

# Analyzing species composition in fragments

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Abstract : Fragmented systems tend to exhibit distinctive patterns of species richness and species composition. Because local extinctions on fragments are no longer balanced by immigration from surrounding areas, their species-area relationships characteristically exhibit high slopes. Small fragments often support many fewer species than an equivalent area of contiguous habitat. In addition, fragments often support "nested subsets" of species, where the species comprising smaller local assemblages constitute a proper or included subset of the species in richer ones. Nestedness appears most prevalent and most strongly developed in fragmented systems, where species composition has been sculpted by local extinction. However, this structure also characterizes other kinds of ecological systems. Extinction, colonization, disturbance, habitat distribution, hierarchical niche relationships, and passive sampling may all shape local assemblages into nested patterns. Although nested structure per se can tell us little about the processes that produced it, the ordering of species and sites in a nested matrix can tell us a great deal about possible causation. Characteristics of species or sites that correlate strongly with these vectors become plausible contributors to the nested structure shown by the system as a whole.

Key words : Biogeography, extinction, habitat fragments, nested subsets, species composition

## Introduction

Fragmentation of natural habitats is a progressive by-product of escalating resource consumption by humans. Continuous tracts of natural landscapes are eroded by human activities into increasingly dissected patches in an anthropogenic matrix. Fragmentation poses an especially severe threat to tropical organisms, which often have relatively small geographic ranges (Rapoport 1982, Terborgh & Winter 1983) and occur at low density because of their generally patchy distributions (Foster 1980).

Fragments differ from isolates in only one fundamental respect: their history. However, biogeographic history has pervasive effects on the types of species that are present on islands (Ricklefs & Schluter 1993, Patterson 1999; table 1). Although colonization, speciation, and extinction must simultaneously affect **all** islands continuously (at least as rates), their cumulative impact on a fauna or flora varies enormously according to its prior history.

Patterns of species richness on fragments commonly differ from those shown on isolates or in non-isolated areas of contiguous habitat. Lawlor (1986) showed that the species-area slope,  $z$  (from regressions of log species on log area), averaged twice as high in archipelagos fragmented by rising sea-levels as in oceanic ones in which islands have always been isolated. In fact, the distribution of slopes for the two classes of islands did not overlap. Smaller fragments are subject to a surfeit of

Table 1: Hallmarks of two distinctive classes of islands

	Isolates	Fragments
characteristic species	Endemics <sup>1)</sup>	Relicts
favoured species	Invaders, r-selected	Generalists, K-selected
species richness	Low species-area slopes	Steep species-area slopes
species composition	Distributional checkerboards	Nested subsets
species flux	Colonization-limited	Extinction-driven

1) Of course, endemics are also produced by vicariance, which involves fragmentation of once-continuous ranges. However, in such cases endemism arises with evolutionary divergence **after** the vicars have become isolated. The former identity of vicars (that is, as surviving daughter lineages of a widespread common ancestor that predated divergence) is underscored by the term relict. In a similar fashion, relicts may exist within currently contiguous habitats.

local extinctions as species number falls to a level commensurate with their newly circumscribed areas. Conversely, the biotas of isolates - regardless of their size - are often limited by rates of colonization (Lawlor 1986).

Historical derivation also influences the species composition of archipelagos. Many insular systems exhibit a pattern of species composition termed **nested subsets**, in which the species comprising a small fauna or flora represent a proper or included subset of those on larger, richer islands, rather than a random draw of those found in the entire species pool (Patterson 1990, Ganzhorn 1998; Wright et al. 1998). Nestedness is especially well-developed in systems thought to have undergone “faunal relaxation” (Patterson & Atmar 1986, Wright & Reeves 1992, Wright et al. 1998). During relaxation, the common species pool that occupied each island prior to fragmentation is ravaged by local extinctions until the species inhabiting the fragment are again in balance with their new surroundings (e.g., Diamond 1976). Because the extinction risk of species is often set by attributes such as body size, trophic position and habitat specialization (Brown 1971, Diamond 1984) in turn influencing their rarity, the same species tend to disappear from each of the islands, and in approximately the same order (Patterson & Atmar 1986, Blake 1991, Bolger et al. 1991, Atmar & Patterson 1993).

Nestedness is a common response to faunal relaxation, as dramatically shown by frogs on Amazonian forest fragments in the “Minimum Critical Size of Ecosystems” project (fig. 1 in Wright et al. 1998; cf. Zimmerman & Bierregaard 1986). Yet most ecological systems are nested, and the factors influencing this ecological structure are as diverse as nature itself. Extinction, colonization, disturbance, habitat distribution, hierarchical niche relationships, and passive sampling may all shape local assemblages into a nested pattern (Patterson 1990, Patterson & Brown 1991, Simberloff & Martin 1991, Cutler 1994, Andrén 1994 a,b). Causes of nestedness in these specific cases are usually identified on the basis of other information available in each study. However, Lomolino (1996) proposed that causality could be assessed directly by organizing rows in the presence-absence

matrix according to each plausible determinant, and measuring the nestedness of each resulting matrix. Thus, matrices organized by area (for extinction) and by isolation (for colonization rate) could be directly compared, and the strength of these often-opposing forces could be directly assessed. However, separate analyses are required to evaluate each potential determinant (Lomolino 1996).

### The Nestedness Calculator

The “Temperature Calculator” of Atmar and Patterson (1993, 1995) seems ideally suited to explore various features of nestedness, including causation. Other metrics (Patterson & Atmar 1986, Cutler 1991, Simberloff & Martin 1991, Wright & Reeves 1992, Lomolino 1996) measure nestedness in relation to the distribution of **each species**. These partial scores are then summed over species to compile community-wide patterns (i.e., counting “up” in a site  $\times$  species matrix, then summing across columns). Each ordering of rows (=sites) produces a potentially different distribution of “holes” and “outliers” and a different nestedness score.

In contrast, “temperature”, *T*, assesses degrees of nestedness **simultaneously across species and sites** (i.e., counting diagonally across the matrix). Just as the species compositions of fragments can be nested within one another, so too can the incidence distributions of species. Neither deserves logical precedence in ecological analyses. Moreover, there is only one arrangement of “presences” in a distribution matrix that maximizes nestedness across both these dimensions. This essential structure can then be compared to numerous possible correlates without matrix reorganization.

Atmar & Patterson (1995) developed a Windows-based Visual Basic program for implementing analyses of *T*. Their “Temperature Calculator” is freely available over the Internet. Subsequent sections detail steps needed to calculate the biogeographic temperature of any set of distributions and to assess their biological determinants: (1) packing matrix elements so as to maximize nestedness; (2) measuring matrix order; (3) assessing the statistical significance of nestedness; (4) identifying and interpreting biogeographic discordance; (5) assessing causation; and (6) calculating state-occupancies.

### Packing the matrix

Presence-absence matrices contain two levels of information. In addition to specifying which species occur at which sites, these matrices also reflect the relative hospitality of sites to the species under study, as well as the prevalence of environmental conditions needed to support each species. This secondary information becomes apparent only after a matrix has been packed into a state of maximal nestedness. The “hospitality” of islands or sites declines from top to bottom of the matrix. Likewise, the prevalence and width of species = niches are ordered from the left to right. Actually, these rankings of rows and columns emerge from reordering the rows and columns of the matrix to minimize the unexpectedness of occurrences.

Although few matrices prove to be perfectly nested, all matrices can be packed into a state of maximal nestedness. Matrices are packed to a condition of maximal

nestedness by reordering entire rows and columns until unexpectedness is minimized. Changing the order of rows and columns does not alter which species occur at which sites, but it does change the overall appearance of the matrix. Nested matrices can be readily distinguished without tests because their presences are tightly clustered into the upper-left corner of the matrix.

The topmost site in a packed matrix is judged the most hospitable. Similarly, the leftmost species is the one whose niche requirements are most commonly and consistently met. In practice, it may be the most resistant to extinction, most prone to colonization, or most probably encounter resources essential to species persistence.

The concept of redundancy can also be appreciated with reference to a packed matrix. When a series of sampled sites each supports all of the species in the pool, the information they provide on the ordering of species and of sites is entirely redundant. For purposes of measuring temperature and depicting matrices, such sites are combined into a single all-inclusive site in the topmost row of the matrix. For purposes of assessing the rank of individual sites (see below), all such sites are tied at first.

### Calculating matrix “temperature”

The concepts of heat, information, noise, order and disorder are all closely related. The calculated metric measures the “biogeographic heat” of the matrix based on the distribution of unexpected presences and absences. In a perfectly nested matrix, the set of species on any island will be a proper or included subset of the species on all islands that precede it in the matrix. The hypothetical line that separates the occupied area of the matrix (i.e., the upper-left corner of the matrix) from the unoccupied portion is termed the **boundary line**.

The boundary line for a perfectly ordered matrix is not arbitrary nor does it depend on specific distribution patterns. Instead, the line is specified only by the size, shape, and “fill” of the matrix (i.e., how many presences it contains). Species absences above and to the left of the line are defined as **unexpected**, as are species presences below and to the right of it. Because the boundary line defines the condition of **maximal nestedness** of species and sites, every unexpected presence beyond the line is accompanied by a corresponding absence within it, and vice versa. When stochasticity is low (i.e., when  $2^\circ$  is low), unexpected presences and absences cluster near the line. As system randomness increases, the unexpected presences and absences move further away from it. The “**temperature**” of the matrix is a measure of that penetration.

Following Atmar and Patterson (1993) the formula for **local unexpectedness** of cell  $ij$  is:

$$u_{ij} = (d_{ij} / D_{ij})^2$$

where  $d_{ij}$  measures the distance of the cell from the boundary line along the skew diagonal, and  $D_{ij}$  is the length of the matrix parallel to the skew-diagonal.

Similarly, **total unexpectedness** is:

$$U = 1 / (mn) \sum \sum u_{ij}$$

summed over  $m$  rows and  $n$  columns, and **system temperature** is calculated using the constant  $K$ , where  $K = 100 / U_{\max}$ , as

$$T = kU.$$

### Assessing probabilities

A nested distribution pattern represents a highly specific type of distribution. Monte Carlo techniques can be used to estimate the probability that the nested structure in any distribution pattern could be produced at random. To assess that probability, any number of matrices can be drawn at random (i.e., 100<sup>00</sup>). However, because random events often clump together, and the matrix-packing algorithm compiles these clustered events to maximize nestedness, the randomized matrices will be cooler after they are packed. The extent to which the **characteristic temperature** of these matrices deviates from 100° depends on the size, shape and degree of fill of the matrix.

Colder characteristic temperatures will be produced in smaller matrices, those that are mostly filled or mostly empty, and in matrices that are highly rectangular (i.e., many more rows than columns, or vice versa). In each case, it is possible for the packing algorithm to cluster clumps of “presences” into the upper-left corner of the distribution matrix.

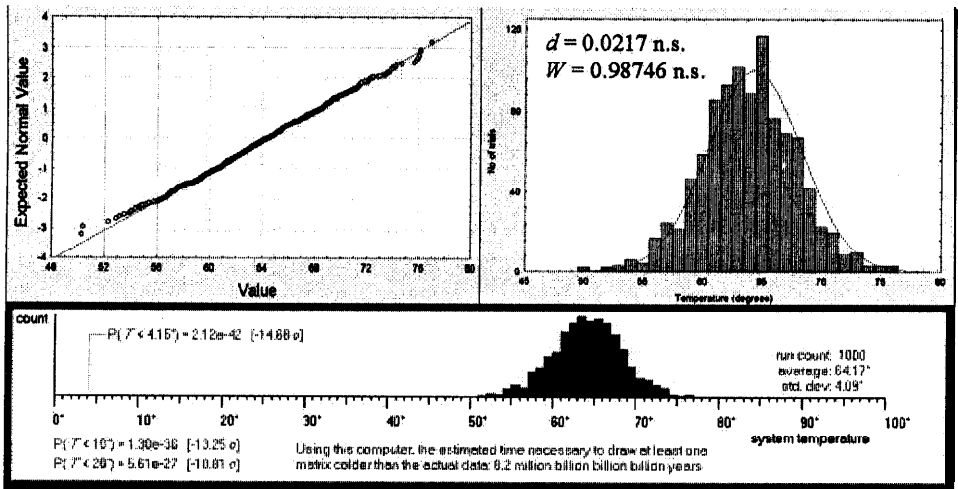


Fig.1: Testing the significance of observed nestedness. The top graphs depict tests of normality for 1000 simulation scores generated for mammals in the southern Rocky Mountain mammals (Patterson & Atmar 1986). Results of both tests for normality, the Shapiro-Wilks'  $W$  and the Kolmogorov-Smirnov  $d$ , showed non-significant differences ( $P < 0.05$ ), validating the probability inference made in the lower graph, in which the likelihood that observed structure was part of the simulated scores is  $\sim 10^{-42}$ .

It then becomes a simple problem to ask “What is the probability of an observed temperature of, say  $4.15^\circ$ , given the trial distribution of simulated scores?” The trial distribution may be taken either as a sample of scores or as a universe. Hugueny & Guegan (1997) criticized the use of normal-probability distributions when assessing the distribution of test statistics that were generated using Monte Carlo techniques. Their argument revolved around the distribution-free nature of Monte Carlo methods, and the often-skewed distributions of test parameters. Fig. 1 contains a test for normality of 1000 temperature scores for the Rocky Mountains mammal data set of Patterson and Atmar (1986), generated using the Nestedness Calculator. Both the Shapiro-Wilks =  $W$  score and the Kolmogorov-Smirnov  $d$  test for normality are non-significant ( $P > 0.05$ ), showing that  $T$  scores are approximately distributed as a normal variable. The result is that after measuring  $T$  in 1000 simulated archipelagos, we have far greater assurance than one in 1000 that the observed temperature of  $4.15^\circ$  falls outside the range of simulated scores. In fact, using a normal approximation, the probability that observed  $T$  is included within the range of simulated scores is  $\sim 10^{-42}$ .

#### Detecting idiosyncratic species and sites

Two forms of noise contribute to the temperature of a matrix: (1) the random variation of environmental, demographic, and genetic stochasticity; and (2) the “coherent” noise of specific biogeographic events or of ecologically distinctive species. Random noise creates a gray band of mixed presences and absences along the entire length of the boundary line. In contrast, coherent noise creates idiosyncratic “spikes” that correspond to species or islands that contribute much more noise than the remainder. Where temperatures are not uniformly distributed across islands and species, contrasting biogeographic histories or current ecologies are implied for those islands and species, respectively, than those that characterize the system as a whole.

Distributions of 82 species of bats along the Eastern Versant of the Andes in Peru (Patterson et al. 1996) illustrate the potential of the Calculator for identifying idiosyncrasy (fig.2). Bat species richness falls precipitously with elevation, so that highland faunas generally represent attenuated versions of those below, forming a nested pattern. However, the individualized responses of highland bat species are strikingly discordant. Each of Manu’s endemic bat species is identified by temperature “spikes” in the lower pane of fig.2.

Auxiliary information is required to determine why given species or islands are idiosyncratic. Idiosyncrasies often indicate unmarked heterogeneity in the original data set. Idiosyncrasies among sites may result from habitat heterogeneity (especially for groups of habitat specialists) or signify sites that experienced contrasting biogeographic histories. Idiosyncratic species might variously recolonize some islands from which they have been locally extirpated, reach their range limits in the midst of the archipelago, or be victims of competitive exclusion or products of local speciation. In this sense, idiosyncrasy may often indicate that the “rules” of the system as a whole have been violated.

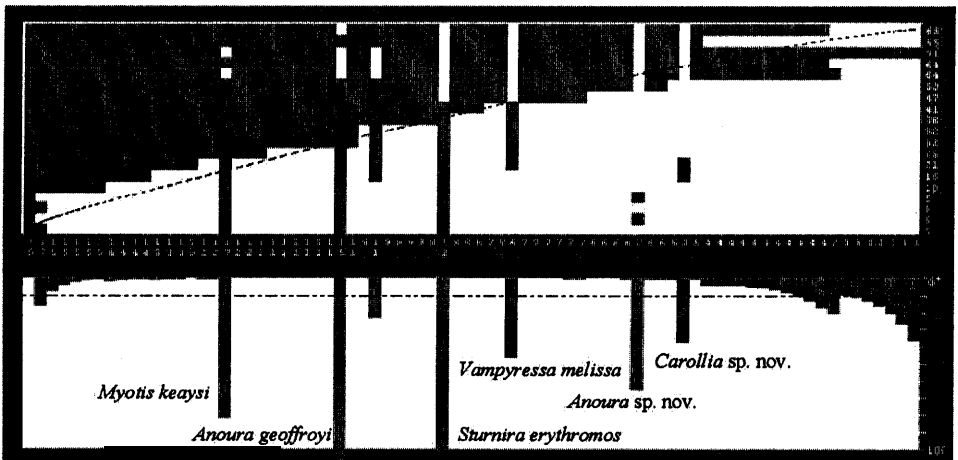


Fig.2: Interpreting idiosyncrasies and assessing the basis for nested distributions. The upper graph shows the nested distributions of 82 bat species (columns) at 19 sampling points (rows) along an elevational gradient in the Andes in southeastern Perú (Patterson et al. 1996). In this region, species richness of bats declines rapidly with elevation and species do not generally replace one another along the gradient; higher-elevation communities are attenuated versions of those below. The temperature of this system is  $10.2^{\circ}$  and the probability that this could be due to chance is  $\sim 10^{-62}$ . The lower graph shows the contrasting distributions of a handful of highland endemics which appear as idiosyncratic “spikes” in the plot of species idiosyncrasies. The Spearman rank-correlation coefficient between rows (in the packed matrix) and elevation equals  $R_s = 0.936$  ( $P < 0.00001$ ); nested structure may be plausibly attributed to elevation (or its correlates).

### Assessing causation

The existence of strongly nested distributions suggests an universal ordering mechanism for species or sites in the system under study. However, the rows and columns of the matrix submitted to analysis have been rearranged in the packing step to maximize nestedness. Where are the matrix alterations recorded, and how can matrix order be compared to independently determined features?

Matrix reorganization vectors record the rearrangements of rows and columns between matrices as submitted and those that emerged from the matrix-packing step. Descriptive vectors for either species or sites (e.g., body size estimates of species or area estimates for sites) may then be compared to the order of each in the packed matrix. Because the ordering of species by the Nestedness Calculator is only relative, rank-correlation analysis of such variables is preferred (cf. Siegel 1956).

Causal analyses are applied to two well-studied biogeographic systems. In the first (table 2), nestedness of montane mammals in the southern Rocky Mountains can be correlated with various physical features of the mountains themselves. The order of rows (mountain ranges) in the packed matrix correlates with their physical characteristics (see table) at tabulated levels. In the second, distributions of Peruvian bats over 19 sampling stations along the Eastern Versant of the Andes

Table 2: Rank-correlations of assemblages of montane mammals on mountaintops in the southern Rocky Mountains (Patterson & Atmar 1986). Row order determined by matrix packing and then correlated with various extrinsic factors.

	$r_s$	a
Elevation	-.327860	n.s.
Latitude	-.808813	<.00001
Longitude	.40640	<.05
Coniferous forest area	-.510545	<.01
Mesic forest area	-.678533	<.0001
Distance to source	.491228	<.05

Notes : Elevation and coordinates determined for the highest peak.

Areal measure taken from Patterson (1984), and distance measure from Lomolino et al. (1989).

are also highly nested. Correlations of row order in the packed matrix with elevation reveal strong correlation ( $R_s = 0.9364$ ,  $P < 0.0001$ ), suggesting that elevation or a co-variate determines nested structure. As in other non-experimental fields, causation of nestedness must be inferred from correlations and appropriate disclaimers are necessary.

### Calculating state occupancy

The preceding steps for measuring nestedness apply to any matrix, regardless of its historical derivation, its current dynamics, or the uniformity of its species and sites. If more stringent assumptions of the system are warranted (such as its being at colonization-extinction equilibrium and with homogeneous resource distributions; cf. Atmar & Patterson 1993), several powerful inferences are possible.

Nested distributions imply that the cell most likely to be occupied in any matrix is the one in the upper left-hand corner; that is, the most ubiquitous species will virtually always be present on the most hospitable island. Similarly, the cell least likely to be occupied will be the bottom, right-most cell, where the most marginal species would be found on the least hospitable island. All other matrix cells vary between these extremes in a manner that is specified by their distance from the boundary line. One may therefore calculate the probability of each matrix cell being occupied. At zero degrees (the condition of perfect order), all cells within the boundary line will be filled. However, as matrix temperature increases, unexpected absences or presences begin to appear in those cells closest to the boundary line, where unexpectedness values are lowest, spreading out across the matrix as a whole.

Two graphs prepared by the Nestedness Calculator can be used to indicate the probability of a cell's occupancy. The first, a "band diagram", shows unexpectedness values for expected occurrences where the species is present, as well as unexpected presences and absences. The second, a cumulative probability diagram, shows state occupancy as a function of unexpectedness for the current matrix. It is from this second diagram that the stability of the various populations can be estimated for each cell in the matrix (fig.3). Calculating state occupancy presumes that the biogeographic noise is random rather than coherent. Thus, unexpected presences resulting from idiosyncratic causes will be deemed more unstable than they actually are. Similarly, the unexpectedness of idiosyncratic absences will be overestimated.

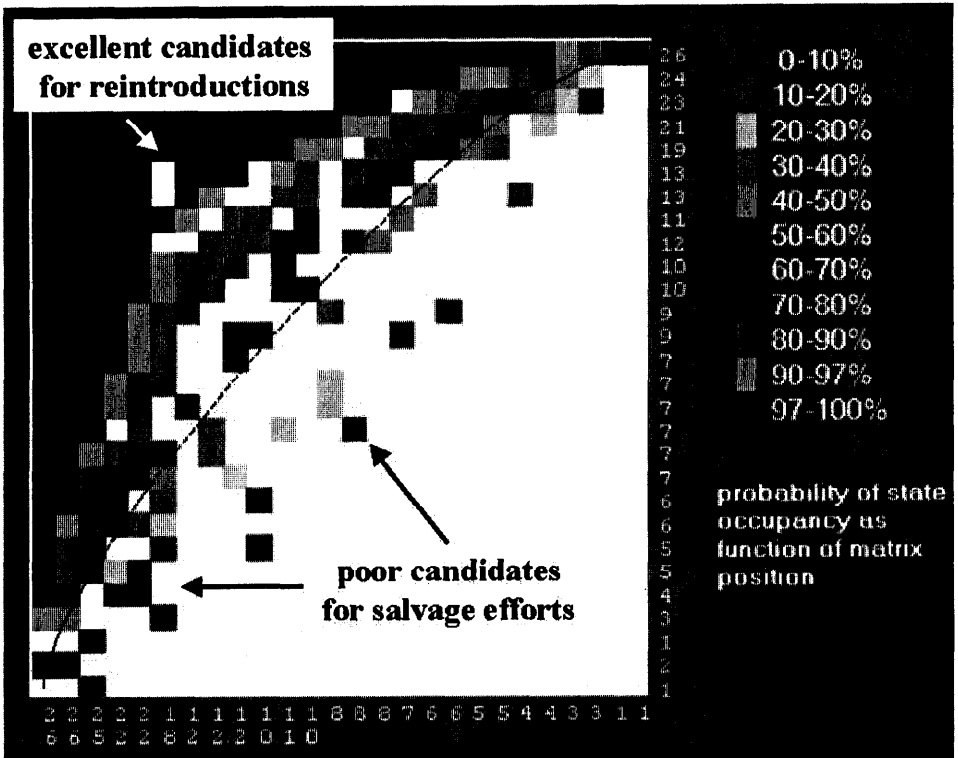


Fig. 3: Using a packed and highly nested matrix to make management decisions; data are boreal mammals of the southern Rocky Mountains (Patterson & Atmar 1986). “Holes” in the packed matrix signify populations that ought to be present, based on species co-occurrence data; introductions of such species are presumably favorable. On the other hand, “outliers” indicate populations not expected under the nested subset pattern, and seemingly a poor risk for strenuous management efforts. In fact, the lower arrow identifies an officially endangered population - *Tamiasciurus hudsonius* - on the Pinaleno Mountains, and one placed under notice of review by the U.S. Fish and Wildlife Service - *Microtus longicaudus*. Both lie outside the boundary line of nested relationships and hypothetically are next at risk of local extinction.

## Discussion

Nestedness appears to be a near-universal property of the assemblages studied by ecologists and biogeographers. Its virtual ubiquity in the natural systems that scientists select for analysis is striking because, like other ecological patterns, nestedness is scale dependent (Patterson 1990). Conditions for the development of nested structure include:

- 1) the species and sites being compared must have a common biogeographic history;
- 2) both must be exposed to similar contemporary ecological conditions; and
- 3) some kind of hierarchical niche relationships among species or sites (Patterson & Brown 1991).

The first two conditions ensure that sites have been open to colonization by a common species pool. The third ensures that there are differences in the numbers of species among sites, and/or differences in the incidence of species among sites. Differences among species in extinction risk, vagility, or habitat affinities affect their incidence, whereas differences in area, isolation, elevation, or habitat composition affect the species richness of sites. Each of these variables may contribute to nested structure and deserves causal investigation.

Nestedness is a property of **assemblages**, not one of **individual species**, so it is reasonable to ask whether nestedness reveals anything that cannot be determined from the ordered distributions of constituent species (cf. Simberloff & Martin 1991). In fact, nestedness analyses can simultaneously track both overall and specific features of distributions, as illustrated in fig.2. The predominant faunal pattern shows Amazonian bat faunas becoming attenuated along the elevational gradient, with highland faunas representing nested subsets of those at lower elevations. However, the responses of a handful of highland bat species exhibit strikingly discordant patterns, as shown in the plot of idiosyncrasies. Some, such as *Sturnira erythromos* and *Anoura geoffroyi* are also perfectly ordered by elevation, only *inversely* with respect to the remaining bat species.

Nestedness requires a hierarchical ordering of sites, species or both. As widely noted (e.g., Williams 1964), habitats are often distributed in a patchy manner, and fragments may differ substantially in habitat composition, in ways affecting both species richness and composition. Sites may also be ordered with respect to isolation, area, or other variables (table 2). Orderings of species are commonly expressed in terms of niche preferences. Most biologists are familiar with the “Hutchinsonian” niche concept, based on the **probability of an organism’s survival/reproduction within a n-dimensional hyperspace**. Over all resources, this probability distribution equals the **fundamental niche**, but because other species preempt resources, the observed or **realized niche** is expressed as the occupancy of species in shared resource space. A different concept was articulated by James et al. (1984) and seems especially appropriate to geographic analyses based on presence-absence data. The “Grinnellian” niche reflects the **range of environmental values that are necessary and sufficient for a species to carry out its life history**. Within a geographic region, species occupy a geographic region congruent with the distribution of its niche. The density and incidence of species within their geographic ranges reflect the prevalence of these conditions (James et al. 1984). Seen in these terms, the rankings of species across an archipelago provide an objective ordering of species with respect to Grinnellian niche width.

Differences in incidence may influence species interactions, as detailed by Hanski (1982) in discussing core and satellite species. The nested ordering of species differs from core-satellite species mainly in being graded, not classified. A fundamental asymmetry of ecological relationships is implied by nested subsets: the “core” species in nested systems (e.g., A) are predictable elements of the environment for more marginal species (e.g., D), but the reverse is not true. Species’ responses to competition and other coevolutionary pressures should

therefore be asymmetric, with direction being set by the prevalence or incidence of the species involved. Moreover, as noted by Simberloff and Martin (1991), nested biotas are not apt to be dominated by competitive exclusion, which tends to produce distributional checkerboards, the opposite of nestedness.

### Guidelines for conservation

The distinctive patterns of species richness and composition in fragments have important implications for conservation. First, the elevated slopes of species richness changes with area means that insular impoverishment with areal reduction is substantially greater on fragments than on islands (Lawlor 1986). The result is that generalized “island” slopes are inappropriate for predicting the species richness values of fragments (Patterson 1991; Doak & Mills 1994). By using such “typical” slopes, previous forecasts of tropical species loss with deforestation (e.g., Simberloff 1986) seriously underestimate the eventual costs of habitat conversion.

Nested subsets also have relevance to biological conservation, most obviously in resolving the SLOSS conundrum. In a perfectly nested archipelago, small reserves each support **the same set of species** (Patterson & Atmar 1986). However, few systems are perfectly nested, and nestedness is seldom perfectly correlated with island area. In addition, systems of small reserves, when selected on the basis of faunal or floral dissimilarity, will often preserve more species than the single largest island (Simberloff & Gotelli 1984). The utility of nestedness in reserve planning appears to be limited, at least when the compositions of all areas are known - “smart” amalgamation routines invariably perform better than those based solely on area considerations, whether from small-to-large or large-to-small (Cook 1995, Lomolino 1996).

But nested subsets have other implications as well. In any strongly nested archipelago, the boundary line marks the distributional limits of the fauna or flora, beyond which population lifetimes are expected to be nil, and species are either absent or expected to be absent. This leads to the expectation depicted in fig.4, that population lifetimes should vary systematically over a nested matrix, reaching their zenith at the origin. In general, we can expect greatest survivorship for the most widespread species on the most hospitable fragment, and declining probabilities for more narrowly distributed species and less hospitable fragments until we reach the boundary line. For a biological system that is undergoing faunal relaxation, the matrix cells distributed along the boundary line denote populations that are most at risk. For a highly dynamic biological system comprised of metapopulations, those boundary populations will wink on and off with greatest frequency, as local populations momentarily recover from local extinctions only to disappear again.

In general, rarity should be inversely correlated with population lifetimes shown in fig.4 (Diamond 1984). The precise position of the boundary line will then depend on the intensity or scale of sampling. Exhaustive sampling (that will uncover the rarest, most narrowly distributed species population in a fragment) or long-scale sampling (that uncovers and records populations that are present only episodically in a given site; cf. Andrewartha & Birch 1954) will shift the boundary line to the lower right of the matrix. This does not, however, render the nested pattern artifactual because nestedness depends on the pattern of co-occurrence, not

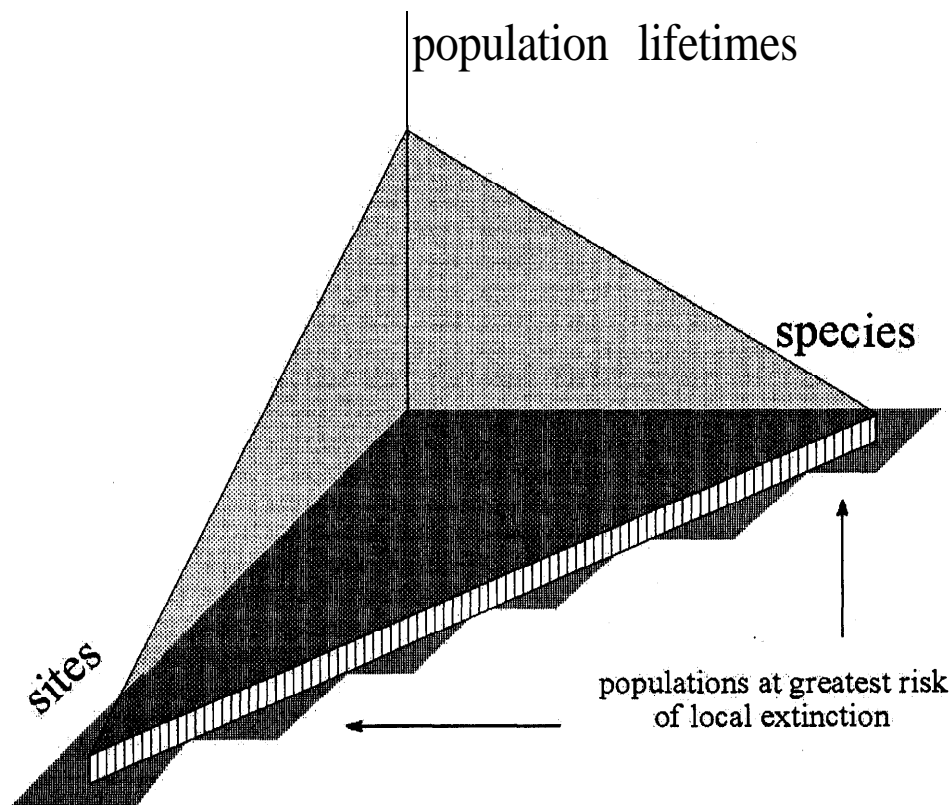


Fig.4: Hypothetical relationship between population lifetimes and the position of populations in a highly nested matrix. By definition, lifetimes fall to zero where the species is absent, but should generally increase - perhaps more-or-less regularly - as one approaches the most widespread species on the most hospitable fragment. All along the boundary line, populations of different species are thought to be most at risk.

the number of occurrences. Livingstone & Grayson (1994) showed that sampling artifacts for Great Basin mammals actually obscured the underlying nested structure, and that additional records of occurrence from more intensive sampling improved the fit of these mountaintop mammals to the nested pattern.

Nestedness is fundamentally a type of hierarchical organization. Hierarchies are familiar to biologists, forming the basis of the Linnean system of nomenclature, as well as the foundation for most attempts to classify the world's biogeographic regions. Despite their simplicity, hierarchies provide a powerful means of storing and retrieving abundant information. As one example, few people can have personal knowledge of *Pseudoryx nghetinhensis*, an animal discovered in central Vietnam in 1992. However, knowing the hierarchical position of this species (Mammalia, Artiodactyla, Bovidae, Bovinae, Boselaphini or Tragelaphini; Schaller & Rabinowitz 1995) permits a host of inferences regarding its morphology, genetics, and evolution. In a similar manner, knowledge of the hierarchical

structure of nested biotas permits numerous inferences - for example, if species M is present, then so too are species A, B, C, . . . . K, and L. Although Simberloff & Martin (1991) questioned whether community-wide statistics had any transcendental value (compared to those calculated on a per-species basis), surely this predictivity is one important reason. The **relative rankings** of species and fragments and the ancillary analyses they permit provides another.

Many questions in ecology and evolutionary biology require knowledge of species-abundance relations, but nestedness analyses are based solely on presence-absence data. Although this limits the potential applications of nestedness, this feature is seen as a distinct advantage because of “data economy”. Even the most rudimentary ecological sampling yields a set of species occurring together at a place and time. Such so-occurrence data are often the best we can manage for many poorly sampled tropical areas. Moreover, given spatial and temporal variation, the presence or absence of species should be more stable than their relative abundance rankings. Development of theory that is compatible with such data should be a high priority for conservationists, again especially in the tropics. Understanding the potential biases of such analyses can only refine our ability to fashion useful predictions from them.

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