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American Naturalist, Volume 119, Issue 3 (Mar., 1982), 345-357.

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American Naturalist
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ISLAND BIOGEOGRAPHIC DISTRIBUTIONS: TESTING FOR RANDOM, REGULAR, AND AGGREGATED PATTERNS OF SPECIES OCCURRENCE

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Submitted March 12, 1980; Revised December 31, 1980; Accepted July 16, 1981

Distributions of animals on islands have been used to infer competitive interactions. For example, two lacertid lizards have mutually exclusive distributions on small islands in the Adriatic Sea. Of 57 islands censused by Radovanovic (1959), 28 were occupied by *Lacerta melisellensis*, 18 by *L. sicula*, and 11 by neither species. Clearly, competitive exclusion of a later colonist by the resident *Lacerta* could maintain the mutually exclusive distributions of the two species. However, there are two questions that must be answered to substantiate the competition hypothesis. First, could random colonization give rise to the observed distribution? The high failure rate of experimental introductions of one species onto islands occupied by its congener suggests that random colonization is not responsible for the observed distribution in the lacertid example (Nevo et al. 1972). Second, one must determine whether alternative mechanisms could explain the exclusive distribution. In the lacertid example, subtle habitat differences between islands could explain both mutually exclusive distributions and failed introductions. Clearly, in the absence of controlled experimentation, the inference that mutually exclusive distributions result from competition will be difficult to prove.

In a series of recent papers, Simberloff (1978) and Connor and Simberloff (1978, 1979) have attempted to answer the first question: Could observed distributions have resulted if species colonized islands randomly and independently of one another? Only after this possibility has been eliminated can observed distributions be used to implicate biological processes. Unfortunately, we believe that the analyses proposed by Simberloff (1978) and Connor and Simberloff (1978, 1979) are not appropriate to determine whether island colonization is random. We will point out the problems inherent in their analyses and propose an alternative analysis which avoids these pitfalls.

THE HYPERGEOMETRIC DISTRIBUTION: I. THE SHARED SPECIES NULL HYPOTHESIS

Simberloff (1978) and Connor and Simberloff (1978) reasoned as follows: Suppose there are P species (or taxa) in a source pool and two islands with m and n species, where $m \leq n$. We seek the probability that there are exactly x species

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Am. Nat. 1982. Vol. 119, pp. 345-357.

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shared between the two islands, where $0 \leq x \leq m$. All x are on the m -species island. Therefore the sample space for the event is the number of ways to choose m species from P species, $\binom{P}{m}$. The number of ways to choose the x species shared between the two islands is $\binom{n}{x}$. The number of ways to choose the remaining $(m - x)$ species from the $(P - n)$ species not found on the island with n species is $\binom{P-n}{m-x}$. It follows the the desired probability distribution is a hypergeometric distribution:

$$p(x) = \frac{\binom{n}{x} \binom{P-n}{m-x}}{\binom{P}{m}}.$$

The expected value of $p(x)$ is

$$E_{ts} = \sum_{x=0}^m x \frac{\binom{n}{x} \binom{P-n}{m-x}}{\binom{P}{m}} = \frac{mn}{P}. \quad (1)$$

Let O_{ts} equal the observed number of species shared by two islands. If O_{ts} is significantly different from E_{ts} , Simberloff (1978) and Connor and Simberloff (1978) reject the null hypothesis (hereafter referred to as the shared species null hypothesis) that "the observed number of species shared between 2 islands (or more generally 2 species lists) is no different than would be expected if the island's species compositions were random samples of a species pool equally likely to colonize" (p. 231). These authors conclude that although O_{ts} is often significantly greater than E_{ts} , "a substantial proportion of the number of species shared between 2 islands can be viewed as resulting from stochastic processes . . ." (p. 244). Simberloff (1978), however, proposes that "competitive interactions would tend to reduce the number of shared species below that expected on the null hypothesis, because pairs or groups of competitors could only exist on different islands" (p. 716). Since O_{ts} is rarely less than E_{ts} , Simberloff concludes that interspecific competition does not greatly affect island colonization.

The shared species null hypothesis is open to three criticisms, two of which are acknowledged by Simberloff (1978) and Connor and Simberloff (1978): (1) To generate E_{ts} , one must know how many species comprise the source pool, P , of potential colonists of an archipelago. In many archipelagoes, it is extremely difficult to determine P . Connor and Simberloff (1978) simply let P equal the number of species in an archipelago. This underestimate of P will lead to an overestimate of E_{ts} .

2. Simberloff (1978) recognized that "a tendency toward higher similarity (between two islands) generated by good colonizers could swamp a real but lesser tendency toward lower similarity generated by competition" (p. 716). To avoid this problem, Simberloff (1978) and Connor and Simberloff (1978) calculated relative colonization abilities from observed frequency-of-occurrence distribu-

tions and calculated E_{ts} and its variance using computer simulations (their hypothesis II). Grant and Abbott (1980) have noted the circularity of this ad hoc procedure. The alternative analysis which we will propose will address differences in colonization ability directly.

3. Independent of the problem posed by good colonists, the shared species null hypothesis is subject to a third, more serious, criticism. Simberloff (1978) and Connor and Simberloff (1978) examine the number of species held in common by all possible pairwise comparisons of islands (this is true for both of their analyses, i.e., their hypotheses I and II). Thus, if a pair of competitors have mutually exclusive distributions, many of the possible pairwise comparisons will include two islands each of which supports the same species from the competing pair. Consider a hypothetical example of a large number of islands each occupied by only one of two competing species, a and b. Let exactly one half of the islands be occupied by species a and one half by species b. Clearly one half of all possible pairwise island comparisons will involve one island with species a and one with species b ($O_{ts} = 0$); one quarter of all possible pairwise comparisons will involve two islands with species a ($O_{ts} = 1$), and likewise one quarter will involve two islands with species b ($O_{ts} = 1$). Here $m = n = 1$, $P = 2$, and $E_{ts} = 0.5$. Thus, given two species with mutually exclusive distributions, half of the pairwise comparisons of islands indicate that competition may occur ($O_{ts} = 0 < E_{ts} = 0.5$), and half indicate that competition does not occur ($O_{ts} = 1 > E_{ts} = 0.5$). Furthermore, note that the average number of species shared between islands equals 0.5, which equals E_{ts} . Thus, the shared species null hypothesis is equivocal; we cannot distinguish our hypothetical checkerboard distribution from a random distribution.

This problem is exacerbated if the species to be analyzed are delimited taxonomically and without regard to autecologies. For example, the class Aves includes species as disparate in their ecologies as hummingbirds and vultures. These species do not interact, and they should not affect one another's island distributions. Returning to our hypothetical archipelago, assume that a third species c neither interacts with species a nor species b and that species c occupies every island in the archipelago. Since the three species are included in the same analysis, one half of all pairwise comparisons of islands will share two species ($O_{ts} = 2$), and one half will share one species ($O_{ts} = 1$). $E_{ts} = 1.33$, and the addition of a noninteracting species has made it more difficult to document the mutually exclusive ranges of species a and b. Because of these biostatistical problems, the shared species null hypothesis cannot distinguish between random distributions and the competitively structured distribution which we present below.

THE COMPETITIVE GUILD MODEL

Let there be n' guilds with no biological interaction between members of different guilds. Let each guild have two member species which have mutually exclusive ranges, and for each guild let one species occupy half and the other species the other half of the islands in an archipelago. Then, the probability that

there are exactly x species shared between two islands, where $0 \leq x \leq n'$, is:

$$p(x) = \frac{\binom{n'}{x}}{\sum_{x=0}^{n'} \binom{n'}{x}}. \quad (2)$$

The expected value of $p(x)$ is

$$E[X] = \frac{\sum_{x=0}^{n'} x \binom{n'}{x}}{\sum_{x=0}^{n'} \binom{n'}{x}} = \frac{n'}{2}. \quad (3)$$

For an archipelago where species are distributed according to the rules of the competitive guild model, $m = n = n'$, $P = 2n'$, and the expected number of species shared by two islands equals $n'/2$, from equation (3). But, given these values of P , m , and n , the expected number of species shared by two islands would also equal $n'/2$ if species were distributed randomly and independently of one another (eq. [1]). Thus, Connor and Simberloff's shared species analysis leads to the spurious conclusion that species distributed according to the rules of the competitive guild model are randomly distributed.

Simberloff (1978) acknowledged that "Expected number of shared species is a weak statistic for detecting diffuse competition, in that any particular pair of islands might share approximately as many species as expected, yet the distributions of species on islands might be highly nonrandom . . ." (p. 723). Indeed, analysis of the number of shared species will not detect "competition" between pairs of species with mutually exclusive ranges. This is especially true if noninteracting species are included. By analyzing large, arbitrary taxonomic groups (all land birds, Simberloff [1978]; all plants or all land birds, Connor and Simberloff [1978]; all bats or all land birds, Connor and Simberloff [1979]), Connor and Simberloff insure that noninteracting species are included in their analyses.

We will now describe an analysis which is better able to detect the effect of competitive exclusion on insular distributions.

THE HYPERGEOMETRIC DISTRIBUTION: II. THE SHARED ISLAND NULL HYPOTHESIS

Rather than investigating the number of species shared by two islands, we ask: What is the probability that two species share x islands? Let there be N islands colonized by two species such that q of the islands are colonized by species 1 and r are colonized by species 2, $q \leq r$. We seek the probability that there are exactly x islands on which both species are present. Again, the desired probability distribution is a hypergeometric distribution:

$$p(x) = \frac{\binom{r}{x} \binom{N-r}{q-x}}{\binom{N}{q}}. \quad (4)$$

The expected value is

$$E_{is} = \frac{\sum_{x=0}^q x \binom{r}{x} \binom{N-r}{q-x}}{\binom{N}{q}} = \frac{rq}{N}.$$

To distinguish between H_0 (the observed number of islands shared by two species, O_{is} , could have arisen through random and independent colonization—hereafter referred to as the shared island null hypothesis) and H_1 (the two species are regularly distributed among islands), we compute the probability that the two species share O_{is} or fewer islands by chance. The desired probability is $\sum_{x=0}^{O_{is}} p(x)$, where $p(x)$ is defined by equation (4). If this probability is less than .05, we reject H_0 and accept H_1 .

To contrast the properties of the shared species and shared island null hypotheses, we will now analyze several observed island distributions. In the Bismarck Archipelago, two species of *Ptilonopus* fruit pigeons, two species of *Pachycephala* flycatchers, and two species of *Macropygia* cuckoo-doves appear to be regularly dispersed among islands (Diamond 1975, figs. 20, 21, 22). The data and analyses for these birds and the *Lacerta* lizards of the Adriatic are summarized in table 1. In each example, the probability that the two species shared O_{is} or fewer islands is less than .05, and the shared island null hypothesis is rejected; species are not distributed randomly and independently of one another. Rather, species are regularly dispersed among islands and competitive interactions may have affected the colonization process.

On the other hand, the shared species null hypothesis of Simberloff (1978) and Connor and Simberloff (1978) gives equivocal results. O_{ts} may be less than, greater than, or equal to E_{ts} (table 1). The reason: For pairwise comparisons of islands which support the same species, O_{ts} is greater than E_{ts} ; and, for pairwise comparisons of islands which support different species, O_{ts} is less than E_{ts} . For example, for the *Pachycephala* flycatchers O_{ts} is greater than E_{ts} 157 times and there are $\binom{12}{2} + \binom{14}{2} = 157$ pairwise comparisons of islands each of which support the same species. O_{ts} is less than E_{ts} 168 times, and there are $12 \times 14 = 168$ pairwise comparisons of islands which support different species. For the remaining comparisons, one or both islands support neither species and $O_{ts} = E_{ts} = 0$. Clearly, the shared species null hypothesis does not give an adequate analysis of these data. The comparison of pairs of islands which both support the same species inflates O_{ts} and may in part explain why Simberloff (1978) and Connor and Simberloff (1978) found that O_{ts} is more frequently greater than E_{ts} .

Connor and Simberloff (1979) point out that there are $\binom{141}{2}$ pairs of bird species in the Bismarck Archipelago and distributions as unlikely as those cited in table 1 could occur by chance. That is, we could be guilty of rejecting a true null hypothesis (type I statistical error). To rectify this problem it is necessary to analyze all possible pairs of species and to determine whether 5% or more of the pairwise distributions could have occurred by chance. Connor and Simberloff (1979) did this for all possible duos (and trios) of West Indian bird and bat species

TABLE 1
ANALYSES OF THE ISLAND DISTRIBUTIONS OF CONGENERIC PAIRS OF SPECIES

| | NUMBER OF ISLANDS WITH | | | Both Species | SHARED-ISLAND NULL HYPOTHESIS | | SHARED SPECIES† NULL HYPOTHESIS | | |
|---------------------------|------------------------|----------------|----------------|--------------|-------------------------------|-------------------|---------------------------------|-------------------|--|
| | Neither Species | Species 1 Only | Species 2 Only | | $\sum_{x=0}^{O_{is}} p(x)^*$ | $O_{is} > E_{is}$ | $O_{is} = E_{is}$ | $O_{is} < E_{is}$ | |
| <i>Ptilonopus</i> | 3 | 18 | 9 | 2 | .000325 | 189 | 145 | 162 | |
| <i>Pachycephala</i> | 17 | 14 | 12 | 0 | .000338 | 157 | 578 | 168 | |
| <i>Macropygia</i> | 13 | 14 | 6 | 0 | .02450 | 106 | 338 | 84 | |
| <i>Lacerta</i> | 11 | 28 | 18 | 0 | .00000111 | 531 | 561 | 504 | |

* For each species pair, $\sum_{x=0}^{O_{is}} p(x)$ is the probability of obtaining a distribution of species among islands as exclusive or more exclusive than that observed. When $\sum_{x=0}^{O_{is}} p(x) \leq .05$, we reject the null hypothesis that the species are distributed randomly and accept the alternative hypothesis that the two species in the pair are regularly distributed among islands. O_{is} is the observed number of islands shared by the member species of a pair. $p(x)$ is defined by equation (4).

† Comparison of observed (O_{is}) and expected (E_{is}) number of species shared between two islands for all possible pairwise comparisons of islands. For each species pair, column entries are the number of times O_{is} is greater than, equal to, and less than E_{is} . E_{is} is defined by equation (1).

and New Hebridean bird species using a shared island approach. This was accomplished by repeated simulation of species' distributions onto islands. For each simulation the number of pairs of species which co-occupied 0, 1, . . . , N islands was tallied. The average number of pairs which co-occupied 0, 1, . . . , N islands in the simulations was then compared to the observed distribution of pairs which co-occupied 0, 1, . . . , N islands. Thus, an excess number of observed pairs which co-occupy 0, 1, or some unspecified but small number of islands constitutes evidence that some unknown number of species have exclusive or nearly exclusive distributions (possibly as a result of competition). However, for competitive interactions to give this result a large number of species must be interacting, and the exact null hypothesis being tested becomes obscure. Moreover, as Grant and Abbott (1980) noted, the two samples being compared (the observed and simulated distributions) are not statistically independent. This introduces a conservative bias to the analysis.

With our shared island statistic, simulations are not necessary and it is possible to retain H_0 : A particular pair of species are distributed randomly and independently of one another. To distinguish between H_0 and H_1 : A pair of species is regularly distributed among islands; it is necessary to calculate the probability that a pair of species co-occupy O_{is} or fewer islands by chance. Again, this probability is $\sum_{x=0}^{O_{is}} p(x)$ where $p(x)$ is defined by equation (4). If $\sum_{x=0}^{O_{is}} p(x) < .05$ for more than 5% of the species pairs, H_0 can be rejected. This analysis was completed for pairwise combinations of West Indian bats (distributions from Baker and Genoways 1978) and New Hebridean birds (distributions from Diamond and Marshall 1976). For every pairwise comparison of species, the desired probability is greater than .05. H_0 is accepted, and there is no evidence that competition has affected these distributions. Computer costs kept us from repeating the analysis for trios of species or for West Indian birds.

To distinguish between H_0 and H_1 : A pair of species is aggregated among islands; it is necessary to calculate the probability that a pair of species co-occupy O_{is} or more islands by chance. This probability is $1 - \sum_{x=0}^{O_{is}-1} p(x)$ where $p(x)$ is again defined by equation (4). For West Indian bats and New Hebridean birds, 9.4% and 8.4%, respectively, of the species pairs co-occupied O_{is} or more islands with probability less than .05 (figs. 1, 2). For both West Indian bats and New Hebridean birds, H_0 can be rejected and H_1 accepted. Some species pairs are aggregated among islands. This should be expected because each archipelago was colonized from several source faunas and species from each source fauna tend to be aggregated on some subset of the islands in each archipelago (Baker and Genoways 1978; Diamond and Marshall 1976).

Connor and Simberloff (1979) did not detect the tendency toward aggregation in the distributions of New Hebridean birds and West Indian bats. In part, this may reflect the fact that their simulated species-island distributions were constrained so that each simulated island supported the same number of species as an actual island in the observed archipelago. Implicit to our analysis is the assumption that islands are equivalent. This assumption should not be violated if one seeks to construct a null hypothesis which is devoid of biological implications. For example, species which occur on a very small number of islands tend to be found on the

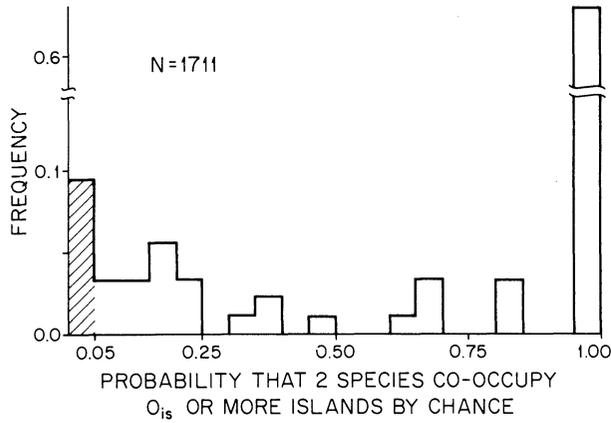


FIG. 1.—Frequency histograms of probabilities that pairs of species co-occupy O_{is} or more islands by chance for all pairwise combinations of bat species in the West Indies. O_{is} is the observed number of islands co-occupied by two species. The probability is calculated as $1 - \sum_{x=0}^{O_{is}-1} p(x)$, where $p(x)$ is defined by equation (4). Most of the bat species occupy a very small number of islands. Therefore $O_{is} = 0$ for many pairs, and the probability that these pairs occupy O_{is} or more islands is 1 by definition.

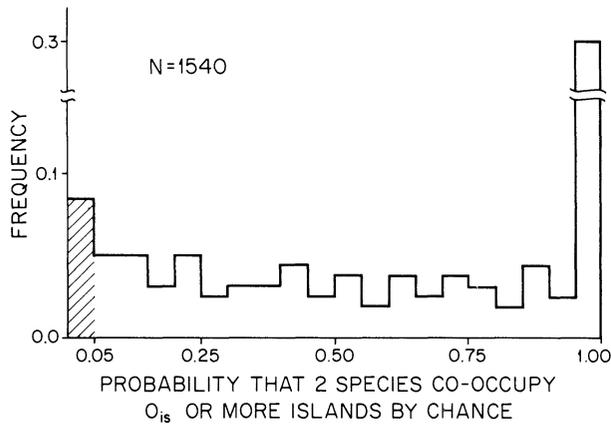


FIG. 2.—Frequency histogram of probabilities that pairs of species co-occupy O_{is} or more islands by chance for all pairwise combinations of bird species in the New Hebrides. See caption to figure 1. Six of the 56 bird species are found on every island in the archipelago. For the 330 pairwise combinations involving these six species, the probability that the pair co-occupies O_{is} or more islands is 1 by definition.

largest islands in an archipelago. This may be true because large islands tend to have greater habitat diversity or because species on large islands have low extinction rates. In either case, species which are found on a few large islands will tend to be aggregated for biological reasons, and the analysis of Connor and Simberloff (1979) will tend to miss this aggregation. Finally, our analysis has the advantage that pairs of species whose distributions are nonrandom are pinpointed. If non-random distributions are detected by the analysis of Connor and Simberloff (1979), one only knows that a large number of species are interacting and not which species.

We now review assumptions implicit to the shared-species analyses of Simberloff (1978) and Connor and Simberloff (1978), the shared-island analysis of Connor and Simberloff (1979), and our own shared-island analysis. Species-island distributions for an archipelago may be recorded as an incidence matrix of ones for presence and zeros for absence where rows represent species and columns islands. The shared-island analysis of Connor and Simberloff (1979) constructs a null model by reshuffling the elements of this matrix while preserving all row and column sums. This amounts to preserving the observed species' incidence functions (*sensu* Diamond 1975) and the observed species-area relation. In the previous paragraph, we showed that preserving the observed species-area relation (column sums) may cause the analysis to miss biologically significant aggregation of species among islands. If it is only important to distinguish between random and regular distributions of species among islands, this will not be a problem. The shared-species analyses of Simberloff (1978) and Connor and Simberloff (1978) also preserve the observed species-area relation (column sums). Our shared island analysis does not. Rather, we conserve observed island number for each species (row sums). This constraint is desirable because it acknowledges the fact that different species have different colonization abilities. Simberloff (1978) and Connor and Simberloff (1978) attempted to incorporate between-species differences in colonization abilities into their shared-species analyses by calculating relative colonization abilities from observed frequency-of-occurrence distributions (their hypothesis II). As noted previously, Grant and Abbott (1980) have criticized this ad hoc procedure. Thus, in addition to the biostatistical problems detailed above, implicit assumptions make: (1) shared-island analyses preferable to the shared-species analyses of Simberloff (1978) and Connor and Simberloff (1978), and (2) our shared-island analysis preferable to the shared-island analysis of Connor and Simberloff (1979) when testing for aggregated distributions of species among islands. Moreover, operational difficulties discussed above make our shared-island analysis preferable to Connor and Simberloff's (1979) when testing for regular distributions of species among islands. Finally, M. C. Grant and J. Williamson (MS) have developed an intricate shared-species analysis which corrects some of the faults of the analyses of Simberloff (1978) and Connor and Simberloff (1978), but maintains the assumption that all species are equiprobable colonists (row sums not constrained).

To demonstrate the versatility of the shared-island null hypothesis, we now consider a more complex example. Five species of small *Myzomelid* honeyeaters are found in the Bismarck Archipelago (Diamond 1975, fig. 23). Of the 40 islands censused, *M. sclateri* occupied 11 islands, *M. pammelaena* four islands, *M.*

cruentata three islands, and *M. erythromelas* and *M. pulchella* one island each. Twenty islands did not support a myzomelid and no island supported two of the congeners. To test the null hypothesis that the myzomelid distributions are the result of random and independent colonization, the distributions of all five species must be analyzed simultaneously. This can be accomplished by modifying the shared-island null hypothesis. Solely for the sake of exposition, the two single-island endemics will be omitted from the analysis, which reduces the number of species to be analyzed to three and the number of islands to 38. If the three species distributions are the result of random and independent colonization, the number of islands which support 0, 1, 2, or 3 species should follow from a random placement of species populations onto islands. However, if interspecific competition affected the colonization process, the number of islands which support two or three species should be fewer than expected from a random model.

Thus, given that three species are present in an archipelago, we seek the probability that X islands support at least two species. Consider figure 3, a schematic diagram representing the possible distributions of three species onto N islands. Let species 1 occupy S islands, species 2 occupy R islands (solid circles), and species 3 occupy Q islands (dashed circle). The diagram is akin to the Venn diagrams of set theory. If species were placed onto islands randomly, the sample space of N islands would be divided into eight types of space: (1) islands occupied by species 1 only, (2) islands occupied by species 2 only, (3) islands occupied by species 3 only, (4) unoccupied islands, (5) islands occupied by species 1 and 2, (6) islands occupied by species 2 and 3, (7) islands occupied by species 1 and 3, and (8) islands occupied by all three species. The sample space for the desired density function is $\binom{N}{Q}\binom{N}{R}\binom{N}{S}$, the total number of ways to place the three species onto N islands. It remains to determine the number of ways in which the three species can be placed onto N islands such that X islands support two or more species. This is equivalent to making the sum of regions 5, 6, 7, and 8 equal X . Imagine placing S populations of species 1, then R populations of species 2, and finally Q populations of species 3 onto N islands. First, there are $\binom{N}{S}$ possible ways to place S populations onto N islands. Then K of the R populations of species 2 are placed on the S islands occupied by species 1 and $R - K$ populations are placed on the $N - S$ empty islands. There are $\binom{S}{K}\binom{N-S}{R-K}$ possible ways to do this, and K will equal the hatched region in the diagram. Recall that the sum of regions 5, 6, 7, and 8 must equal X . The sum of regions 5 and 8 equals K . Hence, the sum of regions 6 and 7 must equal $X - K$. To make the sum of regions 6 and 7 equal $X - K$, $X - K$ of the Q populations of species 3 must be placed onto the $S + R - 2K$ islands occupied by species 1 or species 2. The remaining $Q - X + K$ populations must be placed on the remaining $N - S - R + 2K$ islands. There are $\binom{S+R-2K}{X-K}\binom{N-S-R+2K}{Q-X+K}$ possible ways to do this. Because K can vary between zero and X , the desired probability distribution is:

$$p(x) = \frac{\sum_{K=0}^X \binom{S}{K} \binom{N-S}{R-K} \binom{N-S-R+2K}{Q-X+K} \binom{S+R-2K}{X-K}}{\binom{N}{R} \binom{N}{Q}}, \quad (5)$$

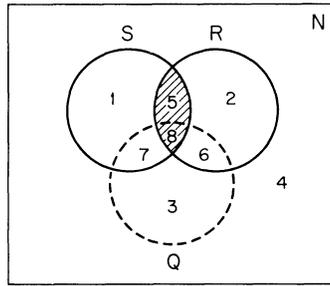


FIG. 3.—Schematic diagram representing the possible distributions of three species onto N islands. Species 1 occupies S islands, species 2 occupies R islands (solid circles), and species 3 occupies Q islands (dashed circle). The diagram is akin to the Venn diagrams of set theory. See text.

where K is the number of islands co-occupied by species 1 (on S islands) and species 2 (on R islands).

In the myzomelid example, $N = 38$, $S = 11$, $R = 4$, and $Q = 3$. From equation (5), the probability that zero islands support two or more species is .0499. The null hypothesis that these species are randomly and independently distributed is rejected, and the alternative hypothesis that the myzomelids are regularly dispersed is accepted.

In an alternative analysis of the myzomelid distributions, one could compute the probability that all islands support zero or one species directly. Let M species occupy an archipelago and let the M species occupy N_1, N_2, \dots, N_M islands, respectively, where $N_1 \geq N_2 \geq \dots \geq N_M$. Now, if species were distributed randomly and independently of one another, the probability that all N islands in an archipelago support zero or one species is:

$$\frac{\binom{N - N_1}{N_2} \binom{N - N_1 - N_2}{N_3} \times \dots \times \binom{N - \sum_{k=1}^{m-1} N_k}{N_M}}{\sum_{k=2}^m \binom{N}{N_k}}$$

In the myzomelid example, with only three species $N = 38$, $N_1 = 11$, $N_2 = 4$, and $N_3 = 3$, and again the probability that all 38 islands are occupied by zero or one species is .0499. If New Britain and New Ireland are added, $N = 40$, $N_4 = 1$, and $N_5 = 1$. The probability that all 40 islands are occupied by zero or one species is .0175, and it is clear that the five myzomelids are regularly dispersed among islands.

In conclusion, our set of shared-island null hypotheses are better able to discriminate between random and nonrandom distributions of species among islands than are the analyses of Simberloff (1978) and Connor and Simberloff (1978, 1979). Moreover, the shared-island null hypothesis can be tailored to test between H_0 and a biologically meaningful H_1 . One point of contention remains: Which species should be analyzed together? Connor and Simberloff (1979, p.

1138) state that "statistical tests . . . will not easily detect . . . competition, since it must be imbedded in a mass of noncompetitively produced distributional data." Of course, this will be true if one insists on analyzing arbitrary taxonomic groups without regard to species' autecologies. Simberloff (1978) and Connor and Simberloff (1978, 1979) do just this. Rather than simultaneously analyzing the distributions of all birds, it might be preferable to analyze the distributions of all insectivorous birds or all insectivorous birds of roughly equal body weight.

The crucial point, if one seeks to detect the effect of competition, is to restrict the analysis to species which are potential competitors. As long as the potential competitors are delimited by objective criteria prior to examining the species-island distributions, our shared-island analysis can be used to determine whether the potential competitors are distributed randomly or nonrandomly among islands.

SUMMARY

We propose tests to determine whether species distributions among islands (or any sampling unit) are random or nonrandom. To distinguish between H_0 : species are distributed randomly and independently of one another and H_1 : species are regularly distributed among islands, we calculate the probability that two (or more) species co-occupy the observed or fewer islands by chance. To distinguish between H_0 and H_1 : species are aggregated among islands; we calculate the probability that two (or more) species co-occupy the observed or more islands by chance. If either probability is less than .05 for 5% or more of the possible pairwise (triplets, etc.) combinations of species in an archipelago, we reject H_0 and accept the appropriate H_1 . Simberloff (1978) and Connor and Simberloff (1978, 1979) attempted a similar analysis. We demonstrate that our analysis is better suited to determine whether species distribution on islands are nonrandom, and we emphasize that statistics cannot be applied indiscriminately without regard to species' autecologies.

ACKNOWLEDGMENTS

Ted Case, Martin Cody, Egbert Leigh, and Daniel Simberloff read and improved upon the manuscript. The University of California provided financial support.

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