

## SPECIES-FOR-SPECIES MATCHING

Few patterns in nature are more spectacular than species-for-species matching, whereby independent, ecologically equivalent sets of species are found in similar habitats at different locations (Cody 1974; Ricklefs and Travis 1980). For example, Brown (1975) noted similarity between the Great Basin and Sonoran deserts in the body-size distributions of rodent species. Heatwole and Levins (1972) observed relative constancy in the number of arthropod species in different trophic classes among mangrove islands defaunated by Simberloff and Wilson (1969). They also noted constancy between the arthropod assemblages of a given island before defaunation and after recolonization. In the rodent example, sets of species in different communities appear to be matched by a continuous variable (body size), whereas matching between sets of mangrove arthropods is by discrete trophic category.

Identifying matching is not trivial, since in virtually all putative cases the correspondence between communities is imperfect. The number of species is rarely identical in different communities, and species present in one community often lack a counterpart in the other. Procedures are thus required to help indicate trends when a precise match is unrealized. Ricklefs and Travis (1980) suggested a criterion for matching that is based on the relative similarities of individual species within and between communities. Their solution is most useful when the number of species is the same in each community and when matching occurs with respect to a continuous variable.

Here I suggest a more general criterion for matching and demonstrate its use. I also consider the implications of matching for the presence of certain interspecific interactions. Finally, I discuss why matching might be infrequent in nature even if convergence between communities is common.

### DETECTING SPECIES-FOR-SPECIES MATCHING

A frequent question is whether the communities under observation are more different than would be expected under the null hypothesis that species values were randomly sampled from a common distribution of possible values. This question forms the basis of virtually all standard comparisons employing  $\chi^2$ ,  $F$ , Kolmogorov-Smirnov  $D$ , and other measures of community difference. However, using the same data, it is possible to inquire whether communities are more similar than expected. That is, rather than ask whether  $\chi^2$ ,  $F$ , and  $D$  are too large to be accommodated by the null hypothesis, ask whether they are too small. Such a "too-small" difference between communities is a simple and very general criterion for matching.

TABLE 1  
THE NUMBER OF ARTHROPOD SPECIES IN DIFFERENT TROPHIC CLASSES ON  
EXPERIMENTAL MANGROVE ISLANDS

Island	H	S	D	W	A	C	P	U	Total
E1	9 (7)	1 (0)	3 (2)	0 (0)	3 (0)	2 (1)	2 (1)	0 (0)	20 (11)
E2	11 (15)	2 (2)	2 (1)	2 (2)	7 (4)	9 (4)	3 (0)	0 (1)	36 (29)
E3	7 (10)	1 (2)	3 (2)	2 (0)	5 (6)	3 (4)	2 (2)	0 (0)	23 (26)
ST2	7 (6)	1 (1)	2 (1)	1 (0)	6 (5)	5 (4)	2 (1)	1 (0)	25 (18)
E7	9 (10)	1 (0)	2 (1)	1 (2)	5 (3)	4 (8)	1 (2)	0 (1)	23 (27)
E9	12 (7)	1 (0)	1 (1)	2 (2)	6 (5)	13 (10)	2 (3)	0 (1)	37 (29)

NOTE.—Figures are taken from Heatwole and Levins (1972), who used data from Simberloff and Wilson (1969). Counts are the number of arthropod species present before defaunation and after about a year of recolonization (in parentheses). Trophic classes: H, herbivore; S, scavenger; D, detritus feeder; W, wood borer; A, ant; C, predator; P, parasite; U, class unknown.

For example, different mangrove islands may be compared with respect to the frequency of arthropod species in different trophic categories (table 1) using a  $\chi^2$  contingency test (Heatwole and Levins 1972). A large  $\chi^2$  value would indicate significant differences between islands. The actual  $\chi^2$  from the pre-defaunation counts is 19.7 (df = 35), more than two standard deviations below the expected value of 35 ( $P = .018$ ; for simplicity, and because I am focusing on differences that are too small,  $P$  values here and below are listed for the one-tailed test; a two-tailed test is obtained by doubling the  $P$  values). The postdefaunation frequencies are not much more similar among islands than expected ( $\chi^2 = 31.4$ , df = 35,  $P = .36$ ), although the overall difference between islands, including both pre- and postdefaunation totals, is too small ( $\chi^2 = 19.7 + 31.4 = 51.1$ , df = 35 + 35 = 70,  $P = .044$ ). Since counts are low in some cells (<1), I repeated the above test after combining adjacent sparse columns (S [scavenger], D [detritus feeder], and W [wood borer] were grouped, as were P [parasite] and U [unknown]; table 1). The modified result is not significant (overall  $\chi^2 = 28.4$ , df = 40,  $P = .085$ ) but remains suggestive. Finally, the differences within a given island between species counts before and after defaunation are also too small, suggesting species-for-species matching by trophic category (overall  $\chi^2 = 22.4$ , df = 39,  $P = .015$ ; combining sparse columns as above, overall  $\chi^2 = 10.4$ , df = 20,  $P = .040$ ).

Brown's (1975) desert rodents (fig. 1) may also be matched. I compared cumulative body-size distributions of the two communities with the Kolmogorov-Smirnov  $D$ . Observed  $D$  was 0.20, considerably below the expected value of 0.46 under the null hypothesis ( $P = .01$ ). Cumulative body-size distributions in the two deserts thus tend to increase in tandem. However, two of the mouse species occur in both deserts (*Peromyscus maniculatus* and *Dipodomys merriami*; fig. 1), a possible violation of the assumption that communities are independent (see below). A more cautious analysis excludes these two species and yields  $D = 0.33$ , still below the expected difference of 0.56, although not significantly so ( $P = .11$ ).

Species-for-species matching as defined above suggests an effect of interactions between species within communities, provided that two general assumptions of the test are met (see the next section). To see this, recall the two main aspects of

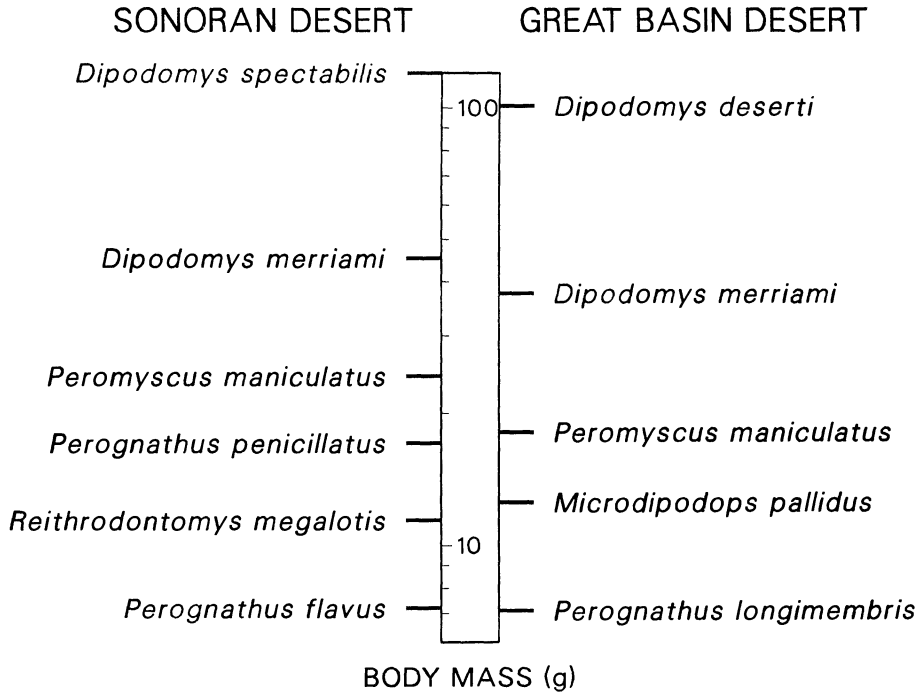


FIG. 1.—Body sizes of rodent species in two desert communities (after Brown 1975)

the null hypothesis being tested: (1) the probability distribution of possible species values is identical for all communities; and (2) sampling is random, such that no species in a community influences the presence or absence or evolution of other species in the same community (i.e., species are independent). A large difference between communities would cause us to reject part 1. Conversely, a too-small difference between communities suggests that part 2 is invalid: species within communities are not independent; that is, they interact.

We are not accustomed to asking whether differences between samples are too small; yet the procedure has some precedence in the literature. An illuminating example is Fisher's (1936) analysis of Mendel's peas. The comparison was made between a sample (observed frequencies of pea plants in different phenotypic classes) and a theoretical prediction (e.g., 3:1, under the simple genetic model), but the two-sample problem is similar. In a combined analysis of all of Mendel's breeding trials, Fisher calculated a  $\chi^2$  of 41.6,  $df = 84$ , well below the value of 84.0 expected under the null hypothesis ( $P = .00003$ ; Edwards 1986). Mendel's data fit his genetic model too well, and Edwards (1986) showed that peas were misclassified in order to yield a closer match to the expectation. Observations were thus not independent; in effect, the pea plants within a trial "interacted," stabilizing their frequencies among the different phenotypic categories.

Conscious manipulation of community attributes in order to further their resemblance is physically impossible (thus, the literal analogy with Fisher's example

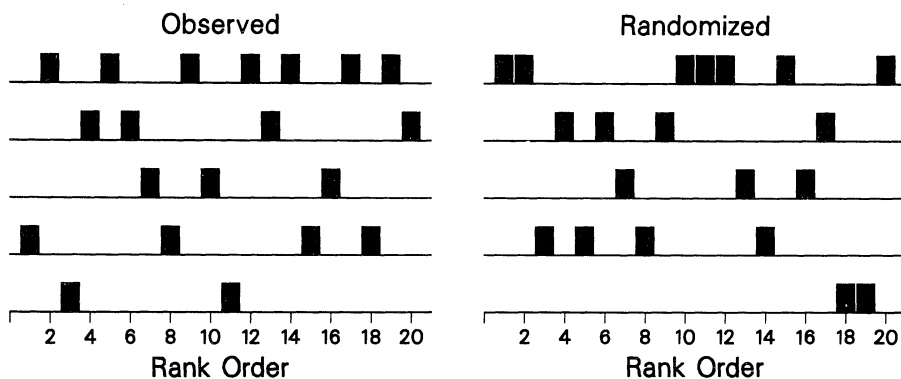


FIG. 2.—Rank order of body sizes (principal-component 1) of finch species in mediterranean habitats compared with a randomized ordering. Morphological variables contributing to size are given elsewhere (Schluter 1986). From top to bottom, the finch communities are from sites in California, South Africa, Chile, Sardinia, and Australia.

breaks down), but interactions between species such as competition can have the same consequence. The direct role of these interactions is to spread species within a community more evenly among resource states, a process that incidentally causes independent sets of species in different communities having the same resources to resemble one another more closely. By itself, the presence of identical resources in two or more communities cannot produce matching; identical resources only help to fulfill part 1 of the null hypothesis being tested (see above), and true matching also requires the nonindependence of species. For this reason, the too-small difference between mangrove islands (table 1) supports Heatwole and Levins's (1972) view that interactions between arthropod species lead to an equitable distribution of species among trophic states on different islands. Similar processes are suggested by the too-small difference between pre- and postdefaunation counts. Matched body-size distributions of rodent communities (fig. 1) suggest that interspecific interactions affect the presence or absence of species of different body size or the direction of body-size evolution.

A final example compares finch communities of mediterranean scrub using data from an earlier study (Schluter 1986; see the Appendix). Body-size distributions (principal-component 1) were compared using a multisample generalization of the Kolmogorov-Smirnov statistic (Lehmann 1975, p. 250). The method is sensitive only to the relative ranks of body sizes, shown in figure 2, and not to absolute sizes. The observed difference between communities,  $D$ , was 0.57, well below the difference of 1.64 expected under the null hypothesis ( $P \approx .0045$ ; estimated from 10,000 simulated randomizations of relative ranks). The inordinate similarity among cumulative body-size distributions reflects the high degree of interspersion of ranks across communities (fig. 2). This contrasts with the greater degree of clumping of ranks within communities in a typical randomization of rank orders ( $D = 1.69$ ; fig. 2). Note that the finch communities are not equally diverse (from two to seven species), and thus a too-small value for  $D$  in this example reflects a kind of two- or three-to-one species matching.

The mediterranean species lists were compiled from several sources (see the Appendix) and are no doubt subject to measurement error. The above result should thus be seen as suggestive, rather than definitive, and as illustrating a pattern that one may encounter when comparing several communities simultaneously in a continuous variable. Measurement error in the lists notwithstanding, matching among finch communities in similar habitats on different continents appears to be a general phenomenon, as shown by too-small values of the  $F$  statistic in ANOVAs comparing different communities in mean finch size (Schluter 1986).

#### STATISTICAL REQUIREMENTS

The above methods assume that each community represents a sample of species from a source pool of possibilities. When islands are colonized from a nearby mainland (see, e.g., table 1), the pool is made up of species potentially able to colonize and persist on islands. When the communities being compared have evolved for a time independently of one another (see, e.g., fig. 2), the pool is the probability distribution of species values that might have evolved. Because communities are compared with one another and not with the source pool, a detailed knowledge of the pool is unnecessary, in contrast to other statistical analyses of community pattern (e.g., "null" models; Harvey et al. 1983; Colwell and Winkler 1984; Schoener 1988). For example, when comparing body sizes among communities using the Kolmogorov-Smirnov statistic (e.g., fig. 2), we require that the distribution of sizes in the species pool be continuous, but not that the distribution itself be specified.

Two general statistical requirements must nevertheless be met before the methods can be applied. First, communities must be independent. This assumption would be violated if species are exchanged between communities. The assumption may also be violated when comparing communities that have evolved separately for a time, if some of the communities share a more recent evolutionary history than others (see Felsenstein 1985).

Second, the source pool must be large relative to the number of species in each community (i.e., the average probability of colonization by species must be small). The necessity of this assumption is intuitive: if only 10 species are available for colonization and communities acquire 8 of them, then the difference between communities cannot be large. The problem of a small relative pool size is apparent when we compare species counts using  $\chi^2$ . Imagine a pool of two herbivores (H) and two predators (P). Assume that all four species have an equal and high probability  $p$  of colonizing a given island, such that many islands acquire three species. The  $\chi^2$  test assumes that four H:P counts are then possible, 3:0, 2:1, 1:2, and 0:3; however, actual counts are constrained by the pool to be 1:2 or 2:1, values closer, on the average, to the expected count of 1.5:1.5. The result is a too-small difference between actual and expected counts (and hence between replicate three-species islands), giving a false impression of matching.

This problem is exacerbated when variation exists between species in probabilities of colonization. To see this, consider the above pool of four species and

islands on which exactly two of them have colonized. Three H:P counts are now possible, 2:0, 0:2, and 1:1. If the probability of colonization,  $p$ , is 0.5 for all four species, then the number of species observed in a given class on an island has an expectation of 1. The average value of the  $\chi^2$  statistic comparing observed with expected class frequencies (i.e.,  $\chi^2$  averaged over the three possible H:P counts) is exactly 0.67. Now consider the case in which  $p$  is 0.7 for one of the two species within each trophic class and  $p$  is 0.3 for the other. The expected number of species in each class remains 1, but the unequal  $p$ 's mean that the observed H:P count will equal the expected configuration of 1:1 more frequently than in the case of equal  $p$ 's (on 79% instead of 67% of the islands). A smaller average value of the  $\chi^2$  statistic results (0.42) and gives a false impression of matching.

To explore further the problem of relative pool size, I carried out a variety of simulations of an island-colonization process involving species in different trophic classes. The results depended on the variability among  $p$ 's, but, in general, the assumptions of  $\chi^2$  were met reasonably well when the number of species on each island was less than about 10% of the number in the pool. The  $\chi^2$  analyses of Heatwole and Levins's table (table 1) is thus probably not greatly affected; the species present on a given island certainly made up less than 10% of local diversity (Simberloff 1969). But effects in general could be larger, and analyses of species counts should therefore be carried out with this problem in mind. The problem is minimized when communities have distinct source pools.

#### DISCUSSION

I have suggested a general criterion for species-for-species matching and have shown from selected examples that the phenomenon indeed occurs. Here I speculate on the frequency of matching in natural communities and clarify the relationship between matching and community convergence.

Too few studies have been carried out to allow a firm conclusion on the prevalence of matching in nature. However, there are two reasons for suspecting that the phenomenon may be relatively rare. First, the few putative cases that do exist often do not hold up when examined in detail. For example, I used the above procedures to compare the mediterranean bird communities of Cody and Mooney (1978; California, Chile, Sardinia, and South Africa). Of seven ecological characteristics presented in their table 1 (trophic category, density, two complex morphological variables, mean foraging height, and two complex feeding-behavior variables), a tendency toward matching was evident only in the first: differences between communities in the proportion of species in each trophic class were too small ( $\chi^2 = 11.4$ ,  $df = 24$ ,  $P = .01$ ; combining categories with low counts yielded  $\chi^2 = 9.3$ ,  $df = 15$ ,  $P = .14$ ). However, these entire avifaunas combine many taxonomic groups, and conceivably a greater degree of matching might be found within some well-defined ecological subgroups or guilds (e.g., finches; fig. 2).

Second, it is easy to imagine situations that would prevent matching. Recall that we are seeking communities more similar than would be expected on the basis of random sampling from the *same* underlying probability distribution of possible species values. Any factor that causes the underlying distributions to differ will

quickly decrease the chance that a too-small difference between communities will arise. For example, habitats superficially alike often differ in important features such as resources (Orians and Solbrig 1977; Cody and Mooney 1978; Milewski 1983). At the very least, we may expect subtle resource differences to prevent all but a crude level of matching. Historical differences between faunas may also prevent underlying distributions of possible species values from being the same. However, even though matching may be uncommon, the phenomenon is still interesting. It would be useful to know in what contexts it is observed and to what extent particular factors prevent matching.

Species-for-species matching is usually discussed in the context of community convergence (e.g., Cody 1974; Cody and Mooney 1978; Ricklefs and Travis 1980). I have avoided relating matching to convergence until now because I feel it is worth distinguishing between the two phenomena. Matching is a measure of absolute community similarity, whereas convergence measures the greater similarity between communities relative to the similarity between their ancestors. When matching is observed, convergence may also have occurred, but it would be erroneous to conclude that convergence has not occurred when communities are found to be unmatched, or even when they are highly dissimilar (see, e.g., Lawton 1984). Note also that although matching suggests the presence of interspecific interactions, convergence without matching usually does not (Schluter 1986).

Though matching might be rare, convergence is conceivably common, because matching requires similar resources and weak historical constraints, whereas convergence requires only that the current environments be more similar than the environments experienced by their ancestors. Elsewhere, I present an indirect test of convergence and its empirical relationship to the degree of community similarity (matching; Schluter 1986).

Matching, like convergence, is one aspect of the more general and largely unresolved question of how well and under what circumstances community structure may be predicted from a knowledge of resource characteristics. It is hoped that the existence of simple, general criteria such as those proposed here will aid in carrying out the necessary tests.

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#### APPENDIX

This section discusses the list of mediterranean finch species (Schluter 1986) on which the observed ranks in figure 2 were based.

To compare the morphologies of nonbreeding finch communities, I modified the breeding lists of Cody and Mooney (1978) where information allowed. One California species absent from chaparral in the winter was deleted (*Pheucticus melanocephalus*), and four winter visitors were added: *Carduelis psaltria* (erroneously listed as *C. lawrencei* in Schluter 1986), *Junco hyemalis*, *Zonotrichia leucophrys*, and *Z. iliaca* (Cody 1974; D. Schluter,

personal observation). A fifth species, *Z. atricapilla*, was not included because it is mainly herbivorous and not granivorous in the winter (Martin et al. 1951; D. Schluter, personal observation). Finch species on other continents are apparently resident in the areas studied (Frandsen 1982; Peterson et al. 1983; Blakers et al. 1984; Olrog 1984), and breeding lists were not adjusted to accommodate migrants. Two species were added to the South African list (*Euplectes capensis* and *Emberiza capensis*) because Winterbottom (1966) described them as frequent. *Serinus leucoptera* was deleted from the same list because it is rare and was unavailable in the museum collections. I added an Australian mediterranean site to the collection of Cody and Mooney, with two resident finch species, *Poephila guttata* and *Emblema guttata* (Schodde 1981; Blakers et al. 1984).

## LITERATURE CITED

- Blakers, M., S. S. J. F. Davies, and P. N. Reilly. 1984. The atlas of Australian birds. Melbourne University Press, Carleton, Victoria.
- Brown, J. H. 1975. Geographical ecology of desert rodents. Pages 315–341 in M. L. Cody and J. M. Diamond, eds. Ecology and evolution of communities. Belknap, Cambridge, Mass.
- Cody, M. L. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, N.J.
- Cody, M. L., and H. A. Mooney. 1978. Convergence versus nonconvergence in mediterranean climate ecosystems. *Annu. Rev. Ecol. Syst.* 9:265–321.
- Colwell, R. K., and D. W. Winkler. 1984. A null model for null models in biogeography. Pages 344–359 in D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, eds. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, N.J.
- Edwards, A. W. F. 1986. Are Mendel's results really too close? *Biol. Rev.* 61:295–312.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1–15.
- Fisher, R. A. 1936. Has Mendel's work been rediscovered? *Ann. Sci.* 1:115–137.
- Frandsen, J. 1982. Birds of the southwestern Cape. Sable, Sloane Park, South Africa.
- Harvey, P. H., R. K. Colwell, J. W. Silvertown, and R. M. May. 1983. Null models in ecology. *Annu. Rev. Ecol. Syst.* 14:189–211.
- Heatwole, H., and R. Levins. 1972. Trophic structure stability and faunal change during recolonization. *Ecology* 53:531–534.
- Lawton, J. H. 1984. Non-competitive populations, non-convergent communities, and vacant niches: the herbivores of bracken. Pages 67–100 in D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, eds. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, N.J.
- Lehmann, E. L. 1975. Nonparametrics: statistical methods based on ranks. Holden Day, San Francisco.
- Martin, A. C., H. S. Zim, and A. L. Nelson. 1951. American wildlife and plants, a guide to wildlife food habits. Dover, New York.
- Milewski, A. V. 1983. A comparison of ecosystems in mediterranean Australia and southern Africa: nutrient-poor sites at the Barrens and Caledon coast. *Annu. Rev. Ecol. Syst.* 14:57–76.
- Olrog, C. C. 1984. Las aves argentinas. Administración de Parques Nacionales, Buenos Aires.
- Orians, G. H., and O. T. Solbrig, eds. 1977. Convergent evolution in warm deserts. Dowden, Hutchinson & Ross, Stroudsburg, Pa.
- Peterson, R. T., G. Mountfort, and P. A. D. Hollom. 1983. A field guide to the birds of Britain and Europe. Houghton Mifflin, Boston.
- Ricklefs, R. E., and J. Travis. 1980. A morphological approach to the study of avian community organization. *Auk* 97:321–338.
- Schluter, D. 1986. Tests for similarity and convergence of finch communities. *Ecology* 67:1073–1085.
- Schodde, R. 1981. Bird communities of the Australian mallee: composition, derivation, distribution, structure and seasonal cycles. Pages 387–415 in F. di Castri, D. W. Goodall, and R. L. Specht, eds. Mediterranean-type shrublands. Elsevier, Amsterdam.
- Schoener, T. W. 1988. Testing for non-randomness in sizes and habitats of West Indian lizards: choice of species pool affects conclusions from null models. *Evol. Ecol.* 2:1–26.

- Simberloff, D. 1976. Trophic structure determination and equilibrium in an arthropod community. *Ecology* 57:395–398.
- Simberloff, D., and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. *Ecology* 50:278–296.
- Winterbottom, J. M. 1966. Ecological distribution of birds in the indigenous vegetation of the South-west Cape. *Ostrich* 37:76–91.

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