

Community Composition and Nested-Subset Analyses: Basic Descriptors for Community Ecology

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MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Community composition and nested-subset analyses: basic descriptors for community ecology

Wade B. Worthen

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Three primary descriptors of community structure are the number, identities (composition), and abundances of species therein. Over the past 35 years, most attention has focused on relationships involving number (species-area and species-energy relationships) or abundance distributions (broken-stick, geometric, log-normal, core-satellite, etc.). Composition patterns have been underemphasized, even though several tools for addressing particular non-random patterns in species composition are available. One non-random pattern in community composition is nested subset structure. A community has a nested subset structure if the species found in depauperate replicates are also found in progressively more species-rich assemblages. In this review, the problems of failing to consider composition patterns like nestedness are described, using species-area relationships and the SLOSS debate (single large or several small reserves) as an example. In addition, nestedness analyses are promoted as: 1) important descriptive tools for determining whether a community has this common non-random pattern of species composition, and 2) as important investigative tools for suggesting mechanisms potentially structuring a community.

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The first step in most community-level studies is to determine the abundances of a taxonomically or trophically defined group of species in a number of habitats. Regression, ordination, or discriminant function analyses are often used to relate species' abundances or species richness (or a derived diversity index) to descriptive variables such as habitat size, climate, or productivity. Although these analyses can reveal critically important patterns, they often fail to address the third basic feature of community structure: the identities of the species themselves (hereafter 'community composition').

Analyzing patterns in community composition has proven far more difficult than analyzing quantitative variables like species richness and abundance distributions. Pairwise analyses of co-occurrence patterns are appropriate for testing particular pairwise interactions like competition (Connor and Simberloff 1979, 1984) and they can reveal some guild structure (Worthen and McGuire 1988), but they fail to address patterns at the level of the entire community. In addition, the large number of pairwise contrasts required for a species-rich assemblage ($[N^2 - N]/2$) can obscure community-level

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patterns and make interpretations difficult or ambiguous (Gilpin and Diamond 1984).

Several community-level analyses have been developed (various neutral models, similarity indices, etc.). Many recent models address one type of non-random composition pattern called nested subset structure. A community has a nested subset structure if the species in depauperate assemblages are a non-random subset of the species that occur in more species-rich assemblages (Patterson and Atmar 1986). Several procedures have been used to examine pattern of nested subset structure. Diamond (1975a) used incidence functions to group species into distributional vagility categories (tramps and supertramps, etc.) and then described nestedness patterns among groups. Others have used Mann-Whitney U tests to test single species distributions and community level patterns related to richness, area, or degree of isolation (Schoener and Schoener 1983, Patterson 1984, Simberloff and Levin 1985, Simberloff and Martin 1991, Kadmon 1995), fit logistic models to presence-absence matrices (Ryti and Gilpin 1987), and created specifically designed nestedness analyses that compare real communities to random models generated by Monte Carlo simulations (Patterson and Atmar 1986, Cutler 1991, 1994) or computations (Wright and Reeves 1992).

Nestedness has several important implications for conservation ecology (Patterson 1987). For instance, certain rare species might be indicators of total species richness because they would typically occur only in species-rich communities. Also, if species richness decreases as habitat area declines (a significant species-area relationship), knowing the nested-subset structure might allow one to predict the ultimate community composition in a habitat subjected to natural or anthropogenic reduction or fragmentation (McDonald and Brown 1992, Lomolino 1994, Brown 1995). In addition, since population size also often correlates with habitat area (Brown 1981, Brown and Maurer 1987) and the number of sites occupied (Hanski 1982), describing composition-area relationships and nestedness could help identify species at risk of extinction should habitat area be reduced below that needed to sustain minimum viable populations (Brown 1981, Soulé and Simberloff 1986; but also see utility of saturation indices, Quinn and Harrison 1988, Cook 1995).

These consequences are well known to conservation biologists, and the uses and limitations of these analyses as practical tools for the selection of nature reserves have been summarized and critiqued in previous reviews (Patterson 1987, Simberloff and Martin 1991, Doak and Mills 1994, Lomolino 1994, Cook 1995). However, the dearth of nestedness studies outside the conservation literature suggests that the utility of these analyses as basic community descriptors is underappreciated by many community ecologists. In this review, the importance of composition analyses and nestedness

are demonstrated in two ways. First, the negative consequences of de-emphasizing composition patterns are described in the context of the SLOSS debate ("single large or several small" reserves). Second, the usefulness of nestedness analyses to basic community ecology is presented. Nested subset analyses are valuable descriptive tools for revealing an ecologically meaningful non-random pattern, and are useful exploratory tools for suggesting mechanisms that may structure a particular community.

Species-area relationships, nestedness, and the "SLOSS" debate

One of the most common patterns in natural communities is the species-area relationship, in which species richness increases with increasing sampling area. It has even been characterized as "one of community ecology's few genuine laws" (Schoener 1976). Initially, the relationship was passively accepted and attributed to greater colonization (Arrhenius 1921) and habitat diversity (Williams 1943) on large islands. However, when Preston (1960, 1962) and MacArthur and Wilson (1963, 1967) showed that log-species vs log-area curves ("power" functions, Arrhenius 1921) could be produced by area-dependent extinction rates in the theory of island biogeography, and suggested that slope analyses could determine whether a community was in equilibrium, the species-area relationship became the focal principle in conservation arguments for protecting "single large" reserves over "several small" ones (SLOSS debate: Terborgh 1974, 1976, Diamond 1975a, b, 1976, Wilson and Willis 1975, Simberloff 1976, Simberloff and Abele 1976, 1982, 1984, Simberloff and Gotelli 1984, Willis 1984, and see reviews by Brown 1984, Simberloff 1988, 1992, Sætersdal et al. 1993, Doak and Mills 1994, and Lomolino 1994). Subsequent analyses revealed the weaknesses of these claims on the following mathematical, theoretical, and empirical grounds: 1) untransformed and exponential (species vs log-area) functions often fit better than the power function (Connor and McCoy 1979, Martin 1981); 2) slope analyses are ambiguous and can not discriminate between the mechanisms of random sampling, colonization-extinction equilibria, habitat diversity, disturbance, or competition (Johnson and Simberloff 1974, Boecklen and Gotelli 1984, McGuinness 1984, Caswell and Cohen 1993, Doak and Mills 1994); and 3) under particular assumptions, island biogeographical theory also predict that several small reserves should support more total species than a single large area (Simberloff and Abele 1976, 1982, 1984, Higgs and Usher 1980). Indeed, most empirical examinations have found higher cumulative richness values on several small islands (Simberloff and Abele 1976, Järvinen 1982, Lahti and Ranta

1985, Niemelä et al. 1985, Boecklen 1986, Quinn and Harrison 1988, Robinson and Quinn 1988, Loman and von Schantz 1991, McNeill and Fairweather 1993). In 1986, Soulé and Simberloff declared that "SLOSS is no longer an issue in the optimal size debate", suggesting that decisions on reserve area be based on the minimum area needed to sustain the minimum viable population of target species, habitat diversity, and autecological data.

The debate hinged on the similarity among the communities in small habitats; in other words, community composition patterns. This is where nestedness relates to the SLOSS debate. If strong nestedness and species-area relationships exist, then small habitats will likely harbor redundant, depauperate subsets that are unlikely to equal the richness of a single large area (Patterson 1987, Wright and Reeves 1992). Protagonists of the SL position correctly defended the theoretical argument that $SL > SS$ if small habitats are homogeneous and contain similar species sets (Terborgh 1974, Diamond 1975a, b, 1976, Diamond and May 1976). Protagonists of the SS position correctly showed that island biogeography could also predict that $SS > SL$ if communities on small habitats are dissimilar (Simberloff and Abele 1976, Connor and Simberloff 1978, Higgs and Usher 1980, Higgs 1981, Margules and Usher 1981). Thus, composition-area relationships were central to the entire debate (Terborgh 1974, 1976, Diamond 1975a, b, 1976, Diamond and May 1976, Whitcomb et al. 1976, Pickett and Thompson 1978). However, the effects of community similarity on SLOSS were not quantified until 1980 (Gilpin and Diamond 1980, 1982, Higgs and Usher 1980, Higgs 1981, Margules and Usher 1981), and methods for quantifying and comparing nestedness at the community level were not developed until 1985 and later (Simberloff and Levin 1985, Patterson and Atmar 1986, Cutler 1991, 1994, Wright and Reeves 1992, Atmar and Patterson 1993). As such, composition-area effects were eclipsed in the SLOSS debate by the quantitative, testable predictions regarding species-area relationships derived from island biogeography. This is understandable but unfortunate; species-area relationships simply do not contain enough information to answer the SLOSS question. Reserve managers charged with the task of actually conserving species were well aware of these shortcomings. As Saunders et al. (1991: 19) stated: "...while of theoretical interest, most of these issues [SLOSS and island biogeography] are of little practical value in managing fragmented systems...the species-area equation, for example, may give a manager a rough idea of how many species will be maintained on a remnant of a given area, but will yield absolutely no information on the practical issue of which habitats contribute most to species richness or which species are most likely to be lost from the remnant".

Nestedness is an important compositional descriptor that can potentially identify risk-prone species (Patterson 1987, McDonald and Brown 1992, Brown 1995, Cook 1995). As such, it could be useful in reserve-selection decisions (Wright and Reeves 1992). However, this index should not be viewed as the sole criterion by which all conservation decisions should be judged. The actual pattern of species distributions across sites is required to identify those that do and do not contribute to nestedness or area patterns (Simberloff and Martin 1991, Doak and Mills 1994, Kadmon 1995). For species that are largely responsible for these patterns, subsequent theoretical predictions or experimental tests might be warranted (Cutler 1994, Kadmon 1995, Worthen et al. 1996). So, even with significant nestedness and species-area relationships, decisions regarding particular species or habitats need species-specific and site-specific information (Simberloff and Martin 1991, Doak and Mills 1994, McCoy and Mushinsky 1994, Kadmon 1995). No single index should be expected to distill the informational content of an entire community, let alone predict how it will react to habitat reduction or fragmentation; not the slope of a line, the exponent of an equation, a species count, a nestedness score, a saturation index, a disorder temperature, a matrix of alpha values, or a connectedness value. In retrospect, it is not surprising that an over-reliance on species-area curves led to erroneous or ambiguous conclusions. Undoubtedly, decisions based exclusively on nestedness scores would meet the same fate. The episode is strong evidence for the failure of the 'magic bullet' approach, and demonstrates the importance of including richness, composition, and abundance patterns in community analyses.

Unfortunately, the bias towards species-area relationships over composition-area relationships continues; despite the growing empirical testimony to the frequency of nestedness and community similarity on habitat fragments in some systems (Galli et al. 1976, Crowe 1979, Willis 1979 (cf. Blake 1991), Ambuel and Temple 1983, Blake and Karr 1984, East and Williams 1984, Jones et al. 1985, Simberloff and Levin 1985, Nilsson 1986, Patterson and Atmar 1986, Patterson 1987, 1990, Blake 1991, Bolger et al. 1991, Cutler 1991, Newmark 1991, Patterson and Brown 1991, Simberloff and Martin 1991, McDonald and Brown 1992, Soulé et al. 1992, Wright and Reeves 1992, Kodric-Brown and Brown 1993, Douglas and Lake 1994, Guégan and Huguény 1994, Lomolino 1994, McCoy and Mushinsky 1994, Kadmon 1995, Telleria and Santos 1995, Worthen and Rohde 1996, Worthen et al. 1996). Widely used introductory ecology texts continue to focus on island biogeography and species-area relationships without adequately describing how validity of these theories depends on nestedness and composition-area relationships (Ricklefs 1990, Pianka 1992, but see Beeby 1993, Krebs 1994). This lack of interest in nestedness and

composition patterns is not unique to introductory ecology texts. In a recent examination of the interface between community ecology and biogeographical theory, there were no references to nested subset structure among the 900+ references cited (Ricklefs and Schluter 1993). Species-area or species-energy relationships, however, were explicitly addressed in nearly half of the thirty chapters (Ricklefs and Schluter 1993).

Nestedness: a basic descriptor in community ecology

Computing a nestedness score – the Patterson and Atmar (1986) method

Nested subset analyses are useful tools for revealing an important type of non-random community structure. The relative merits and faults of different nestedness indices, and the relative merits of richness or area based compositional descriptors, have been summarized elsewhere (Cutler 1991, 1994, Simberloff and Martin 1991, Wright and Reeves 1992, Doak and Mills 1994, Cook 1995). Only a brief summary of Patterson and Atmar's (1986) two basic options will be presented here. To calculate a nestedness score, community replicates are ranked by their species richness values. For example, for the guild of ground-feeding Galapagos finches (data from Grant and Schluter 1984), the islands are ordered from five-species communities to single-species sets (Table 1). For each species, the most depauperate community containing that species is identified. Absences from all richer communities are tallied (x_i 's and n_i 's, Table 1), and these values are summed across all the species to generate a nestedness score (N). Nestedness scores will increase with the size of the matrix, so scores from communities with different matrix dimensions can not be compared. (Wright and Reeves (1992) introduced a standardized metric, C , which can be compared between communities.)

Benefit no. 1: Testing a composition pattern against a null model

By rejecting a null hypothesis of random richness, composition, or abundance, it is implied that this aspect of community structure is probably a meaningful pattern and not a chance occurrence. Of course, whether a null model is rejected depends as much on the model as it does on the data. In the Patterson and Atmar (1986) nestedness analysis, the actual nestedness value is compared to a distribution of 1000 nestedness values (z value and t -test) computed for randomly constructed communities (Patterson and Atmar 1986). Two different models can be used to create the random communities. In both models, species are randomly assigned to assemblages until a set of communities is created that has the same distribution of species richness values as

the natural data set. In the first model (R_0), species are assigned to assemblages with equal probability. Statistically significant departures from the random communities are common with this method, because differences in species' frequencies can cause a degree of nestedness. (The Wright and Reeves (1992) statistic N_c also assumes equiprobable species occurrences and is equally liberal.) The second model (R_1) of Patterson and Atmar (1986) is more conservative; it assigns species to the randomly constructed communities based upon their frequencies in the natural data set (but see criticisms of Simberloff and Martin 1991, and Wright and Reeves 1992). In theory, these null communities already account for differences in species' incidence values; statistically significant departures from the randomly constructed communities should indicate ecologically meaningful patterns that are not sampling artifacts of unequal frequency distributions. The Galapagos finch data show how these analyses yield different results. There is a significant difference between the actual guild and the equiprobable null models (R_0), but no statistically significant difference between the actual guild and the frequency-based null models (R_1 , Table 1).

Species-level patterns can also be addressed with this statistic and with Mann-Whitney U tests (Schoener and Schoener 1983, Patterson 1984, Simberloff and Levin 1985, Simberloff and Martin 1991, Kadmon 1995). Species-level analyses are important because they can identify the species contributing to the nestedness pattern (Simberloff and Martin 1991, Kadmon 1995, Worthen et al. 1996). In the Galapagos finch data set (Table 1), four of the six species have nested patterns (using Mann-Whitney U). Again, however, nestedness across the entire community is insignificant when compared to conservative R_1 models.

Although nestedness is probably a common pattern (Patterson 1990, Simberloff and Martin 1991), rejecting null models is not a moot exercise; many communities do not exhibit nested subset structure when compared to the conservative R_1 null model (as in Table 1) and many species within a significantly nested community may not have significantly nested distributions (Kadmon 1995, Worthen et al. 1996). In a recent analysis of 38 communities of metazoan ectoparasites on marine fishes, there was only one case of a significantly nested pattern (after a Bonferroni correction for multiple comparisons, Worthen and Rohde 1996). This was an important analysis because it provides a definitive test (and support) for previous hypotheses regarding the random nature of these communities (Rohde et al. 1994, 1995).

It is important to realize, however, that failure to reject the null hypotheses in these nested subset analyses does not necessarily mean that the communities are 'random assemblages' unaffected by ecologically meaningful processes; it just means that these communities do not have this particular type of composition pattern.

Table 1. Community composition patterns for Galapagos ground finch guilds (data from Grant and Schluter 1984) and Patterson and Atmar (1986) nestedness analyses. (Species, from left to right: *Geospiza fuliginosa*, *G. fortis*, *G. scandens*, *G. magnirostris*, *G. difficilis*, and *G. conirostris*.)

a. Guild composition patterns (1 = species occurrence, x = absence deviating from perfect nestedness)

Island	Richness	<i>G. ful.</i>	<i>G. fort.</i>	<i>G. scan.</i>	<i>G. diff.</i>	<i>G. magn.</i>	<i>G. con.</i>
Santiago	5	1	1	1	1	1	x
Pinta	5	1	1	1	1	1	x
Isabela	4	1	1	1	1	x	x
Fernandina	4	1	1	x	1	1	x
Rabida	4	1	1	1	1	x	x
Santa Cruz	4	1	1	1	1	x	x
Santa Fe	4	1	1	1	1	x	x
Marchena	4	1	1	1	1	x	x
Genovesa	3	x	x	x	1	1	1
Seymour	3	1	1	1	x	x	x
Pinzon	3	1	1	x	1	x	x
Baltra	3	1	1	1	x	x	x
San Cristobal	3	1	1	1	x	x	x
Floreana	3	1	1	1	x	x	x
Plazas	3	1	1	1	x	x	x
Espanola	2	1					1
Gardner (by Espan.)	2	1					1
Darwin	2	x			1	1	
Wolf	2	x			1	1	
Daphne Major	2	x	1	1			
Champion	2	x	1	1			
Daphne Minor	2	1	1				
Bainbridge	x	1					
Bartolome	x	1					
Beagle	x	1					
Caldwell	x	1					
Cowley	x	1					
Eden	x	1					
Enderby	x	1					
Gardner (by Flor.)	x	1					
Hermanos	x	1					
Tortuga	x	1					
Frequency		27	17	14	12	6	3
Nestedness subscore (n_i)		5	1	3	5	11	14
Nestedness score ($\Sigma(n_i)$)		39					

b. Species-level analyses

Z-scores⁺ (* = $p < 0.05$)
(Mann-Whitney U tests)

0.26 ns 4.47* 3.99* 4.07* 2.01* 0.20 ns

c. Community-level analyses

	R0 (Equiprobable)	R1 (Frequency based)
Nestedness score	39	39
Null scores ($\bar{X} \pm 1\text{sd}$, 1000 runs)	58.46 \pm 3.84	50.46 \pm 7.63
z value ⁺	-4.95	-1.44
p value (t-test)	$p < 0.01$	$p > 0.05$, ns

⁺ = includes (+0.5) continuity correction (Wright and Reeves 1992).

Community composition may have a different, non-random composition pattern (checkerboard), or non-random richness or abundance patterns. All three aspects of community structure should be considered. The contrast between the Galapagos finch guild and the ectoparasites of marine fishes demonstrates this point. Neither community exhibits nested subset structure. However, it is incorrect to say that both are random, non-interacting assemblages. In the Galapagos finch guild, there are non-random patterns in bill morphology and species abundances suggesting that competitive interactions affect this community (Grant and Schluter

1984, Simberloff 1984). However, in the ectoparasite communities, there are extremely few significant relationships among species abundances; all analyses indicate that competition is unimportant and that community composition is determined only by colonization (Rohde et al. 1995). Thus, nestedness analyses address the remaining possibility that differential colonization causes a non-random, nested composition pattern (as described below). In this case, demonstrating that these communities are not nested reinforced the abundance patterns and provides compelling evidence that local communities are truly unstructured, random

assemblages from the local species pool. There are global patterns in species richness, however; tropical fish support more ectoparasite species than temperate or arctic fishes (Rohde et al. 1995).

These comparisons show that community structure is a function of all three descriptors: richness, composition, and abundance. Concluding that a community is a 'random assemblage' based on analyses of only one descriptor is potentially incorrect, because structure may exist for one of the other variables. It would be interesting to know whether other communities, purported to be 'random assemblages' based on species richness or relative abundance analyses, are random with respect to composition patterns and nested subset structure. More attention to composition patterns is needed.

Benefit no. 2: Focusing on the determinants of nested community structure

Differential extinction. Four mechanisms have been proposed to explain nestedness patterns: differences in extinction probabilities, differences in colonization abilities, nested habitat requirements, and passive sampling (Cutler 1994). Basically, these are factors that influence species incidence functions (Wright and Reeves 1992). The results of nestedness analyses can focus an experimenter's attention on (or away from) these variables. For most nested communities, subset structure has usually been attributed to differential extinction probabilities (Schoener and Schoener 1983, Jones et al. 1985, Patterson and Atmar 1986, Roughgarden 1989, Bolger et al. 1991, Newmark 1991, Patterson and Brown 1991, Soulé et al. 1992). This is not surprising, given that nestedness studies followed species-area work that focused on land-bridge or mountaintop 'islands' (Brown 1971, Diamond 1975a, b, Diamond and May 1976). Since these islands were once continuous and connected to a mainland, it is assumed that they originally contained the full complement of mainland species and that subsequent fragmentation and isolation caused the communities to 'relax' to their present assemblage; perhaps as a consequence of diffuse competition for reduced resources and/or stochastic extinction of populations fluctuating close to their minimum viable population sizes.

Differential colonization. Differences in colonization rates have long been recognized as a potential cause of nestedness (Darlington 1957, Diamond and May 1976, Gilpin and Diamond 1982, Patterson and Atmar 1986, Patterson 1990, Patterson and Brown 1991). Isolated islands (far from source populations, or isolated by an inhospitable matrix) should only harbor species with the greatest dispersal capabilities. Islands that are easier to colonize (closer, or with corridors or an easily traversed matrix) should include poorer dispersers in addition to the subset of vagile species found in depauperate

isolates. For instance, in a complete species level analysis of woody plant communities on islands formed by the flooding of a reservoir, Kadmon (1995) demonstrated that the communities were nested with respect to isolation but not island size; suggesting that differential dispersal was important. Kadmon (1995) also demonstrated that wind-dispersed, vagile species contributed little to the nestedness pattern, whereas species with limited dispersal abilities were strongly nested. This is an excellent example of how a nestedness analysis can be used to form and test hypotheses regarding the factors affecting community structure.

Some authors have suggested that oceanic islands, structured by both colonization and extinction, should have less nested communities than land-bridge islands dominated by extinction, alone (Quinn and Harrison 1988, Patterson 1990, Cutler 1991, 1994, Wright and Reeves 1992). Wright and Reeves (1992) suggested that their standardized C metric might distinguish these two groups. However, ectoparasite communities that are largely structured by colonization have Wright and Reeves (1992) C-scores as high as extinction dominated systems (Worthen and Rohde 1996). While the Wright and Reeves (1992) C-value may not resolve this distinction, it is possible that extinction-dominated systems may have other recognizable properties. Cutler (1994) suggested that communities dominated by extinction seem to have 'hole-rich' matrix patterns identified by his metric U (not the Mann-Whitney U).

It might be possible to distinguish the relative effects of colonization and competition on community-wide composition patterns. In communities where particular pair-wise competitive interactions affect composition patterns, nestedness should be reduced (as in the Galapagos finch guild, Table 1). In contrast, a significant nestedness score suggests that pairwise competitive effects are not the primary determinants of community-wide composition patterns. For example, consider the avifauna of the New Hebrides archipelago that was central to the null model debate of the 1970–80's (data from Diamond and Marshall 1976). After an extensive examination of richness and co-occurrence patterns, Connor and Simberloff (1979, 1984) concluded that competition was not the primary determinant of community composition. They continued by stating (1979: 1138): "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". If the distributional patterns are determined more by non-random colonization and stochastic extinction patterns than by competition, one might expect significantly nested composition patterns. The avifauna of the New Hebrides archipelago does exhibit significantly non-random nested subset structure (Cook 1995). This supports

Connor and Simberloff's (1979) argument; rejecting the hypothesis that the communities are structured by competition does not mean that they are random assemblages – the nestedness analysis demonstrates that they have a significantly non-random composition structure. Likewise, although competition does not determine community-wide species richness and composition patterns, it is still possible that competition affects the abundance patterns of particular species pairs or the structure of particular guilds (Gilpin and Diamond 1984). Again, all three descriptors must be addressed.

Nested habitats or niche space. Nested habitat requirements can also produce nested subset structure (Blake 1991, Kodric-Brown and Brown 1993, Worthen et al. 1996). Generalists should be found in most habitats, whereas specialists will only occur in the subset of sites where their more limited requirements are also met. Given that large areas typically have greater habitat diversity than small areas, one might expect communities governed by nested niches to show the strongest relationship between nestedness, richness, and area. Again, however, nestedness in these systems is strongly affected by the habitat variability among small islands. If small islands vary, they may each harbor a few different specialists; creating a strong species-area relationship without the community having a nested subset structure (Patterson and Brown 1991).

Nestedness resulting from nested environmental tolerances might be expected in certain types of situations. For instance, in some types of primary succession, initial colonists alter the environment and make it more hospitable for other species. These facilitative dependencies (Connell and Slatyer 1977) would encourage nested subset structure if the 'pioneers' persisted while new species colonize. Successional changes in heterotrophic communities can be facilitative, as well. Typically, initial colonists breach the protective covering of the resource (skin, bark, or seed coat, for example), providing access for subsequent species. The effects of species facilitations, commensalisms, and mutualistic interactions on nestedness and community composition have not been adequately addressed and demand further study.

Passive sampling. Cutler (1994) suggested that passive sampling can also produce significant nestedness. Differences in species' frequencies can certainly produce nestedness; that was the impetus for the construction of more conservative models (R1) that attempted to account for these random effects. However, Cutler (1994) demonstrated that 100 random archipelagos, constructed through the passive sampling of individuals from 100 species with a specific log-normal relative abundance curve ($\alpha = 0.2$), were all significantly nested *even when using conservative R1 criteria* (my italics). However, with only one combination of parameters

tested, it is possible that nestedness is dependent on the particular characteristics of this model. For instance, the ten sites were created with different 'sizes' by varying individual abundances across three orders of magnitude (2, 4, 8, 16, 32, 64 ...1024). 60% of the sites have fewer than 100 individuals and therefore will necessarily contain fewer species than the sites with 256, 512, and 1024 individuals. When the effects of a skewed species abundance distribution (log-normal, $\alpha = 0.2$) are added, the effects become even more pronounced by increasing the similarity among the six smallest sites (particularly those containing only 2, 4, and 8 individuals) and increasing their nestedness within medium and large sites. These constraints would increase nestedness relative to R1 models where richness is not related to individual abundances. Finally, the particular log-normal species abundance curve ($\alpha = 0.2$) may also have biased the test in another manner. In a study that created random communities using real species frequencies and Coleman's (1981) random placement model, random communities were not significantly nested when compared to R1 models (Bolger et al. 1991). Williams (1995) suggested that Coleman's model (1981) is more appropriate than power functions (that assume log-normal distributions) for testing species-area relationships; perhaps the same is true for nestedness patterns (particularly where sites have a dramatic 'area' component where size/abundance varies by three orders of magnitude). Cutler (1994) demonstrated that passive sampling can produce a nested subset pattern under specific conditions. However, the high species pool/site ratio, and the limiting effects of the species pool/individual abundance ratios (compounded by the effects of a log-normal species abundance distribution), may have artificially constrained this 'random' model. More passive sampling models with different parameter states need to be tested to determine the generality of this mechanism. In any case, it may be appropriate to test the richness distribution against a random placement model (such as Coleman 1981) to 'protect' subsequent nestedness analyses.

Conclusions

Nested subset analyses are not the 'magic bullets' of conservation biology; given the multivariate nature of community composition, it seems unreasonable to expect any single descriptor to satisfy this role. Nonetheless, nested subset analyses can provide important descriptive information about community structure. These analyses can be used to determine whether a particular non-random pattern exists, and they can be used to suggest what factors might be contributing to the composition patterns within a community (see Kadmon 1995, Worthen et al. 1996). It has been more than a decade since the use of null models in community

ecology was promoted (see articles in Strong et al. 1984), and nearly a decade since the introduction of analyses specifically designed to test these patterns (Patterson and Atmar 1986). However, these useful null models for testing nested subset patterns have been underexploited. The time is long overdue for determining the frequency of non-random nestedness patterns in natural communities, and for recognizing that composition patterns, in general, are important descriptors of community composition.

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