecific competition. Even if competition were the only factor affecting the $p(i, j)$, the correspondence between hypothesized competition and similarity for only three groups would not be statistically significant.

Connor and Simberloff's Tests of Hypotheses

Connor and Simberloff (1978) studied the number of species shared by pairs of islands in the Galápagos to test the null hypothesis that species occur independently of one another. They concluded that observed similarities were consistent with independent colonization and persistence and discounted the importance of interspecific interactions. Simberloff (1978) cited their results in discounting the hypothesis that interspecific competition, in particular, affects the distributions of species on islands.

The approach used by Connor and Simberloff (1978) differs from that of Power (1975) because they tested for the effects of interspecific interaction on similarity after controlling for effects from the $p(i, j)$. Specifically, they tested two null hypotheses for all bird species in the Galápagos Islands. (For reasons we discuss later, we temporarily disregard their simultaneous analysis for lists of plant genera.) Expected similarities among species lists under both of their hypotheses are identical to those given by equation (9). In other words, their expected similarities are based on the assumption that the intraspecific interisland covariances are zero. Stating this assumption by describing the species as independently located, they sought evidence that similarity differs from that expected from the $p(i, j)$ alone. We have shown that such evidence would support the hypothesis that intraspecific interisland covariances are nonzero and that interisland colonization and possibly interspecific interactions have therefore affected species distributions.

Expected similarities under their null hypotheses require estimates of the $p(i, j)$, and their null hypotheses I and II differ in the assumptions leading to these estimates. Null hypothesis I assumes that all species are alike, such that $p(i, j) = p(h, j)$ for all i, h . Null hypothesis II differs only in that it does not include this assumption of equiprobable species. Under null hypothesis I, the estimate of a $p(i, j)$ is proportional to the number of species on island j . Under null hypothesis II, each estimated $p(i, j)$ is proportional to both the number of species on island j and the number of islands occupied by species i . Under both hypotheses, the distributions of similarities were calculated following the additional assumption that column sums were fixed (the number of species on an island under the null hypothesis equals the number observed in the data). This assumption does not affect expected values of similarity.

Connor and Simberloff (1978) did not state whether they expected interspecific interactions, if important, to increase or decrease similarity in comparison with values predicted by their null hypotheses. Simberloff (1978), however, stated that the hypothesized effect of competition would be to decrease similarity below their expected values. Connor and Simberloff rejected both null hypotheses for

Galápagos bird species. They found greater similarity among species lists than expected in either case. Although they rejected these null hypotheses, they concluded that their results failed to support the importance of interspecific interactions.

Our theoretical analysis has shown that significantly greater similarity than expected under their null hypotheses is consistent with the importance of interspecific interactions, including competition, in determining species distributions. Connor and Simberloff's (1978; Simberloff 1978) failure to draw this conclusion was probably due to their expectation that competition would decrease similarity. Since we now see that increased similarity is consistent with the importance of interisland colonization and possibly interspecific interactions, we must consider the possibility that their results provide support for the importance of these phenomena.

Before addressing Connor and Simberloff's test of null hypothesis I, we point out a relationship between mean similarity and the row sums of the occupancy matrix. Mean similarity, $S(\cdot, \cdot)$, is the average value of $S(j, k)$ over all pairs of islands (columns) in the matrix. The number of unique pairs of islands is

$$N = \binom{C}{2} = C(C - 1)/2, \tag{11}$$

and mean similarity is given by

$$S(\cdot, \cdot) = \sum_{j=1}^C \sum_{k=1}^C S(j, k)/N, \quad j \neq k. \tag{12}$$

Now consider a single species (row) in the occupancy matrix. The number of islands occupied by species i is given by the row sum, $r(i)$, where

$$r(i) = \sum_{j=1}^C m(i, j). \tag{13}$$

Each unique pair of 1's in a row contributes 1 to the total similarity (the double sum in eq. 12). The number of such pairs in a row is $r(i) [r(i) - 1]/2$, and the total similarity is the sum of the contributions of all the rows; thus,

$$S(\cdot, \cdot) = \sum_{i=1}^R r(i) [r(i) - 1]/2N. \tag{14}$$

Mean similarity is determined by the row sums. Moreover,

$$\begin{aligned} S(\cdot, \cdot) &= \left[\sum_{i=1}^R r(i)^2 - \sum_{i=1}^R r(i) \right] / 2N \\ &= R \text{ var } r(i) / 2N + \left\{ \frac{1}{R} \left[\sum_{i=1}^R r(i) \right]^2 - \sum_{i=1}^R r(i) \right\} / 2N. \end{aligned} \tag{15}$$

When column sums are fixed, as in Connor and Simberloff's (1978) analyses, then the sum of the row sums is also fixed (the sum of the row sums equals the sum of

the column sums). Thus, the second term in equation (15) is fixed, and mean similarity increases with the variance of the row sums.

Recall that Connor and Simberloff's null hypothesis I includes the equiprobable species assumption. When species are identical, the expected values of the row sums are also identical, and the variance of these sums is minimized. When species differ, the expected values of the row sums also differ, and the variance of the observed row sums tends to be larger than expected under null hypothesis I. Since mean similarity increases with the variance of the row sums, expected similarity under null hypothesis I tends to be lower than observed values as a simple consequence of the assumption of no differences among species.

This, of course, was the result when Connor and Simberloff (1978) tested null hypothesis I against data from the Galápagos. Since their result would be a direct consequence of the assumption of equiprobable species, an assumption we know to be false, there is no reason to infer any other causes for the rejection of null hypothesis I.

For their null hypothesis II, Connor and Simberloff (1978) relaxed the assumption of equiprobable species. They proposed a method for simulating expected similarities under this hypothesis. The proposed simulations follow the assumptions that column sums are fixed and that species occupying each island are drawn at random from a pool in which each species appears as often as the number of islands it occupies in the Galápagos data. For example, the simulated biota of an island with 10 species would be filled by drawing at random from the pool until 10 different species were chosen. A species occurring on eight islands would be twice as likely to be chosen (on any draw) as one appearing on four islands. Draws must be with replacement in the pool to avoid creating negative intraspecific interisland correlations as an artifact of the procedure. Each island pair must be simulated separately rather than simulating entire matrices and using these for all pairs. The latter approach would produce estimates of null distributions that are dependent because of nonindependent sampling of the species pool.

Although this approach does not calculate estimates of the $p(i, j)$, such estimates are implied by the assumptions and could be calculated. The proposed simulations seem reasonable since the islands vary in the number of species they tend to hold and the species vary in the number of islands they tend to occupy. Both tendencies are estimated in a reasonable way from the data. That column sums are still fixed is troublesome and unnecessary, but it does not affect expected values.

The effect of dropping the equiprobable-species assumption can be predicted from equation (15). More-variable species will result in increased variation in the row sums and, therefore, expected similarity will increase. For bird species, however, the mean similarity in Connor and Simberloff's (1978) simulated archipelagos (expected similarity under null hypothesis II) was less than expected under null hypothesis I. We cannot explain this result. We have performed simulations for Galápagos bird species using the same data (Harris 1973), following the procedures described in Connor and Simberloff (1978). Our results differ from theirs; we found that, as predicted from equation (15), expected similarity under hypothesis II was greater than under hypothesis I.

The simulations we performed resulted in Monte Carlo distributions of similarity under null hypothesis II. Using these distributions we found that 11 of the 105 island pairs (10.5%) had bird faunas that are significantly more similar than predicted by null hypothesis II (one-sided 5% test). This result differs from the 69.5% reported by Connor and Simberloff (1978).

What can be concluded about the adequacy of null hypothesis II when it is rejected in 11 of 105 tests? The two approaches Connor and Simberloff (1978) suggested are flawed. First, they suggested that if the null hypothesis is true, half of the observed similarities will lie above those expected and half will lie below. They tested this prediction using a χ^2 test. However, observed values are equally likely to fall above and below the expected only when the mean of a distribution equals its median. The hypergeometric distribution of similarities used for null hypothesis I does not have this property, nor did the Monte Carlo distributions we developed under null hypothesis II.

In their second approach, Connor and Simberloff used a χ^2 test to compare the number of rejections with an expected number based on 5% of the tests performed. This approach, however, assumes that all tests performed are independent, which they are not. Each species list is used (for birds) in 14 different tests; thus, the tests are clearly interdependent. With 15 islands, there are actually only seven possible independent pairs of islands. If we had chosen seven independent pairs at random for our Monte Carlo tests, we would probably have found zero or one pair in which observed similarity was significantly greater than expected. Neither result would be sufficient evidence to reject null hypothesis II.

We have not discussed the details of Connor and Simberloff's (1978) results for Galápagos plant genera for two reasons. First, the theoretical analysis of similarity we presented in the first section of this paper is not directly applicable to similarities among lists of genera. It is not clear what effects competition or other biological phenomena would be expected to have on such similarities, and results for plant genera are therefore difficult to interpret. In addition, because we did not have the data for plant genera analyzed by Connor and Simberloff (1978), we could not attempt to replicate their results. They found significantly higher similarities among plant genera lists than expected under their null hypothesis II; but recall that this was also their result for bird species, and our replication of their simulations failed to reproduce that result.

To summarize our examination of Connor and Simberloff's (1978) analysis, we agree with their basic conclusion that similarities among species lists for Galápagos birds fail to support the importance of interspecific interactions in determining species distributions. Their conclusion, however, was apparently based on the expectation that competition would decrease similarity below that predicted by independent colonization and persistence and on their result that similarities were significantly higher than expected. In contrast, our conclusion is based on our theoretical result that interspecific interactions in combination with interisland colonization tend to increase similarity and on our reanalysis of the Galápagos bird data (Harris 1973), which shows that similarities were not significantly higher than expected under Connor and Simberloff's (1978) null hypothesis II.

CONCLUSIONS

The most important result of our theoretical analysis is that, beyond their effects on unconditional probabilities of occurrence, all types of interspecific interactions tend to increase similarity. This result contradicts the intuitive predictions of Power (1975) and of Simberloff (1978) that competition would decrease similarity. In addition, we find that for interspecific interactions to have such effects, they must combine with the effects of interisland colonization. In contrast, interisland colonization can increase similarity operating alone. Our examinations of the analyses by Power (1975) and Connor and Simberloff (1978) in light of these theoretical results suggest that the similarity of species lists for the Galápagos Islands does not provide evidence for the importance of competition or any other type of interspecific interaction in determining species distributions.

A question of more-general interest here is whether or not any analyses of similarity among biota can provide evidence that competition, or any type of interspecific interaction, is important in determining species distributions. The failures of Power (1975) and of Connor and Simberloff (1978) to find convincing evidence in the Galápagos Islands do not answer this general question.

A modification of the simulation approach proposed by Connor and Simberloff (1978) might detect a significant contribution to similarity by the intraspecific interisland covariances. Such an approach would (1) test only the similarities among randomly selected, independent pairs of islands, (2) use simulations to estimate probability values for the significance of differences for each pair, and (3) combine these probability values for a single overall test of significance (Sokal and Rohlf 1981, p. 779). The assumption of fixed column sums need not be included in the simulations.

Using this approach, a rejection of the null hypothesis, with observed similarity greater than expected, would be evidence that interisland colonization and perhaps interspecific interactions are important in determining species distributions. Any effects of interspecific interactions, however, could not be separated from the effects of interisland colonization; and even if this were possible, any effects of competition could not be separated from the effects of other interspecific interactions. Moreover, failure to find significant effects of the intraspecific interisland covariances would not negate the importance of interspecific interactions. Even if competition or other interspecific interactions had important effects on species distributions, low rates of interisland colonization could prevent such interactions from having significant effects on similarity.

SUMMARY

To resolve the controversy initiated by Connor and Simberloff's (1978) analysis of similarity among the biota of the Galápagos Islands, we analyze the theoretical relationship between interspecific interactions and similarity. A counterintuitive result from our analysis is that all interspecific interactions, including competition, tend to increase similarity (given their effects on unconditional probabilities of occurrence). To have this effect, however, they must combine with the effects of

interisland colonization. The results of Power (1975) and those of Connor and Simberloff (1978) suggest that interisland colonization and possibly interspecific interactions have had important effects on similarity in the Galápagos, but several difficulties prevent us from accepting their results. We conclude, with Connor and Simberloff, that the similarity of bird species lists for the Galápagos Islands does not support the importance of interspecific interactions in determining species distributions. In general, we conclude that although a combined positive effect of interisland colonization and all types of interspecific interactions on similarity might be detectable using a modification of Connor and Simberloff's approach, the effects of these phenomena cannot be disentangled to provide evidence for or against the importance of competition.

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