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THE ASSEMBLY OF SPECIES COMMUNITIES: CHANCE OR COMPETITION?¹

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Abstract. We challenge Diamond's (1975) idea that island species distributions are determined predominantly by competition as canonized by his "assembly rules." We show that every assembly rule is either tautological, trivial, or a pattern expected were species distributed at random. In order to demonstrate that competition is responsible for the joint distributions of species, one would have to falsify a null hypothesis stating that the distributions are generated by the species randomly and individually colonizing an archipelago.

Key words: *assembly rules; bird communities; competition; exclusive distribution; island species distribution; species pairs.*

In a widely cited new approach to the interpretation of biogeographic distributions, Diamond (1975) asserts that the assembly of bird communities manifests the following patterns:

- a. "If one considers all the combinations that can be formed from a group of related species, only certain ones of these combinations exist in nature."
- b. "Permissible combinations resist invaders that would transform them into forbidden combinations."
- c. "A combination that is stable on a large or species-rich island may be unstable on a small or species-poor island."
- d. "On a small or species-poor island, a combination may resist invaders that would be incorporated on a larger or more species-rich island."
- e. "Some pairs of species never coexist, either by themselves or as a part of a larger combination."
- f. "Some pairs of species that form an unstable combination by themselves may form part of a stable larger combination."
- g. "Conversely, some combinations that are composed entirely of stable subcombinations are themselves unstable."

Examining data from 147 species of land birds distributed in various combinations over 50 islands in the Bismarck Archipelago near New Guinea, Diamond

concluded that these "assembly rules" can be explained by (1) interspecific competition for resources, (2) "overexploitation strategies" whereby certain "permissible combinations" of species together lower resources to a point such that other species are usually starved to extinction, (3) differences among species in dispersal rates, and (4) low transition probabilities between "permissible combinations" such that combinations A and B might both be "permissible," but transition from A to B might only be possible through combinations which are very unlikely, presumably for the three preceding reasons. This latter phenomenon is not unlike the genetic landscape of Wright (1967), with adaptive peaks separated by impassable low-fitness troughs.

We will show that every assembly rule is either a tautological consequence of the definitions employed, a trivial logical deduction from the stated circumstances, or a pattern which would largely be expected were species distributed randomly on the islands subject only to three constraints: (1) that each island has a given number of species, (2) that each species is found on a given number of islands, (3) and that each species is permitted to colonize islands constituting only a subset of island sizes. The last constraint is an acceptance, for the purpose of this paper, of Diamond's contention that each species has an "incidence function" of probabilities of being found on islands of given sizes. The allowable subset of island sizes constitutes the domain for which the values of the incidence function are nonzero. Diamond (1975), Diamond et al. (1976), and Diamond and Marshall (1977) all synonymize island size with the number of species on the island, a convention which we adopt here. We

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regret we cannot use the same Bismarck data which Diamond first used, but its publication has been delayed by various unforeseen complications (J. M. Diamond, *personal communication*, E. Mayr, *personal communication*). In lieu of these, we have used the New Hebridean bird data (Diamond and Marshall 1976), plus data for West Indies birds (Bond 1971) and bats (Baker and Genoways 1978) to examine the assembly rules.

RULES *a* AND *e*

"If one considers all the combinations that can be formed from a group of related species, only certain ones of these combinations exist in nature."

"Some pairs of species never coexist, either by themselves or as part of a larger combination."

These rules are identical, except that rule *a* is restricted to related species and rule *e*, though unrestricted taxonomically, is concerned only with pairs of species. We deal with them together. Diamond's "proof" of rule *e* consists of five examples from the Bismarcks of exclusively distributed related species (his Figs. 20–24). Although he does not do so, it is possible for each example to calculate the probability of an arrangement as exclusive as that observed. For instance, the *Macropygia* doves (his Fig. 20) consist of two species, *M* and *N*, such that *M* is on 14 islands, *N* on 6 different ones, and 13 surveyed islands have neither. Presumably the remaining 17 islands have not been censused. The probability of an arrangement this exclusive over these 33 islands for randomly placed species with the same frequencies is:

$$\frac{\binom{33}{14} \binom{19}{6}}{\binom{33}{14} \binom{33}{6}} = .0245.$$

The terms in the numerator are the number of ways species *M* can be placed, and the number of ways species *N* can be placed on islands not occupied by species *M*, respectively. The terms in the denominator are simply the numbers of ways the two species can be placed irrespective of which islands are already occupied. Similarly, for the *Pachycephala* flycatcher example (his Fig. 21), species *P* is found on 11 islands, *D* on 18 different islands, and 21 islands have neither. The probability of such an exclusive arrangement for species placed randomly, subject only to their being on 11 and 18 islands, respectively, is:

$$\frac{\binom{50}{11} \binom{39}{18}}{\binom{50}{11} \binom{50}{18}} = .00345.$$

When one recalls that there are $\binom{141}{2} = 9870$ pairs

of birds in the Bismarcks, it is clear from the above probabilities that by chance alone certain species pairs would not occur together on any island. What one wants to know is how many such pairs, trios, etc. would be expected for randomly distributed birds, and how many such pairs, trios, etc. are actually observed.

It is impossible, lacking the data, to treat these rules for the Bismarcks, but for the New Hebrides and West Indies avifaunas and West Indies bats one would expect a large fraction of the species pairs and trios, whether related or not, not to coexist even were the species placed randomly within each archipelago subject only to three constraints:

- i) For each island, there is a fixed number of species, namely, that which is observed.
- ii) For each species, there is a fixed number of occurrences, namely, that which is observed.
- iii) Each species is placed only on islands with species numbers in the range for islands which that species is, in fact, observed to inhabit. That is, the "incidence" range convention is maintained.

We simulated such a random placing 10 times, with the result that the total number of species occurrences was maintained, allocated as in nature among islands and among species. We then scanned each simulated arrangement for number of pairs not found anywhere (and number of trios for New Hebrides birds and West Indies bats), number of pairs (or trios) found on only one island, only two islands, only three islands, etc. Finally, we examined the actual arrangements. All analyses were performed with and without constraint (iii) "incidence functions". However, since relaxing incidence constraints does not affect the results, only the results including incidence constraints are presented. Details of the simulation are described in the Appendix.

For the New Hebrides birds (56 species on 28 islands), there are 1540 possible species pairs of which 63 are not found on any island. But by chance alone one would have expected 63.2 such pairs ($SD = 2.9$). Further, the entire distribution of number of species pairs vs. number of islands shared (Fig. 1) shows a close match to the random expectation; with the last two classes lumped so that expected number in each class is >5 , $\chi^2 = 16.34$ (27 df), $.95 > P > .90$. Of the 27 720 trios of New Hebrides birds, 3070 do not coexist on any island, but the expected number of such trios is 3068.0 ($SD = 105.1$). For the entire distribution of number of species trios vs. number of islands shared, with the last three classes lumped so that expected number in each class is >5 , $\chi^2 = 13.57$ (26 df), $.98 > P > .95$. If we restrict our attention, as in rule *a*, to birds within families (cf. Terborgh 1973), we find that there are 99 pairs in the New Hebrides that are confamilial in one or another of the 15 families, of

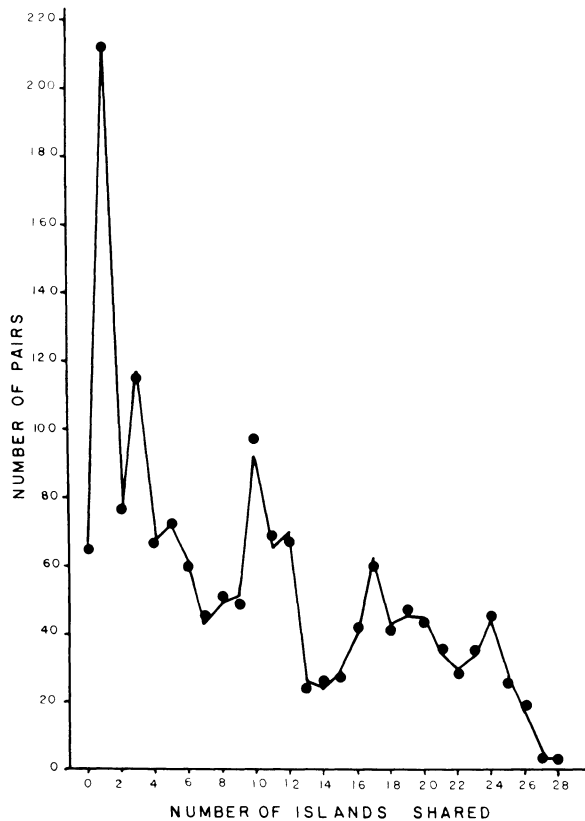


FIG. 1. Distribution of number of species pairs vs. number of islands shared for New Hebrides birds. Solid line is the expected distribution given the three constraints discussed in text. Dots are the observed values.

which only one is not found on any island; one would have expected 0.9 ($SD = 0.3$). For the entire distribution, lumping classes so that denominators are >5 , we find $\chi^2 = .63$ (11 df), $P > .99$. For confamilial trios, we find that of 304 possible, seven are found nowhere in the archipelago, while one would have expected 6.4 ($SD = 1.9$) exclusive confamilial trios even had the birds been randomly distributed. For the entire distribution, with lumped classes as before, $\chi^2 = 1.04$ (17 df), $P > .99$. In a nutshell, there is nothing about the absence of certain species pairs or trios, related or not, in the New Hebrides that would not be expected were the birds randomly distributed over the islands as described above. Since there are so many possible sets of species, it is to be expected that a few sets are not found on any island; this does not imply that such sets are actively forbidden by any deterministic forces.

For West Indies birds (211 species on 19 islands), there are 22 155 pairs of which 12 757 are found on no island. But had the birds been randomly distributed on the islands as described above, one would have expected 12 448.1 ($SD = 79.2$) such exclusive pairs. For the entire distribution of number of species pairs vs. number of islands shared (Fig. 2), we find the observed

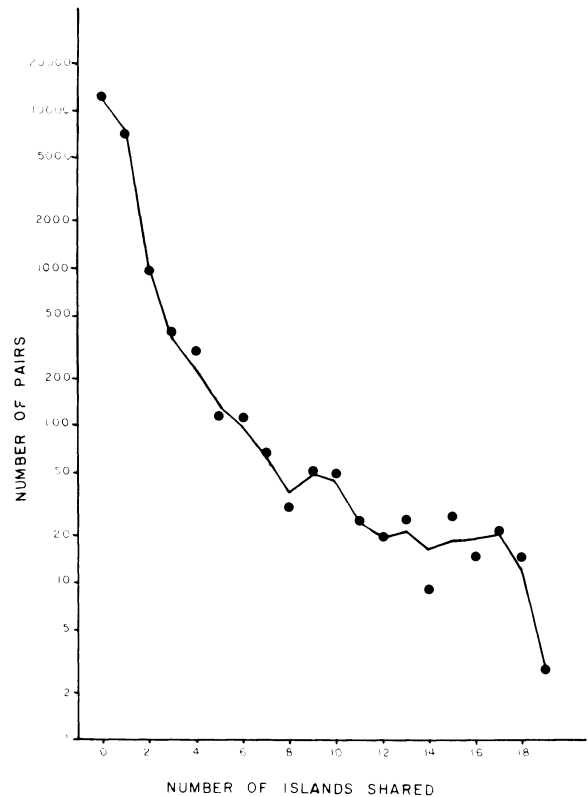


FIG. 2. Distribution of numbers of species pairs vs. number of islands shared for West Indies birds. Solid line is the expected distribution given the three constraints discussed in text. Dots are the observed values.

and expected values to be not nearly so close as in the New Hebrides: $\chi^2 = 66.18$ (18 df), $P < .01$. It is nevertheless clear from Fig. 2 that not only is the number of completely exclusive species pairs only slightly greater than expected for randomly distributed birds, but also there are no major anomalies in the degree of partial exclusivity which some species pairs achieve. Of 1029 pairs of birds which are confamilial in one or another of the 24 West Indian families, 621 are mutually exclusive. But a random arrangement would have 437.0 ($SD = 18.3$) such exclusive confamilial pairs; for the entire distribution, $\chi^2 = 271.44$ (17 df), $P < .01$. If we relax constraint (ii), that of specified total number of islands for each species, we find the fit to be much better, though observed and expected distributions still differ by a χ^2 test. Since there are 1 543 465 possible trios of West Indian birds, computing time limitations forbade our extending this analysis to cover trios.

Finally, for the West Indies bats (59 species on 25 islands) there are 1711 possible species pairs, of which 996 are exclusively distributed while a random arrangement would have produced 941.7 ($SD = 11.6$); for the entire distribution (Fig. 3), $\chi^2 = 15.26$ (6 df), $.02 > P > .01$. Of the 32 509 trios of West Indies bats,

27 397 do not coexist on any island, and the expected number of such trios is 26 965.7 ($SD = 84.2$). For the entire distribution of number of species trios vs. number of islands shared, with shared island classes 6 and 7, 8–11, and 12–25 lumped so that expected number in each class is >5 , $\chi^2 = 91.96$ (8 df), $P < .01$. Within the five families are 499 confamilial pairs, of which 325 are found on no single island while 208.6 ($SD = 5.5$) such pairs would have been expected. For the entire distribution, $\chi^2 = 183.99$ (7 df), $P < .01$; as with the birds, relaxing constraint (ii) brings the observed and expected distributions much closer together. Of the 3850 confamilial trios, 3519 are mutually exclusive, while one would expect 2564.4 ($SD = 47.2$) given a random arrangement with all three constraints; for the entire distribution $\chi^2 = 851.15$ (7 df), $P < .01$, with classes 6 and 7 lumped. Relaxing constraint (ii) yields a much better fit for confamilial trios, $\chi^2 = 10.29$ (3 df), $.025 > P > .01$.

For the West Indies birds and bats, then, there are as many mutually exclusive species pairs as would have been expected had the species been randomly distributed on the islands subject only to constraints of incidence ranges (iii), some species being more widely distributed than others (ii), and some islands having more species than others (i). Although more of these exclusive pairs are of related species than chance alone would have dictated, one would have expected many exclusive related pairs even under the random hypothesis. For our three test biotas, we summarize the data on mutually exclusive pairs and trios in Table 1. It is clear that five examples of exclusive distribution, as Diamond (1975) presents, provide no support for assembly rules *a* and *e*.

The New Hebrides bird distribution fit the random hypothesis even more closely than the West Indies birds and bats for both related and unrelated species. We can suggest two possible reasons. First, our simulation placing birds on islands (at least without incidence range restriction) is analogous to randomly placing 0's and 1's in an $m \times n$ matrix (with m = number of species, n = number of islands) with row and col-

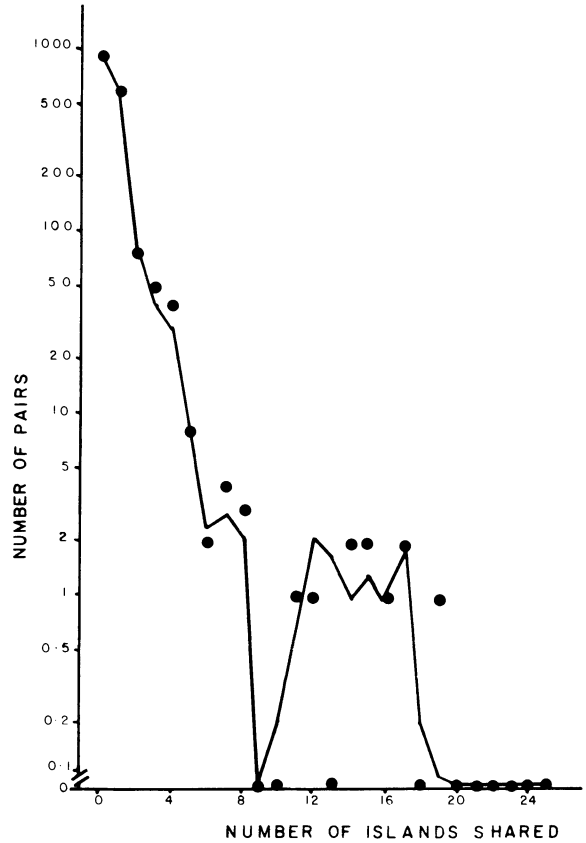


FIG. 3. Distribution of number of species pairs vs. number of islands shared for West Indies bats. Solid line is the expected distribution given the three constraints discussed in text. Dots are the observed values.

umn sums fixed. There are a limited number of such matrices, and since we would even allow row and column interchanges (which correspond, respectively, to exchanging species names or island names), the number of different arrangements is even smaller. Exactly how many such arrangements there are, given a set of row and column sums, is an old, unsolved combina-

TABLE 1. Observed and expected exclusive species groups for several taxa.

Taxon	Group size	Confamilial	Total groups	Observed exclusive groups	Expected exclusive groups
New Hebrides birds	pair	No	1 540	63	63.2 (2.9)*
New Hebrides birds	pair	Yes	99	1	0.9 (0.3)
New Hebrides birds	trio	No	27 720	3 070	3 068.0 (105.1)
New Hebrides birds	trio	Yes	304	7	6.4 (1.9)
West Indies birds	pair	No	22 155	12 757	12 448.1 (79.2)
West Indies birds	pair	Yes	1 029	621	437.0 (18.3)
West Indies bats	pair	No	1 711	996	941.7 (11.6)
West Indies bats	pair	Yes	499	325	208.6 (5.5)
West Indies bats	trio	No	32 509	27 397	26 965.7 (84.2)
West Indies bats	trio	Yes	3 850	3 519	2 565.4 (47.2)

* Parenthetic values are standard deviations.

torics problem (N. Heerema, *personal communication*), but we noticed that all our West Indies random matrices looked very different, both from one another and from the matrix depicting the observed arrangement, while all the random New Hebrides matrices were similar, and similar to the observed matrix. We infer that for the species and island totals of the New Hebrides birds, there are very few possible arrangements even without the incidence ranges (which, incidentally, span the whole range of island sizes for 36 of the 56 New Hebrides species, and almost the whole range for most of the rest). Since these are all similar, it is not surprising that the observed distribution is not very different from a random one with respect to exclusive pairs and trios. But unless one is willing to ascribe to competition the facts that islands have different numbers of species and that species are found on different numbers of islands, the New Hebrides data still argue heavily against the claim that competition determines most aspects of the distribution of species on islands.

Second, where a distribution includes single-island endemics (as do two of Diamond's examples, *Myzomela* honeyeaters and *Zosterops* white-eyes) a statistical analysis like ours exaggerates the degree of biological exclusion, since the evolution of specific differences between two formerly conspecific populations would generate an exclusive pattern independent of competition. Such species should probably be excluded from the analysis, as Terborgh (1973) did for identical reasons in his examination of West Indian bird distributions. We used complete lists because we were uncertain which species pairs, trios, etc. represented recent cases of allopatric speciation. Much of the excessive exclusivity in West Indies birds and bats is "pseudo-exclusion" arising from either unsettled taxonomy, or the inclusion of superspecies. For example, Bond (1971) mentions that among the vireos, *Vireo modestus*, *V. crassirostris*, *V. griseus*, and *V. gundlachi* can be considered conspecific, as well as *V. altiloquus* and *V. magister*. Several other genera (*Contopus*, *Elaenia*, *Mimus*, *Quiscalus*, *Loxigilla*, *Melanerpes*, *Saurothera*, *Amazona*, and *Chlorostilbon*) contain two or more exclusive species, but it is likely that this represents allopatric speciation without subsequent reinvasion, rather than active competitive exclusion. Diamond (1975) provides a striking example of this problem in his discussion of *Zosterops* in the Bismarcks. Five of 12 species of white-eyes belong to a superspecies, and are by definition allopatric or parapatric in distribution. From a zoogeographic standpoint these are all one species. Yet he contends that this "checkerboard" distribution results from competitive exclusion, not geographic speciation without reinvasion. We conclude by observing that to the extent that such taxa are included in the analysis, they distort the results in the direction of increased number of observed exclusive pairs or trios (the 0-class in Figs.

1-3). It may be that such taxa are more common in the West Indies than in the New Hebrides.

RULE *b*

"Permissible combinations resist invaders that would transform them into forbidden combinations."

This is clearly a deduction from the definitions of "permissible combination" and "forbidden combination," plus Diamond's explanation of the assembly rules. Since Diamond defines a permissible combination to be one which exists somewhere in the archipelago and a forbidden one to be one which does not exist, and believes that forces 1-4 on page 1132 are the deterministic explanations for these observed combinations or absences, it follows that he believes the permissible combinations actively "resist" transformation into forbidden ones. Our discussion of rules *a*, *e*, and *g* makes it clear that the statistical distributions themselves do not demand an explanation of active resistance.

Nor is there compelling experimental evidence that any particular combination is actively forbidden by any force(s), or actively "resists" transformation. Diamond claims that five cases directly document active resistance of "forbidden" invaders, but examination of these suggests otherwise. Case 1 is that three cuckoo-doves (*A*, *N*, *R*) have been resident on New Britain during this century, while a fourth (*M*), "whose addition would create a combination forbidden by compatibility rules," is resident on islands 1.6 km away, but is only a vagrant on New Britain. But a "compatibility rule" is an ad hoc rationalization: "knowledge about species ecologies may suggest to us that a given pair . . . is incapable of coexistence . . ." Diamond believes that "distributional information" can also lead us to infer a compatibility rule, but his reasoning is flawed here. He calculates the no-coexistence probability Z_{AB} of not finding coexistence on any of a set of n islands as the product of n terms of the form $1 - J_A J_B$, where J_A and J_B for each island are the incidence probabilities for species *A* and *B*, respectively, on an island of that size. If the no-coexistence probability Z_{AB} is low, yet *A* and *B* are never seen together in the archipelago, incompatibility is inferred. But as our discussion of rules *a*, *e*, and *g* shows, there are a vast number of possible combinations of any size, so many that even for a large archipelago there will be so few islands that many combinations would not exist even were the species randomly distributed, whether or not constrained by incidence rules.

Now, the "combination forbidden by compatibility rules" in case 1 could be *MN*, *MNR*, *AMN*, or *AMNR*, since Diamond earlier has said that these four are all forbidden by compatibility rules. "The first two of these combinations are also forbidden by incidence

rules," which simply means that in this set of 50 islands all islands that have *N* also have *A*, so that "any combinations containing *N* but not *A* . . . are forbidden" (page 394). Obviously he does not mean "actively forbidden" by the incidence rules! As for the compatibility rule which forbids these four combinations, we are left only with Diamond's assertion that their ecologies preclude their coexistence; he concedes that even his method of calculating no-coexistence probabilities does not support this particular compatibility rule (page 396). Whether *M* bred on New Britain in this century is not even clear; Diamond did not find it in 1969. Even if one concedes that it has not bred there in this century, where is the evidence of active resistance? So long as we accept that some species (including *M*) are not found on all islands, and that one can *conceive* of noncompetitive reasons for this, the absence per se of a species from an island is not evidence for active resistance by other species. Cases 3 and 4, that *N* has not bred on Vuatom and Karkar, can be explained similarly.

Case 2 is that species *A* and *M* are resident on Vuatom, while *R* is believed not to have bred there this century in spite of its occasional presence there. It is said that the combination which would have resulted, *AMR*, is "forbidden by combination rules." Now, "combination rules" are defined strictly statistically, and are exactly the statistical part of the assembly rules. That is, when the no-coexistence probability of a combination, calculated as described above, is not so high that one would not have expected to see the combination, yet the combination is not seen in the archipelago, a "combination rule" of active exclusion is inferred. The flaw in the statistical reasoning has already been demonstrated, and once again there is no evidence of active resistance, unless one believes *in advance* that there can be *no* explanation of any species' failure to colonize all islands, except for competition. Case 5, that *M* has not bred on Umboi, is analogous to case 2.

Diamond's section title for these cases is "Historical proof of resistance to invasion . . ." yet the proof seems always to consist of an aprioristic combination or compatibility rule which itself lacks proof. In no case is there evidence that active resistance occurs, unless one *begins* with the assumption that a distributional gap must be explained by active resistance, in which instance we have a tautology and why bother with the exercise of producing evidence?

RULE c

"A combination that is stable on a large or species-rich island may be unstable on a small or species-poor island."

First, since all Diamond's statistical analyses use species number as the operational definition of island size, we may omit "large" and "small" and restate

rule *c* thus: "A combination that is stable on a species-rich island may be unstable on a species-poor island." Nowhere are "stable" and "unstable" defined. If persistence is meant, no evidence is even attempted, so we presume that stable is here a synonym for "permissible" and unstable a synonym for "forbidden." We have in our discussion of rule *b* shown that there is no evidence for active resistance, and that permissible simply means exists somewhere in the archipelago (Diamond, page 344, appears also to define permissible thus), while forbidden means not found in the archipelago. So rule *c* becomes: "A combination which is found on species-rich islands may not be found on species-poor islands." Need we add that any species-rich island will contain far more combinations of all sizes than a species-poor island, so that one would expect by chance alone to find some combinations on species-rich islands which are found on no species-poor islands? And that by chance alone there should be many more of these than of combinations found on species-poor islands but not species-rich islands? For that matter, a certain number of combinations by chance alone ought not to be found on any island, species-rich or species-poor! We discuss this in our treatment of rules *a*, *e*, and *g*, but for now suffice it to say that rule *c* is a trivial consequence of the definitions of rich and poor plus the most elementary laws of combinatorial mathematics.

RULE d

"On a small or species-poor island, a combination may resist invaders that would be incorporated on a larger or more species-rich island."

This rule seems to be a composite of rules *b* and *c*, and thus both a tautology (since active resistance must be assumed, if one is to prove active resistance) and a direct consequence of the definitions of poor and rich. As discussed for rule *c*, one would expect by chance alone certain combinations to be found on species-rich but not species-poor islands. As discussed for rule *b*, there is no experimental or statistical evidence that any particular combination (on *any* size island) actively resists transformation to some other particular combination.

RULE f

"Some pairs of species that form an unstable combination by themselves may form part of a stable larger combination."

Suppose one had a pair of species, *A* and *B*, which he claimed exemplified this rule. That is, they are unstable by themselves, but stable as part of some larger combination (say, *ABC*). There are no islands with published faunal lists of only two species in the Bismarcks, New Hebrides, or West Indies, and for the Bismarcks just one island with only three species. This fact renders the "rule" an untestable proposition.

How is one to know that *A* and *B* are an unstable duo by themselves? Whenever they appear, they will have to be with some other species (say *C*), likely several other species. By its existence, the resultant larger combination (*ABC*) is defined as stable. So the rule boils down to: "Some pairs of species which are not found alone (but they couldn't be, since no island is small enough) *are* found together with other species." Or should it be, "Every pair of species which is found at all is found with other species"? And what has this to do with competition?

RULE *g*

"Conversely, some combinations that are composed entirely of stable subcombinations are themselves unstable."

It turns out that if the species were distributed randomly, subject to the three constraints described in our discussion of rule *e*, one would *expect* a number of species trios *not* to exist on any island even though each of the species pairs contained in the trio is found on one or more islands. For the New Hebrides birds, 27 720 trios are possible, of which 3070 do not occur on any island. Of these 3070 noncoexisting trios, 169 have all three of their component pairs existing on at least one island. For the random simulation in our test of rule *e*, the expected number of exclusive trios is 3068.0 (*SD* = 105.1), and one would expect 162.9 (*SD* = 7.2) of these to have each of their three component pairs represented on at least one island. For the West Indies bats, 32 509 trios are possible, of which 27 397 do not occur on any island. Of these 27 397 noncoexisting trios, eight have all their component pairs on at least one island, while one would expect 130.8 (*SD* = 33.9). Clearly, for the West Indies bats, few trios are composed entirely of stable subcombinations. The simulated and real data could as well be examined for species quartets and their component trios, etc., but the computer bookkeeping is expensive and we trust that our point is made.

CODA

We have shown that at least one of the assembly rules is untestable, three are tautological consequences of definition plus elementary laws of probability, and the remaining three describe situations which would for the most part be found even if species were randomly distributed on islands. Clearly the assembly rules do not compel us to posit interspecific competition as a major organizing force for avian communities. That such an all-encompassing theory should be built on so little evidence invites an examination of the procedures used in its construction, and one point stands out. At no time was a parsimonious null hypothesis framed and tested. Instead of asking what biogeographical distributions would arise were *no* biological forces acting to produce them other than

dispersal differences among species, and whether observed distributions differ from these, Diamond (1975) assumed competition to be the primary determinant and then sought post facto to rationalize the observed data in the light of this assumption. As Popper (1963) points out, it is easy to find confirmatory evidence for most reasonable hypotheses, but science progresses by a different route: by posing testable hypotheses and then attempting to falsify them.

Further, at least two other attempts to use biogeographic data to demonstrate that interspecific competition structures island communities suffer from the same defect: failure to pose and to test a null hypothesis (Simberloff 1979a). First, that species/genus ratios on islands are lower than the mainland has been invoked as evidence for intense island competition (Grant 1966) in spite of Williams' prior demonstration (1951) that such a situation would obtain even for random subsets of any mainland species pool (Simberloff 1970). Second, Schoener (1965), Grant (1968), and Abbott et al. (1977) claim that size ratios of "adjacent" species in a size ranking are greater on islands than mainland, and greater on small islands than large ones, because of more intense interspecific competition on small islands. But the proper null hypothesis for such a study is that random subsets of a mainland pool would produce these trends, and a test of the null hypothesis for several archipelagoes provides no cause for rejection (Strong et al. 1979).

All this is not to say that species *are* randomly distributed on islands, or that interspecific competition does not occur. Rather, statistical tests of properly posed null hypotheses will not easily detect such competition, since it must be embedded in a mass of non-competitively produced distributional data. Instead, one must make a strong argument for competitive exclusion via observed active replacement of one species by another (Simberloff 1978 reviews several cases), experiment, or very detailed autecological study.

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- that species are distributed at random with the matrix constrained as described above, the matrix is first sorted such that row sums (N_j) decrease from top to bottom and column sums (S_i) increase from left to right. Proceeding species by species (row by row), each species j is placed sequentially on N_j islands chosen by generating a sequence of random numbers. Before each species is placed on an island, a check is performed to determine if the species has already been placed on that island, or if that island has received its full complement if S_i species. If either of these conditions is met, another island is chosen on which to place the species. This procedure is repeated until species j has been placed on N_j islands. At this point the procedure is repeated for the next species, etc., performing the same checks to insure that each species j is placed on N_j islands and that after placing all species, each island i has S_i species.
- When incidence constraints are used the selection of an island on which to place species j is limited to the range of island sizes (as measured by S_i) on which species j occurs in the actual matrix. As the simulation proceeds species by species, more and more islands are filled to their values of S_i . Occasionally the situation arises where the j th species cannot be placed on N_j islands all falling within its incidence range. In this event the incidence range constraint is expanded by one island in each direction (smaller and larger), and the random selection procedure repeated. The incidence range is continually expanded until species j can be placed on N_j islands.
- Once the random matrix is constructed, it may be inspected in the same manner as the actual data set, to enumerate values of the statistics of interest. To count the number of species pairs sharing 0, 1, 2, . . . N islands, each pair of rows (species) is scanned for the number of positive matches (1's in the same column in both rows). To generate this distribution for trios, one need only to repeat this procedure for groups of three rows at a time. Obviously, larger groups could be examined in a similar manner, but even for a moderately large archipelago (e.g., the New Hebrides birds, 56 species \times 28 islands) the number of computations necessary to perform this counting sequence rapidly becomes prohibitive (for pairs, 43 120 computations; for trios, 776 160; for quartets, 10 284 120 etc.). To compute expected values for these statistics, the entire sequence, matrix construction and counting, is repeated a number of times and the means and variances computed from this pool of values.
- To determine the number of "unstable" trios that have 0, 1, or 2 "stable" component pairs, an "expected" matrix is again randomly constructed and all groups of three rows (species) having 0 positive matches are inspected. For each of these trios of rows all three component pairs are examined to determine how many (0, 1, or 2) have at least one positive match. These results are summed for all groups of three rows to generate the distribution of number of "unstable" trios with 0, 1, or 2 "stable" component pairs. Expected values and their variances are again computed from a number of repeated runs of the same simulation with different random number sequences.
- The success of the matrix construction component of this simulation depends on the topology of the actual matrix from which row and column constraints are derived. If the N_j are mostly small (many species distributed on only a few islands, with few species widely distributed), the simulation can easily fill the matrix randomly subject to the specified constraints (e.g., West Indies birds and bats). However, if many N_j are large (species widely distributed) the simulation "hangs up" without completely filling the matrix according to the specified constraints. What happens is that since the matrix rows are sorted from large to small values of N_j , widely distributed species are placed early in the simulation, when each column (island) has few 1's (presences of species). Usually however,

APPENDIX

To examine rules a , c , and g we generated values of expected number of species pairs or trios sharing 0, 1, 2, . . . N islands, for confamilial and nonconfamilial pairs and trios, as well as expected numbers of "unstable" trios with 0, 1, or 2 stable component pairs. The simulation algorithm to produce these expected values had two major parts: one to fill randomly a 0–1 matrix constrained by restrictions (i) row sums, (ii) column sums, and (iii) incidence ranges, and a second to inspect and to count the actual as well as expected values of the above-mentioned statistics.

The constraints (i, ii, and iii) to the randomly constructed matrix were determined by inspecting the actual matrix for a particular archipelago. Hence, the column sums (island species numbers), and row sums (species occurrences) for the random matrix are exactly equal to those for the actual matrix. The incidence ranges are as nearly equal to those in the actual matrix as we could make them (see below). Given these fixed constraints the random matrix can then be constructed.

Envision a matrix of 0's and 1's where each row is a species and each column an island. Presence is indicated by a 1 and absence by a 0. To construct an "expected" matrix given

that species are distributed at random with the matrix constrained as described above, the matrix is first sorted such that row sums (N_j) decrease from top to bottom and column sums (S_i) increase from left to right. Proceeding species by species (row by row), each species j is placed sequentially on N_j islands chosen by generating a sequence of random numbers. Before each species is placed on an island, a check is performed to determine if the species has already been placed on that island, or if that island has received its full complement if S_i species. If either of these conditions is met, another island is chosen on which to place the species. This procedure is repeated until species j has been placed on N_j islands. At this point the procedure is repeated for the next species, etc., performing the same checks to insure that each species j is placed on N_j islands and that after placing all species, each island i has S_i species.

When incidence constraints are used the selection of an island on which to place species j is limited to the range of island sizes (as measured by S_i) on which species j occurs in the actual matrix. As the simulation proceeds species by species, more and more islands are filled to their values of S_i . Occasionally the situation arises where the j th species cannot be placed on N_j islands all falling within its incidence range. In this event the incidence range constraint is expanded by one island in each direction (smaller and larger), and the random selection procedure repeated. The incidence range is continually expanded until species j can be placed on N_j islands.

Once the random matrix is constructed, it may be inspected in the same manner as the actual data set, to enumerate values of the statistics of interest. To count the number of species pairs sharing 0, 1, 2, . . . N islands, each pair of rows (species) is scanned for the number of positive matches (1's in the same column in both rows). To generate this distribution for trios, one need only to repeat this procedure for groups of three rows at a time. Obviously, larger groups could be examined in a similar manner, but even for a moderately large archipelago (e.g., the New Hebrides birds, 56 species \times 28 islands) the number of computations necessary to perform this counting sequence rapidly becomes prohibitive (for pairs, 43 120 computations; for trios, 776 160; for quartets, 10 284 120 etc.). To compute expected values for these statistics, the entire sequence, matrix construction and counting, is repeated a number of times and the means and variances computed from this pool of values.

To determine the number of "unstable" trios that have 0, 1, or 2 "stable" component pairs, an "expected" matrix is again randomly constructed and all groups of three rows (species) having 0 positive matches are inspected. For each of these trios of rows all three component pairs are examined to determine how many (0, 1, or 2) have at least one positive match. These results are summed for all groups of three rows to generate the distribution of number of "unstable" trios with 0, 1, or 2 "stable" component pairs. Expected values and their variances are again computed from a number of repeated runs of the same simulation with different random number sequences.

The success of the matrix construction component of this simulation depends on the topology of the actual matrix from which row and column constraints are derived. If the N_j are mostly small (many species distributed on only a few islands, with few species widely distributed), the simulation can easily fill the matrix randomly subject to the specified constraints (e.g., West Indies birds and bats). However, if many N_j are large (species widely distributed) the simulation "hangs up" without completely filling the matrix according to the specified constraints. What happens is that since the matrix rows are sorted from large to small values of N_j , widely distributed species are placed early in the simulation, when each column (island) has few 1's (presences of species). Usually however,

midway through the matrix-filling process a species is encountered that must be placed on, say, 10 islands, but of the, say, 28 islands (columns) in the archipelago, 19 have already been "filled up" (received S_i species) by the simulation. Hence, the expected matrix cannot be completed. We have determined that the reason for this hang up is not the simulation itself, but simply that when most N_j are large the population of non-equivalent matrices is very small (by non-equivalent we mean that the matrices are not derivable from the actual matrix by interchanges of the rows and/or columns).

This problem arose when we attempted to construct the New Hebrides bird matrix according to the simulation. To circumvent this problem we developed an alternative algorithm to insure that the random matrices generated for the New Hebrides birds were in fact all nonequivalent. This procedure involves placing the actual New Hebrides bird matrix in a canonical form. We did so by putting the row and column sums in echelon form. This involved first placing rows in decreasing row sum order from top to bottom, and then column sums in decreasing order from left to right. Among the tied row sums, the row translating to the largest binary number was placed first, etc., and this was repeated for all groups of tied rows. After the rows were sorted, tied columns were

treated similarly. When in canonical form, the full matrix was then scanned for submatrices of the form:

$$\begin{array}{ccc} & & N_j \\ & 1 & 0 & 1 \\ S_i & 0 & 1 & 1 \\ & 1 & 1 & \end{array}$$

although they need not be this closely spaced. When located, these submatrices were switched so that the 1's and 0's appear on the opposite diagonal:

$$\begin{array}{ccc} & & N_j \\ & 0 & 1 & 1 \\ S_i & 1 & 0 & 1 \\ & 1 & 1 & \end{array}$$

This allows the row and column sums to be maintained since the changes exactly balance. After several of these changes are made, the new matrix was placed in canonical form (as described above). If the actual and new matrices when placed in canonical form are not completely identical then they are nonequivalent and can be used to compute the statistics of interest using the counting part of the simulation. A number of matrices were thus created to generate means and variances of the statistics for the New Hebrides birds.