

The role of stochastic processes in producing nested patterns of species distributions

Christopher L. Higgins, Michael R. Willig and Richard E. Strauss

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Nestedness has received considerable attention in community ecology and conservation biology from both theoretical and empirical perspectives. This has led to the creation of various metrics and null models to analyze nested subsets, all of which rely on the random placement of species to assess significance. However, if immigration and extinction are the processes that underlie species distributions on island systems, then null models might be better determined on the basis of randomly placed individuals. Consequently, we examined the effects of species–abundance distributions (uniform, dominance–decay, random–assortment, and dominance–preemption), island–size distributions (uniform and linear decrease), and total abundances (128, 256, 512, 1024, 2048, 4096 and 8192) on the degree of nestedness and its significance. Generally, matrices of species presence and absence created from the random placement of individuals were nested significantly according to null models based on the random placement of species. Island size and abundance had less of an effect on nestedness in systems dominated by only a few species than in systems in which abundances were distributed more evenly. Stochastic processes, such as the random placement of individuals, predispose systems to evince patterns of nestedness at the species level, which may account, in part, for the ubiquity of nestedness in nature.

C. L. Higgins, M. R. Willig and R. E. Strauss, Dept of Biological Sciences and the Museum, Texas Tech Univ., 6 Lubbock, TX 79409-3131, USA (higgins@tarleton.edu). Present address for CLH: Dept of Biological Sciences, Box T-0100, Tarleton State Univ., Stephenville, TX 76402, USA. Present address for MRW: Center for Environmental Sciences and Engineering, and Dept of Ecology and Evolutionary Biology, Univ. of Connecticut, Storrs, CT 06269, USA.

Studies of island biotas have played a major role in advancing ecological and evolutionary understanding of community structure. The seminal work of MacArthur and Wilson (1963, 1967) catalyzed research by developing a model to describe the dynamic relationship between immigration and extinction in effecting patterns of species richness on islands of different size. This focus on immigration and extinction eventually led to the idea of nested subsets or nestedness, which describes the idealized situation in which taxa found on species-poor islands are proper subsets of those on species-rich islands (Patterson and Atmar 1986). Since its formaliza-

tion, nestedness has received considerable attention in community ecology (Kadmon 1995, Brualdi and Sanderson 1999, Roberts 2002, Hausdorf and Hennig 2003) and conservation biology (Patterson 1987, Simberloff and Martin 1991, Cook 1995, Boecklen 1997), with many biological systems exhibiting at least partially nested patterns of species distributions (Patterson 1990, Cook and Quinn 1995, Wright et al. 1998).

Despite increased attention to documenting empirical patterns of nestedness, consensus has not been reached concerning the underlying mechanisms that lead to nestedness as opposed other patterns of community

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composition. In addition to historical constraints that restrict the pool of available species that potentially can occupy a set of islands (Brown and Lomolino 1998), three main ecological mechanisms have been proposed to cause nestedness. These include differential colonization (Darlington 1957, Cutler 1991, Cook and Quinn 1995), differential extinction (Patterson and Atmar 1986, Wright and Reeves 1992), and hierarchical habitat distributions (Honnay et al. 1999, Martínez-Morales 2005). Differential colonization could result in nestedness if highly vagile species occupy most islands and less vagile species inhabit only the closer, larger islands. Similarly, differential extinction could result in nestedness if species exhibit particular area requirements and island areas differ in the system of analysis. In this situation, species with larger area requirements would only be found on larger islands and those species with smaller area requirements should be ubiquitous. Hierarchical (i.e. nested) habitats may produce nested subsets if most species are habitat specialists; however, the structure produced by hierarchical habitats is ameliorated if most species are euryecious. Passive sampling (i.e. sampling from the species pool in proportion to species abundances) also has been shown to result in patterns that appear nested (Andrén 1994, Cutler 1994, Fischer and Lindenmayer 2002), but passive sampling is not an ecological mechanism; rather, it results from the random sampling of individuals from species pools.

Passive sampling describes a situation in which rare species are underrepresented in the community compared to abundant species, at least within a particular area (Connor and McCoy 1979). Cutler (1994) examined the role of passive sampling in creating nestedness by sampling individuals randomly from a log-normal distribution and placing them on islands until reaching specified abundances. He repeated this process for 100 iterations and found that all 100 simulations were nested significantly at the 1% level, suggesting that the random placement of individuals alone could give rise to nestedness. Andrén (1994) used both a traditional null model (RANDOM1) and the random sample hypothesis to analyze nestedness in two empirical data sets. He concluded that random samples of species with different relative abundances could result in nestedness without additional ecological mechanisms. Fischer and Lindenmayer (2002) also analyzed the role of passive sampling in nestedness by developing a null model that accounted for differences in species incidence and demonstrated that the Nestedness Calculator (Atmar and Patterson 1995) overestimates the degree of nestedness because it assumes all species are equally ubiquitous.

Although these studies documented that passive sampling can lead to nested patterns of species composition, a clear understanding is elusive regarding the degree to which characteristics of species–abundance distributions affect such assessments. Without this

understanding, it is virtually impossible to elucidate mechanisms that give rise to nested patterns. The objective of this study is to examine the effects of differing species–abundance distributions, island–size distributions, and total abundances on the degree of nestedness and its significance, as influenced by the random placement of individuals.

Material and methods

Species–abundance distributions

Historically, species–abundance distributions (SADs) have been characterized by several common species, several rare species, and many species of intermediate rarity (May 1975). A more contemporary view of SADs suggests that most species are represented by a small number of individuals (i.e. most species are rare), whereas most individuals belong to only a few species (Gaston 1994). The mathematical description of the relationship between species and their abundances has taken many forms, ranging from discrete distributions such as the geometric series (Motomura 1932, May 1975) to continuous distributions such as the lognormal (Preston 1948, 1962a, 1962b). Although each model may correspond to certain biological situations, for this study we used variations of the geometric series (uniform, dominance–decay, random–assortment, dominance–preemption) in which differences in niche apportionment distinguish the models (Tokeshi 1990, 1999). Each model assumes that the fraction of niche space sequestered by a species is proportional to its relative abundance and that the niche space is divided sequentially. The models differ in how available niche space is divided among species, resulting in various degrees of evenness (Fig. 1). The

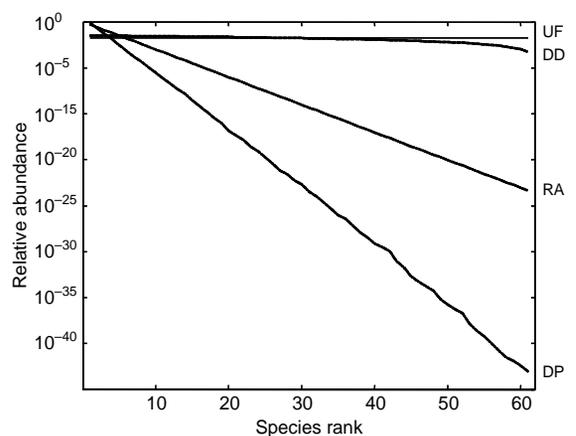


Fig. 1. Diagrammatic representation of the differences in form among species–abundance distributions (uniform, UE; dominance–decay, DD; random–assortment, RA; and dominance–preemption, DP) used to assess the consequences of the random placement of individuals on nestedness.

uniform model (UF) is deterministic. It produces a perfectly even SAD in which each species has the same niche breadth and abundance. The dominance–decay model (DD) is stochastic. Each species sequesters less than half of available niche space, but the exact amount is uniformly random between 0 and 0.5. The random-assortment model (RA) results in abundances that independently differ from one another and are unrelated to niche breadth. The dominance–preemption model (DP) is the converse of the DD model in that each additional species sequesters more than half of the available niche space, but the exact amount is uniformly random between 0.5 and 1. For each of these four models, we held the number of species constant at 61, corresponding to the mean number of species per island system analyzed by Wright et al. (1998).

Island–size distributions

Island area plays a major role in the distribution and abundance of species on islands, with larger islands supporting more species than do smaller islands (Connor and McCoy 1979). In fact, the relationship between species richness and island area is one of the most robust and general patterns in ecology (Williamson 1988, Rosenzweig 1995). This pattern holds for most assemblages of organisms and has been quantitatively described by a simple power function ($S = cA^z$, where S is the number of species within area A , and c and z are mathematical constants describing the intercept and slope of the relationship between $\log S$ and $\log A$) that seems to fit many island systems (Williamson 1988, Rosenzweig 1995), although a number of alternate models might be considered as well (Scheiner et al. 2000). We held the number of islands constant at 16, corresponding to the mean number of islands per system analyzed by Wright et al. (1998), and used only two island size distributions (ISD) in assessing the effect of random placement of individuals on nestedness. One ISD was characterized by a linear decrease of island sizes ($y = -0.0074x + 0.1250$, where y is the relative area of an island and x is the size rankings of islands in the archipelago), whereas the other was defined by a uniform distribution of sizes ($y = 0.0625$, where y is the relative area of an island). The linear decrease in island size is not intended to accurately reflect size distributions of actual archipelagos; rather, it is intended to serve as a primary framework in which island sizes within an archipelago differ. Moreover, the linear decrease in island size assumes a corresponding linear decrease in the number of individuals a particular island can maintain viably.

Abundances

Because we were interested in randomly placing individuals into an incidence matrix based on values from a probability matrix, we varied the total number of individuals (IND) for each of the different combinations of SAD and ISD. We simulated seven values for IND (128, 256, 512, 1024, 2048, 4096 and 8192), which represent evenly spaced values on a logarithmic scale. Although these values do not represent the entire range of possibilities, they provide insight into how changes in total number of individuals might alter the degree of nestedness.

Simulations

For each combination of SAD and ISD, we created a probability matrix by multiplying two vectors (ISD \times SAD). We then randomly assigned 128, 256, 512, 1024, 2048, 4096 or 8192 individuals into a corresponding incidence matrix based on the probability matrix, allowing each cell to receive a probabilistic number of individuals. Once all individuals were placed into the matrix, we converted abundance to a binary code (presence or absence) to facilitate quantification of the degree of nestedness using traditional approaches (reviewed by Wright et al. 1998). We calculated the total number of species absences from biotas richer than the most depauperate on which it occurs (N0; Patterson and Atmar 1986), the total number of species presences in biotas more impoverished than the richest on which it occurs (N1; Cutler 1991), the standardized number of times a species presence correctly predicts its occurrence at equally rich or richer sites (C; Wright and Reeves 1992), and the amount of disorder in the system relative to perfect nestedness (T; Atmar and Patterson 1993). Statistical significance for each measure was determined through randomization (R0 and R00; *sensu* Wright et al. 1998) with 1000 iterations per measure and an alpha level of 0.05. All of these measures were calculated with algorithms written in Matlab, including a program that implements the methodology from the Nestedness Calculator of Atmar and Patterson (1993). Because the original matrix was simulated using randomly placed individuals, we repeated this entire process with 100 iterations, which we judged to be sufficient to characterize the mean and variance in random placement of individuals by monitoring changes in the statistics with each additional iteration.

Results

In general, presence-absence matrices based on the random placement of individuals, regardless of SAD, ISD, or IND, were nested significantly compared to null

distributions created by the random placement of species (Table 1). The dominance–preemption and random–assortment models, both of which produced abundance distributions dominated by only a few species, resulted in significant nestedness that was relatively unaffected by island size or abundance (Fig. 2, 3). The nested patterns produced by these models consistently had more holes than outliers (Fig. 4). The dominance–decay model resulted in patterns that were non-nested at low abundances but became nested at higher abundances. This

pattern was the same for both uniform and linear decreases in island size. At low abundances, the dominance–decay model resulted in patterns that had more holes than outliers, but the opposite was true for higher abundances. The same pattern was observed for the uniform SAD. The uniform SAD resulted in much more variable levels of nestedness, especially at higher abundances. In fact, the uniform SAD in combination with a linear ISD resulted in significant nestedness when assessed with the nestedness calculator.

Table 1. Means of the various metrics of nestedness and their significance. Species–abundance distributions (SAD) include uniform (UE), dominance–decay (DD), random–assortment (RA), and dominance–preemption (DP) models.

SAD	ISD	N0	P (N0)	N1	P (N1)	NC	P (NC)	C	P (C)	T	P (T)
UF	Uniform	392.2	0.880	105.5	0.499	109.0	0.933	0.027	0.368	58.9	0.280
		490.0	0.575	196.6	0.487	386.9	0.600	0.005	0.540	42.0	0.514
		457.4	0.527	337.4	0.423	1219.6	0.503	0.000	0.542	30.9	0.571
		293.4	0.501	481.1	0.514	3095.0	0.510	0.001	0.549	32.4	0.577
		104.8	0.407	385.9	0.467	5637.1	0.480	0.002	0.489	60.5	0.097
		11.5	0.098	43.3	0.415	7100.2	0.611	0.001	0.693	74.6	0.126
		0.0	0.980	0.0	0.980	7316.3	1.000	0.918	0.020	99.0	1.000
		306.5	0.843	98.2	0.570	103.9	0.905	0.032	0.393	70.5	0.000
	Linear	375.4	0.605	175.6	0.525	354.1	0.648	0.009	0.493	62.6	0.000
		344.8	0.497	278.8	0.519	1059.9	0.524	0.001	0.521	56.9	0.000
		237.3	0.449	333.0	0.500	2514.3	0.509	0.000	0.521	60.8	0.000
		115.8	0.437	227.5	0.483	4426.3	0.468	0.004	0.549	81.9	0.000
		42.0	0.470	74.1	0.453	5930.6	0.511	0.003	0.558	92.3	0.003
		10.4	0.414	14.6	0.442	6778.7	0.589	0.002	0.617	92.8	0.013
		338.5	0.666	102.2	0.455	139.0	0.495	0.002	0.655	58.0	0.240
		419.4	0.211	186.4	0.271	459.4	0.015	0.053	0.022	47.9	0.051
DD	Uniform	397.4	0.026	305.2	0.110	1308.5	0.000	0.129	0.000	44.6	0.000
		295.2	0.005	389.0	0.001	2930.9	0.000	0.244	0.000	51.3	0.000
		163.0	0.000	293.2	0.000	4785.0	0.000	0.377	0.000	58.4	0.000
		79.7	0.001	150.5	0.000	6038.4	0.000	0.468	0.000	68.0	0.000
		36.0	0.001	65.2	0.000	6707.5	0.000	0.525	0.000	80.0	0.001
		265.5	0.708	93.7	0.382	128.0	0.550	0.002	0.697	70.4	0.000
		319.9	0.251	161.8	0.217	408.4	0.024	0.062	0.040	67.5	0.000
		307.2	0.044	243.1	0.035	1113.6	0.000	0.156	0.000	69.1	0.000
	Linear	239.4	0.014	262.9	0.000	2355.8	0.000	0.291	0.000	73.1	0.000
		156.9	0.004	202.5	0.000	3843.3	0.000	0.419	0.000	83.5	0.000
		86.7	0.001	113.8	0.000	5172.9	0.000	0.524	0.000	92.7	0.000
		43.3	0.006	58.4	0.000	6123.2	0.000	0.593	0.000	96.9	0.000
		26.3	0.011	20.3	0.001	279.8	0.000	0.637	0.000	83.9	0.000
		25.4	0.000	21.4	0.000	403.1	0.000	0.688	0.000	85.1	0.000
		26.0	0.000	20.7	0.000	514.2	0.000	0.724	0.000	83.8	0.000
		27.2	0.000	20.9	0.000	636.5	0.000	0.754	0.000	83.5	0.000
RA	Uniform	24.1	0.000	20.1	0.000	765.5	0.000	0.776	0.000	84.2	0.000
		26.0	0.000	20.5	0.000	881.3	0.000	0.782	0.000	84.1	0.000
		26.0	0.000	19.5	0.000	1004.4	0.000	0.795	0.000	83.1	0.000
		22.2	0.026	15.7	0.001	228.3	0.000	0.640	0.000	87.2	0.000
		22.8	0.002	17.0	0.000	345.8	0.000	0.723	0.000	88.4	0.000
		23.7	0.002	15.7	0.000	458.4	0.000	0.757	0.000	88.7	0.000
		21.7	0.000	16.3	0.000	578.1	0.000	0.788	0.000	88.0	0.000
		22.6	0.000	16.8	0.000	695.9	0.000	0.801	0.000	88.9	0.000
	Linear	22.2	0.000	16.3	0.000	812.6	0.000	0.817	0.000	88.2	0.000
		22.3	0.000	16.7	0.000	935.4	0.000	0.826	0.000	88.7	0.000
		10.0	0.002	9.0	0.001	204.6	0.001	0.759	0.001	93.5	0.000
		8.5	0.002	7.5	0.000	266.5	0.000	0.813	0.000	93.3	0.001
		8.0	0.006	7.0	0.000	328.2	0.000	0.849	0.000	93.4	0.000
		8.2	0.001	6.7	0.000	386.7	0.000	0.868	0.000	94.7	0.001
		8.7	0.000	7.3	0.000	444.0	0.000	0.869	0.000	94.2	0.000
		8.4	0.001	7.3	0.000	506.6	0.000	0.876	0.000	94.6	0.001
DP	Uniform	9.0	0.000	7.8	0.000	558.8	0.000	0.865	0.000	93.8	0.000
		8.7	0.029	5.8	0.000	176.0	0.000	0.794	0.000	94.0	0.001
		8.2	0.014	6.4	0.000	234.6	0.000	0.828	0.000	95.0	0.000
		8.6	0.004	5.8	0.000	292.5	0.000	0.850	0.000	95.3	0.000
		8.4	0.007	5.1	0.000	351.4	0.000	0.868	0.000	94.5	0.000
		8.5	0.000	6.2	0.000	410.1	0.000	0.870	0.000	95.1	0.000
		7.3	0.001	5.5	0.000	472.7	0.000	0.896	0.000	95.0	0.000
		7.4	0.000	5.9	0.000	532.0	0.000	0.892	0.000	95.4	0.000
	Linear	8.7	0.000	7.8	0.000	558.8	0.000	0.865	0.000	93.8	0.000
		8.7	0.029	5.8	0.000	176.0	0.000	0.794	0.000	94.0	0.001
		8.2	0.014	6.4	0.000	234.6	0.000	0.828	0.000	95.0	0.000
		8.6	0.004	5.8	0.000	292.5	0.000	0.850	0.000	95.3	0.000
		8.4	0.007	5.1	0.000	351.4	0.000	0.868	0.000	94.5	0.000
		8.5	0.000	6.2	0.000	410.1	0.000	0.870	0.000	95.1	0.000
		7.3	0.001	5.5	0.000	472.7	0.000	0.896	0.000	95.0	0.000
		7.4	0.000	5.9	0.000	532.0	0.000	0.892	0.000	95.4	0.000

Fig. 2. Percent nestedness, based on the total number of times a species presence correctly predicts its occurrence at equally rich or richer sites (C), for each simulated combination of species–abundance distribution, island–size distribution, and total abundances. Perfect nestedness is represented by more extreme values. Boxes represent mean values ± 1 sd and whiskers represent the range.

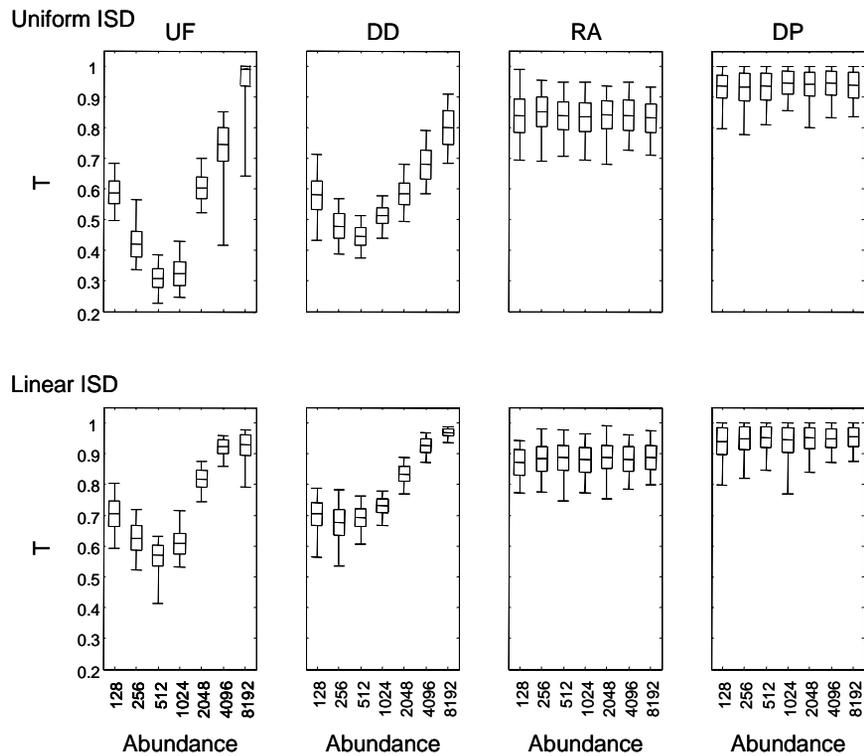
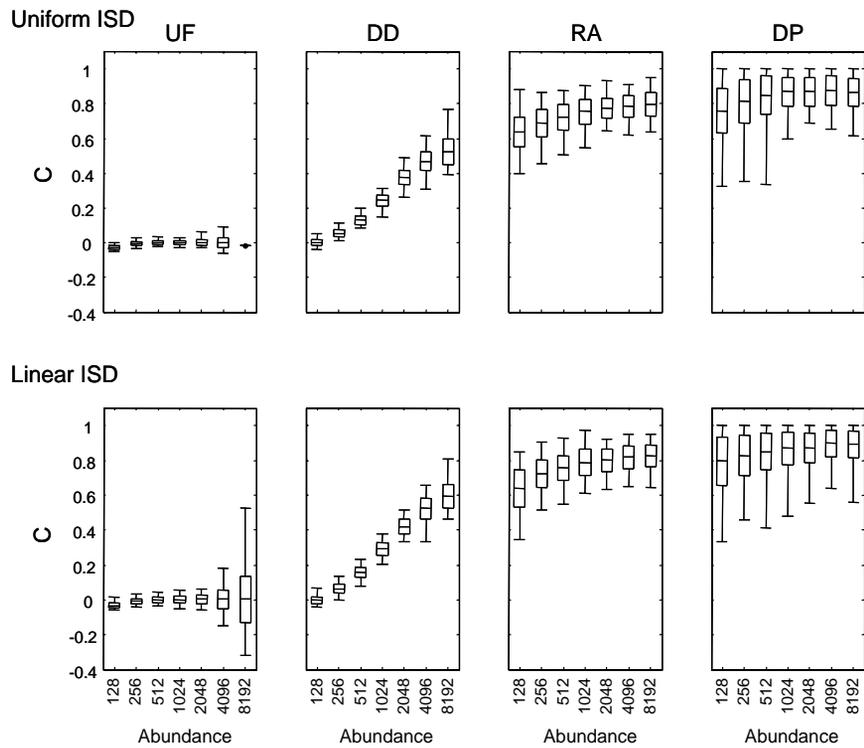


Fig. 3. Percent nestedness, based on the amount of disorder in an island system relative to perfect nestedness (T), for each simulated combination of species–abundance distribution, island–size distribution, and total abundances. Temperatures were scaled between zero and one, and subtracted from 1 to facilitate comparisons with other measures. Perfect nestedness is represented by more extreme values. Boxes represent mean values ± 1 sd and whiskers represent the range.

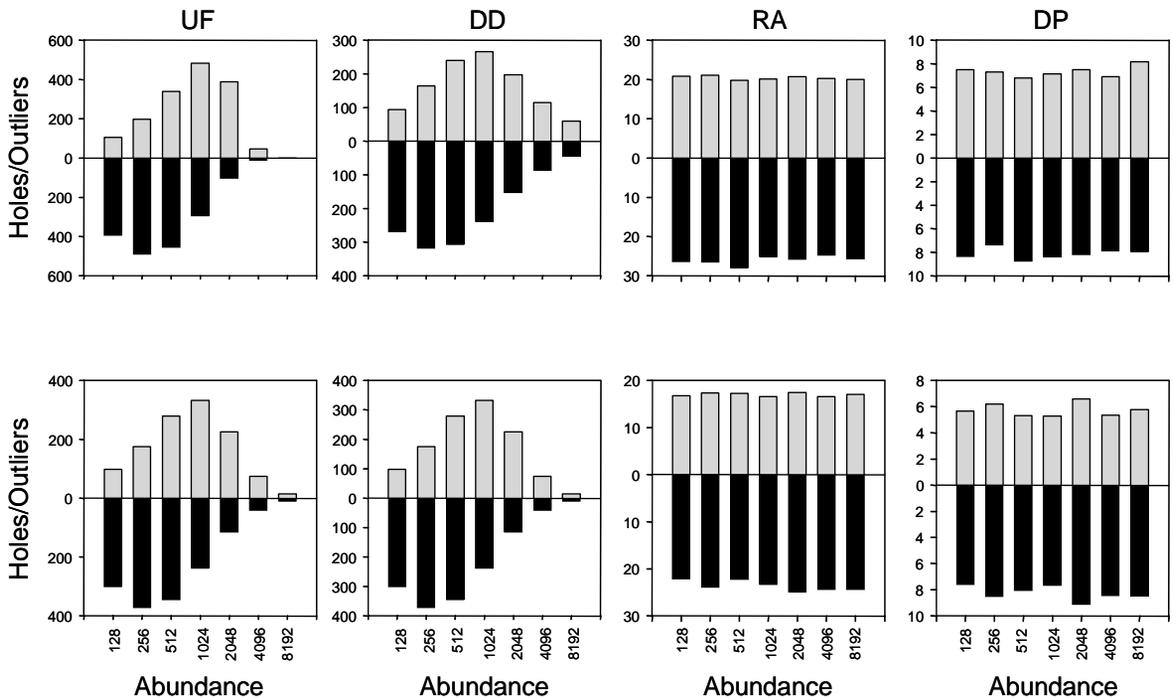


Fig. 4. The mean number of holes (N_0) and outliers (N_1) from simulations for each combination of species–abundance distribution, island–size distribution, and total abundances. Holes (black bars) are beneath the horizontal axis and outliers (gray bars) are above the axis

Discussion

This study indicates that stochastic processes, such as the random placement of individuals, predispose systems to evince patterns of nestedness at the species level, which may account, in part, for the ubiquity of nestedness in nature. Although this study is not the first to document the role of stochastic processes in producing nestedness, it advances current understanding by thoroughly and systematically examining the influence of various SADs, ISDs, and total abundances on producing nested patterns of species distributions. This work directly relates to several common themes pertaining to the study of nestedness, including the role of unexpected absences (holes) and presences (outliers) in producing nested subsets, the dynamics of extinction and colonization in producing nestedness, and the use of null models in evaluating statistical significance of empirically derived patterns of nested species composition.

Holes vs outliers

Cutler's (1994) pioneering work on passive sampling and nestedness suggested that island systems created from the random placement of individuals would tend to have more unexpected presences (U_p) than unexpected absences (U_a). That is, the resulting matrices are outlier-rich. At first glance, our results only partially support

the claim made by Cutler because the majority of simulations resulted in patterns with more holes (N_0) than outliers (N_1). However, the discrepancy is resolved by considering the strong positive correlation between U_a and N_0 (Wright et al. 1998), although the positive correlation is counterintuitive. One might think that as U_p increased, so would N_1 . The difference, however, involves how the measures are calculated. One unexpected presence (U_p) could easily result in multiple holes (N_0) or vice-versa (Cutler 1991), thereby creating the strong positive relationship.

Wright et al. (1998) reasoned that sampling from SADs should on average underestimate the incidence of rare species while overestimating the incidence of abundant species, predisposing systems to appear to be nested. They argued that rare species should persist on islands as long as their niche requirements are met, even if the probability of placement on that island is low from a statistical standpoint. Similar reasoning was used for abundant species: an individual may have a high probability of being placed on an island, but this does not necessarily mean that it can survive there. Although both arguments may be valid from a biological standpoint, the validity is dependent on sample sizes from a statistical point of view. Highly dominated systems, such as those created from DP, often result in nested patterns when biologically realistic densities are assigned randomly to islands. In this case, the occurrences of rare

species are indeed underestimated and the occurrences of abundant species are overestimated. Of course, if enough individuals were placed randomly on islands, the resulting species incidences would consist exactly of all species from the sampling pool and there would be no nestedness (i.e. all islands would contain the same species). In this case, the incidence of both abundant and rare species is estimated accurately because all species in the system are included in the presence–absence matrix. In either scenario, the total numbers of holes and outliers decrease in simulated systems as dominance increases, but the exact relationship between the relative number of holes and outliers is dependent on species–abundance distributions and abundance (Fig. 4).

Dynamics of extinction and colonization

Assessments of nestedness facilitate the prediction of extinctions and colonizations (Patterson 1990). In terms of the Nestedness Calculator (Atmar and Patterson 1993), species that have unexpected presences farthest from the extinction threshold, which is the line that separates the occupied portion of the matrix from the unoccupied portion, should have a higher probability of local extinction on that island compared to taxa closer to the boundary. Similarly, islands with unexpected species absences farthest from the extinction threshold should have higher probabilities of invasion by that species compared to islands closer to the threshold. Consequently, the reorganization of rows and columns in the Nestedness Calculator, which might or might not be in order of species richness or incidence, is meaningful. Such insight is lost when examining interactive island systems in which extinction and colonization are solely a consequence of metacommunity dynamics (*sensu* Hubbell 2001) to the point at which random placement of individuals adequately characterizes island-specific species composition. In these systems, larger islands contain, on average, higher abundances of individuals, increasing the probability that a particular species occurs on that island. Thus, novel colonizations would occur more likely on larger islands independent of the extinction threshold. Similarly, smaller islands should, on average, be subject to more localized extinctions. As a result, the reorganization of rows and columns should be based solely on species abundance, ranked from high to low, for both islands and species if the island system is interactive. In this context, holes and outliers become more reliable indicators of future extinctions and colonizations.

Null models

Inference in ecological and biogeographical studies is strengthened by the use of null models to determine if an

observed pattern is significantly different than that expected by chance alone. Although incisive overviews of the use of null models in ecology exist (Gotelli and Graves 1996, Gotelli 2001), two key points require reiteration. First, null models do not describe what the world would look like in the absence of ecological mechanisms. Rather, null models describe what the world would look like in the absence of specified mechanisms (Connor and Simberloff 1986). Second, null models emphasize the importance of stochastic processes in producing empirical patterns (Cutler 1994, Gotelli and Graves 1996). In terms of nestedness, we have shown that the random placement of individuals, according to various species–abundance and island–size distributions, can by itself produce nested patterns of species composition. This finding supports previous research on passive sampling (Cutler 1994) and demonstrates the degree to which nestedness is affected by stochastic mechanisms. Our results complement other studies examining the role of randomized individuals in creating empirical patterns, such as commonness and rarity (Storch and Sizing 2002), species richness (Chave et al. 2002, He and Legendre 2002), and species–area relationships (Coleman et al. 1982, Williams 1995, Plotkin et al. 2000).

With few exceptions (Cutler 1994, Roberts 2002), studies of nested subsets on island systems have used the random placement of species to assess significance of nestedness, without regard to absolute or relative abundances of individuals per species. We have shown that traditional methods can be biased in assessments of nestedness whenever species have non-uniform abundance distributions, whenever islands within a system differ in size or quality (i.e. the number of individuals which they support), or whenever total abundances are above a threshold. Under these conditions, the rate of rejecting the null hypothesis when it is in fact true (type I statistical error) is much greater when species incidences are randomized as opposed to species abundances. This does not imply that previous methods should be abandoned; rather, it highlights the importance of individual-based processes in generating patterns of non-random species composition. Indeed, individual-based models are extensions of the traditional species-based models that can be tailored to include probabilistic density and scale factors that affect the distributions of individuals. Under certain circumstances (e.g. when island systems consist of landmasses that are highly dispersed from each other in which case the SAD of each island likely arises from *in situ* dynamics), the random placement of species may serve appropriately as a null model. However, in studies that focus on interactive systems in which the SAD of each island arises from colonization dynamics rather than from *in situ* reproduction, consideration of null models based on the random placement of individuals is useful. If both

species-based and individual-based models yield similar results, whether significant or not, then generality of conclusions is enhanced. If the two methods provide different results, the uncertainty requires an examination of the extent of interactiveness of the system to decide which method more appropriately characterizes the island system.

Although additional insights may be gleaned by incorporating information at the level of individuals, many systems cannot benefit from such an approach because of a lack of individual-based data or because the system itself is not appropriate. For abundances to play an important role in species-level patterns such as nestedness, migration behavior must have an overriding effect on local abundance. This arises primarily within interactive island systems, such as the breeding birds on islands in Lake Pymatuning (Coleman et al. 1982), where individuals are easily capable of flying among islands in a single day. Importantly, the designation of interactive versus non-interactive island systems depends on both the inherent nature of the islands (e.g. their sizes and distances from each other) and the ecological and demographic attributes of study organisms. For example, the islands in Lake Pymatuning may be interactive with regard to the birds that inhabit them, but the island system might be non-interactive with regard to soil invertebrates. For birds of the Greater Antilles, distances among islands are so great that population dynamics would arise primarily as a result of birth and death processes within islands rather than from migration behaviors. Thus, studies of nestedness must critically evaluate the interactive nature of island systems before using the random placement of individuals as a null model with which to assess significance of nested subsets. However, when the island system is interactive and species abundances are available, greater ecological understanding (Allen and Hoekstra 1992, Pickett et al. 1994) may be achieved by integrating such information into consideration of nestedness.

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