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The measure of order and disorder in the distribution of species in fragmented habitat

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Abstract. Species distribution patterns within naturally fragmented habitat have been found to often exhibit patterns of pronounced nestedness. Highly predictable extinction sequences are implied by these nested species distribution patterns, thus the patterns are important to both the philosophy and practice of conservation biology. A simple thermodynamic measure of the order and disorder apparent in the nested patterns is described. The metric offers (i) a measure of the uncertainty in species extinction order, (ii) a measure of relative populational stabilities, (iii) a means of identifying minimally sustainable population sizes, and (iv) an estimate of the historical coherence of the species assemblage. Four presumptions govern the development of the metric and its theory: (i) the fragmented habitat was once whole and originally populated by a single common source biota, (ii) the islands were initially uniform in their habitat heterogeneity and type mix, and have remained so throughout their post-fragmentation history, (iii) no significant clinal (latitudinal) gradation exists across the archipelago so as to promote species turnover across the archipelago, and (iv) all species of interest are equally isolated on all islands. The violation of these conditions promotes species distributions which are idiosyncratic to the general extinction order expected in fragmentation archipelagos. While some random variation in extinction order is to be expected, idiosyncratic distributional patterns differ from randomness and are readily segregatable from such noise. A method of identifying idiosyncratic species and sites is described.

Key words: Extinction – Nestedness – SLOSS –Conservation – Disorder

Extinction has often been regarded as a random process, thus it has been somewhat surprising to repeatedly find species distribution patterns which suggest that the order of species extinction is highly determined (Brown 1986). The inherent orderliness of these extinction patterns has become increasingly apparent over the past 70 years (Arrhenius 1921; Gleason 1922, 1925; Preston 1960, 1962; Brown 1971; Diamond 1975, 1984; Connor and McCoy 1979; Brown and Gibson 1983; Murphy 1983; Cody 1983; Case and Cody 1983; Schoener and Schoener 1983; Patterson 1984; Simberloff and Levin 1985; Patterson and Atmar 1986; Ryti and Gilpin 1987; Cutler 1991; Bolger et al. 1991; Soulé et al. 1992; Wright and Reeves 1992; among others).

The thesis for ordered extinctions is simple: an area of suitable habitats, initially inhabited by a common ancestral biota, is fragmented into an archipelago of islands by climatic change. On each island of an archipelago, there will be one species which is nearest its minimum sustainable population size, and thus at greatest risk of local extinction. As area continues to shrink, populations of the archipelago's constituent species will tend to go extinct in order of their specific extinction risks. Because each island of an archipelago (if fully isolated) may be regarded as an independent trial, an archipelago undergoing "faunal relaxation" becomes a profound natural experiment which offers the possibility of (i) resolving the order of extinction among the constituent species, and (ii) identifying individual populations which are at or near their minimum sustainable sizes, information which would be very difficult to determine by any other means.

If species-extinction order were perfectly replicated on each island of the archipelago, the result would be a set of perfectly nested subsets, such that each smaller island would contain only a proper subset of the species found on all larger islands. But some degree of disorder is to be expected. Often, the extinction order will be perturbed by the statistical noise of local opportunity and catastrophe. Statistical stochasticity is a concept closely related to heat, information, noise, order and disorder. The metric to be described here will measure the *heat of disorder* inherent in the historical biogeography of an archipelago.

The system "temperature" of an archipelago's biogeography is easily visualized. Imagine an assemblage of *n* species present on a single island which is continuously

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shrinking. Further imagine that we can reset the island back to its initial conditions and rerun the extinction process repeatedly. In a perfectly "cold" system each species present in the assemblage would go extinct in turn as each species falls below its minimum sustainable population size, and that order would not change no matter how many times the experiment were repeated. But if the system temperature of the biogeographic event were raised, extinction order would concomitantly become less determined due to the increasing influence of random processes acting on the individual populations and islands. Species extinction order will no longer be perfectly replicable. Rather, the precise extinction order will be made to some degree uncertain. Some species will go extinct out of turn. Nevertheless, at all system temperatures less than complete disorder, the general extinction order will hold. System temperature becomes a relative measure of the disorder apparent in extinction order and will be defined to vary from 0° (completely replicable extinction order) to 100° (completely random extinction order).

Extinction is not the only ecological process which will generate nested patterns of species presences (Patterson 1990; Simberloff and Martin 1991). Immigration into depauperate areas may produce somewhat the same form of nesting, although it appears to do so on shorter timescales and with less definitiveness. Certain species will be the first to invade a defaunated region, ordered principally by their respective vagilities. Other conditions, such as differences in habitat heterogeneity among island sites, can be argued as well to be probable nesting mechanisms. But extinction-dominated archipelagic systems are the simplest process for generating patterns of nested species order and will be the only process considered for the remainder of this exposition.

Extinction-dominated island systems are not rare; they are common in both real and virtual archipelagos. Among the most clearly defined virtual islands are the "sky islands" of the Sierra Madre and Rocky Mountains of western, temperate North America. Boreal and alpine ecological communities, which were once present on the intervening plains, moved up the slope of the mountains with the retreat of the last Pleistocene glaciation, effectively fragmenting and isolating many species populations, 9–11,000 years ago.

Four presumptions are explicit in the theory to follow: (i) the islands of fragmented habitat were originally populated by a single common source biota, (ii) the islands were initially uniform in their habitat heterogeneity and type mix, and have remained so throughout their post-fragmentation history, (iii) no significant clinal (latitudinal) gradation exists across the archipelago so as to promote species turnover cross the archipelago, and (iv) all species of interest are equally isolated on all islands. The degree to which these conditions are matched in natural circumstance will suggest the degree to which the following theory should be applied or modified.

The measure of order and disorder

The metric to be described reverses the perspective taken in Patterson and Atmar (1986). Their earlier metric, N, was devised to demonstrate that species distributions on an archipelago are not random. Although the original N metric is attractive because of its simple calculability, it is incomplete and possesses several deficiencies as a practical measure. The value N is obtained by counting the number of unexpected absences of species from islands when the island-species pairs are arranged in nested order. This counting scheme has several shortcomings: (i) the count emphasizes unexpected presences more than absences, (ii) all absences are given equal weight, and (iii) the metric is matrix-size dependent (number of islands × number of species), thus a calculated N value cannot be compared between archipelagos.

The metric to be described corrects these problems. The new metric is a measure of unexpected species absences and presences on individual islands; in that, it is similar to Cutler's (1991) definition of unexpectedness, but otherwise differs in its details. *Unexpectedness* is the key concept in the theory to follow. Unexpectedness is similarly central to Boltzmann's definition of entropy and Shannon's definition of information.

The ideas of heat, entropy and information are historically intertwined, yet it is rare to find situations in which it is philosophically advantageous to call on all three ideas simultaneously. Clausius (1865) first defined *entropy*, S, as that fraction of energy that is lost to irrecoverable heat in every ordered energy transaction. Boltzmann (1872), who had been earlier greatly influenced by Darwin's rules of selection acting on individuals within populations (Boltzmann 1905; Prigogine 1980), almost immediately redefined Clausius' entropy as the relative disorder apparent within a statistical population of system states. Under Boltzmann's interpretation, heat becomes equivalent to disorder. Seventy years later, Shannon (1948; Shannon and Weaver 1949), in imitation of Boltzmann, redefined entropy a third time as an informational measure of *surprise*, I, as

$$I = -\log(p_i)$$

where p_i is the probability of encountering the ith state in a collection of system states. Taking the logarithm of a specific state's probability reflects no fundamental physical property; it is done only to emphasize the mathematical effects of rare events and diminish the effects of common events (Fano 1961).

The presence or absence of a particular species on a specific island is a system state. The unexpected presence or absence of a species on an island is similar to informational surprise. But not all unexpected species presences and absences are of equal informational value, and those specific differences in informational value must be taken into account.

The definition of U

Two forms of information appear in a presence-absence matrix. The primary information indicates which species appear on which islands. The secondary information is extinction order and island site suitability. This secondary information only becomes apparent after a matrix has been packed into a state of maximum nestedness.

Consider an $m \times n$ species-island presence-absence matrix of arbitrarily large size. Species presences will be marked with a black square, absences with white. A *perfectly nested* matrix is defined to be one where every island contains a proper subset of the species on all of the islands above it. While few actual data matrices will prove to be perfectly nested, all matrices can be packed to a state of maximum nestedness. The most species-rich island, by convention, is placed along the top row and the most widely distributed species is placed in the leftmost column. All other islands and species are packed towards the upper-left corner of the matrix, ordered in a manner to minimize unexpected species absences and presences.

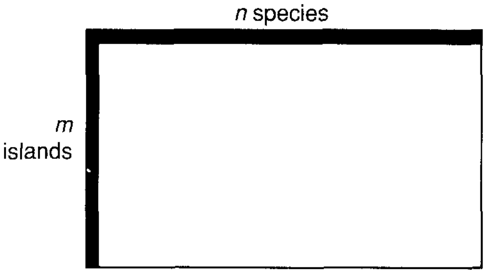


Fig. 1. A minimum, "all-white" matrix

The minimum such matrix that may be defined is an "all-white" matrix, where one island has n species and the remaining $m-1$ islands possess only one species each (Fig. 1). Although such a matrix is perfectly nested, it contains very little information about species' extinction order. We would not be surprised if any one of the $n-1$ right-lying species present on the most species-rich island were next to go extinct. Given this specific presence-absence matrix, we have no information about which of these species lies closest to its extinction threshold on the topmost island. The same lack of information is true of island habitat suitability concerning the ubiquitous species on the lower $m-1$ islands. The only exception to these statements is the upper-leftmost island-species pair. The uppermost island is demonstrably hospitable to all n species. Similarly, the leftmost species is demonstrably the most resistant to extinction. It would therefore come as great surprise should the leftmost species on the uppermost island be the first population to succumb to extinction.

An "all-black" matrix, where all species are present on all islands, is informationally valueless. All row (island) and column (species) reorderings are informationally equivalent because all rows and columns are identical. No extinction-order information is gained or lost in the reordering. Only a *maximally nested* matrix is intolerant of reordering. A maximally nested matrix is a special case of a perfectly nested matrix such that no reordering of islands of species is possible and still maintain the same degree of system order.

The maximally informative matrix will be a maximally nested square matrix of 50% fill, where species-island presences are packed into an upper-left triangle. Species extinction order will be maximally resolved, as will island habitat suitability. As each island is traversed in succession, one species will drop away. Two independent orderings are explicitly defined in any unexpectedness-minimized matrix: (i) the order of species extinction risk, and (ii) island habitat suitability. Such a matrix defines and maximally resolves the probable viability of each species on each island.

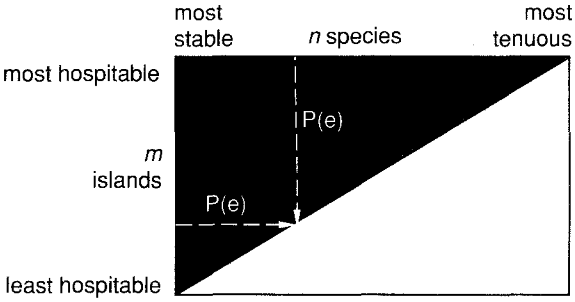


Fig. 2. The extinction probability vectors implicit in a maximally packed matrix

Two extinction probability vectors are similarly defined (Fig. 2). For each island in the matrix, a maximally nested matrix explicitly orders the constituent species in terms of their respective extinction probabilities, increasing left to right. On all islands, the species most susceptible to extinction will always be the rightmost. In the same manner, for any one species, the probability of extinction, $P(e)$, increases in ordered sequence, top-to-bottom. Although no data explicitly exists in a simple presence-absence matrix to directly support the contention, it is strongly presumed that the matrix also orders the species' population sizes, top-to-bottom.

The line that separates the occupied area of the matrix from the unoccupied may be termed either the "extinction" or "occurrence" boundary threshold. Species on this line are at – or very near – their absolute minimum sustainable population sizes and are at great risk of near-term extinction. The extinction of a species' population residing on the line would carry little or no surprise, and thus little or no information. In contrast, the extinction of the most prevalent species from the most hospitable island in the next epoch would be highly unexpected. Indeed, no other event could be more surprising. The same level of surprise would similarly result with the unexpected appearance in the next epoch of the most tenuous species on the least hospitable island.

Unexpectedness therefore runs diagonally. Unexpectedness is measured by the distance an unexpected presence or absence of a species is from the extinction threshold, measured along a line running parallel to the skew diagonal (Fig. 3). Local unexpectedness, u_{ij}, may be defined as

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

where D_{ij} is the length of the full line running through the jth species on the ith island, and d_{ij} is the specific length along that line. The ratioed distance is squared to exaggerate the information inherent in unexpected absences or

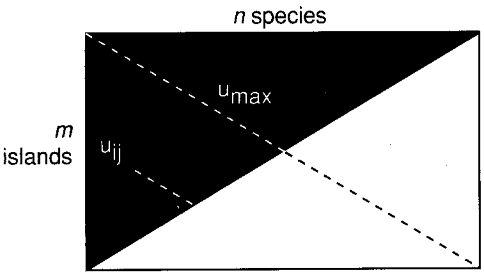


Fig. 3. The measure of local unexpectedness

presences located some distance away from the extinction threshold. Total unexpectedness, U, is defined as

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

The double normalization of the metric, U, results in a measure which is insensitive to matrix size or shape. A *perfectly ordered* matrix will have a $U=0$. A matrix of maximum unexpectedness will have a $U_{\max} \approx 0.04145$. System temperature is defined as the ratio

$$T = kU$$

where $k = 100/U_{\max}$. System temperatures will assume values in the range 0–100°. Because of the manner in which system temperature has been defined, it becomes a matrix-independent noise-to-signal ratio.

The extinction line for a matrix of perfect order is not arbitrary, nor is it dependent on internal data; the line is determined only by matrix shape and fill. The matrices drawn to this point have been drawn with a 50% fill (that is, 50% of the elements reflect species presences), but a nested matrix of maximized order exists for any arbitrary fill percentage.

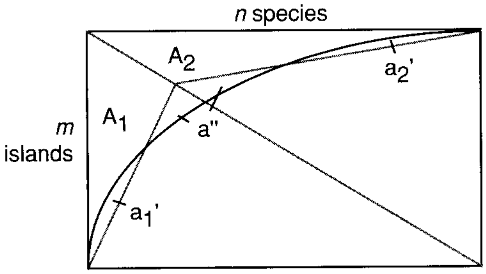


Fig. 4. The graphical determination of the line of perfect order for an arbitrary matrix

The determination of the extinction line is simple and geometric. If the percentage fill of a matrix is ϕ, then a point ϕD is chosen along the skew diagonal (Fig. 4). Lines are extended to the opposite corners. The areas $A_1 + A_2$ equal the desired fill. Moreover, $A_1 = A_2$. A line of smoothest transition is then drawn from corner to corner such that the areas $a'_1 + a'_2 = a''$. The line of smoothest transition will also be the line of perfect order, where *order* is defined by degree of impact that the rearrangement of any two rows or columns (islands or species) would have on the divergence of U from the absolute minimum.

For fills less than 50%, a perfectly ordered matrix forms a concave meniscus in the upper-left corner of the matrix. For fills greater than 50%, the curvature is reversed and forms a convex meniscus. Because the threshold line is defined by the line of perfect order, unexpected absences and presences will always appear in pairs. At all $T > 0°$, there will be as many unexpected absences as unexpected presences. As the matrix cools, the unexpected presences and absences will coalesce towards the extinction line. At 0°, they disappear.

Matrix temperature

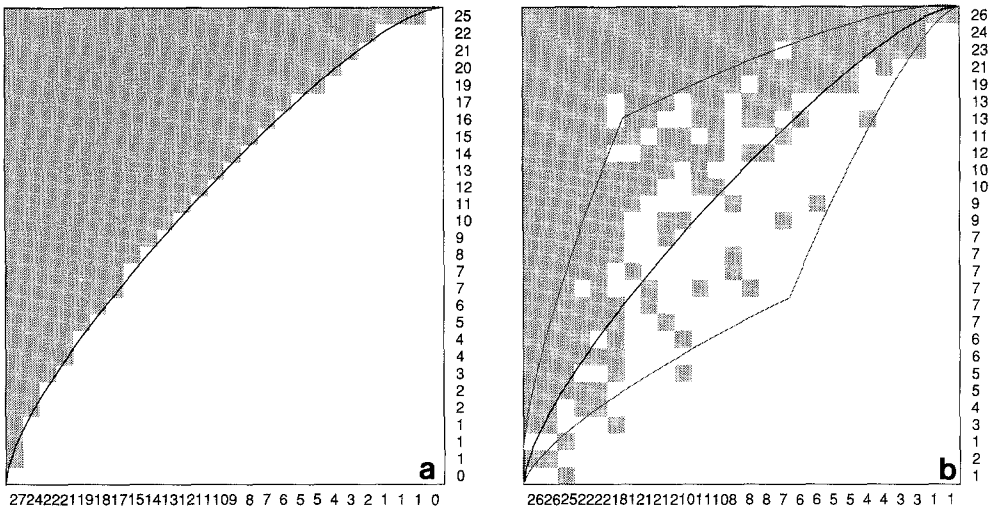
A matrix of perfect order assumes the attributes of a frozen liquid, where, by definition, complete order exists only at 0°. As the temperature is raised, a turbulence (noise) is imposed on the system and the sharp boundary between presences and absences is replaced by a gray "melt" band of disorder. At 100°, no discernible extinction order remains; the presence-absence matrix has become a free gas. The history of all populations on all islands have become wholly independent of one another and correlatable predictability has disappeared from the matrix. A scaled increase in disorder as a function of T (and U) is visible in the sequence of matrices in Fig. 5.

For a matrix's temperature to be calculated, a matrix must first be packed to a state of minimum unexpectedness. Column-to-column and row-to-row swaps do not harm the primary information of the matrix (i.e., which species appear on which islands). However, a matrix can be packed only to a specific minimum temperature and no further. The temperature of a matrix is inherent to the manner in which species are distributed throughout the matrix. Row and column totals (species richness and incidence totals) cannot be used as a reliable guide for packing; reversals are common in minimized warm matrices (Fig. 5–7). Rather, the matrix must be packed so as to minimize the distance of unexpected presences and absences from the calculated extinction threshold line.

Idiosyncratic species

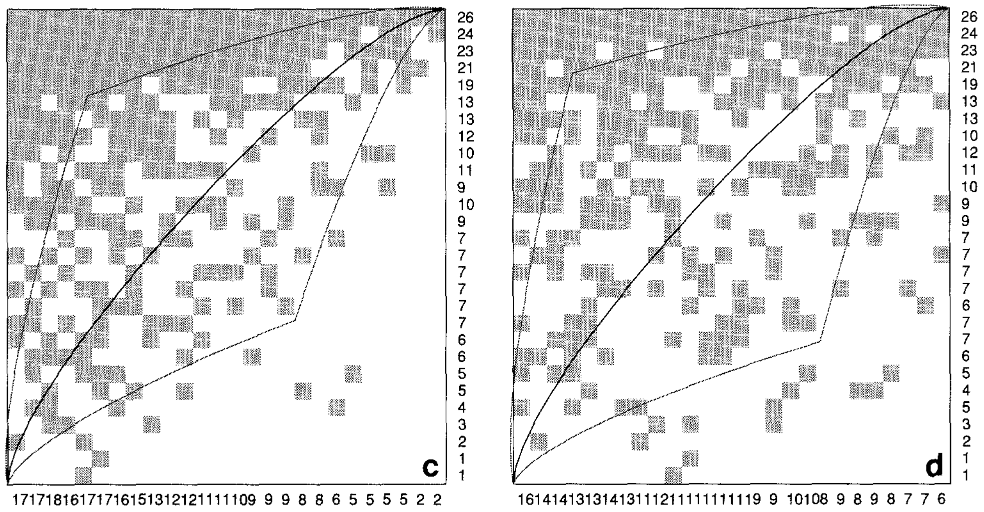
Two distinctly different forms of noise contribute to the temperature of a matrix: (i) the random variation of stochastic environmental, demographic, genetic, and catastrophic events, and (ii) the "coherent" noise of specific idiosyncratic biogeographic events. These are different phenomena, and they exhibit readily discernible patterns in a packed matrix.

Random events, regardless of their specific causes, work to create a gray noise band uniformly along the entire length of the extinction threshold boundary line. In contrast, species which are idiosyncratically distributed among the archipelago's islands generate specifically higher temperatures than the matrix as a whole (Fig. 6). (The idiosyncratic species patterns of Fig. 6 can be visually exaggerated by tilting the page. This foreshortens the vertical axis. The idiosyncratic species will appear as noticeable "streaks" in a packed matrix.) These elevated temperatures act as indicator flags to suggest that these



(a) $T = 0.03°$
Maximally
cold matrix

(b) $T = 3.81°$
Small mammals
Rocky Mountains
(Patterson 1984)



(c) $T = 18.96°$
RANDOM1

(d) $T = 37.21°$
RANDOM0

Fig. 5a–d. Biogeographic temperature. Four matrices of equal size (28 islands, 26 species) and equal fill (37.77%) are presented in increasing "temperature" sequence: (**a**) a maximally cold matrix, (**b**) actual data, (**c**), (**d**) matrices randomly filled under successively relaxed constraints [see Patterson and Atmar (1986)]. The probabilities that RANDOM1 and RANDOM0 would generate a matrix of equal or lower temperature than that observed in the Rocky Mountain small mammal biogeography are $P < 10^{-20}$ and $P < 10^{-40}$, respectively

species were disconnected from the primary biogeographic extinction event of the archipelago.

Among the simplest ecological mechanisms which will generate idiosyncratic distributions is the post-isolation immigration of new species onto the archipelago. Immigrating species may appear on only a subset of the islands, biased towards those islands which are closest to their respective sources. Idiosyncratic species distribution patterns will be similarly generated by the presence of a fundamental disjunction in the historical evolution of community structure (Fig. 6), such as that seen in Wallace's Line or the sharp disjunction in herpetofauna that Lowe (1992) has described for the northern Madrean Archipelago in southeastern Arizona. A third process which will foster distinctly idiosyncratic distributions is competitive exclusion (Fig. 7). Ecological and behavioral generalist species may be excluded from larger sites dominated by competitively superior specialists and relegated to small peripheral islands (Yeaton and Cody 1974; Simberloff and Martin 1991). A fourth process which will promote idiosyncratic species distributions is the presence of unique ecogeographic features (e.g., a river) on a random subset of islands. Species closely associated with such ecogeographic features will appear only on the islands where the features occur.

The two forms of divergence from perfect order may be readily segregated in the following manner: idiosyncratic species may be detected by defining an idiosyncratic species temperature, $I(j)$, as

$$I(j) = k/m \sum_i u_{ij}$$

where u_{ij}, k, and m are defined as above. If the source of disruptions from perfect extinction order is random and uniform across all species, $I(j)$ will approximately equal the system temperature, T, for all j species. But if there

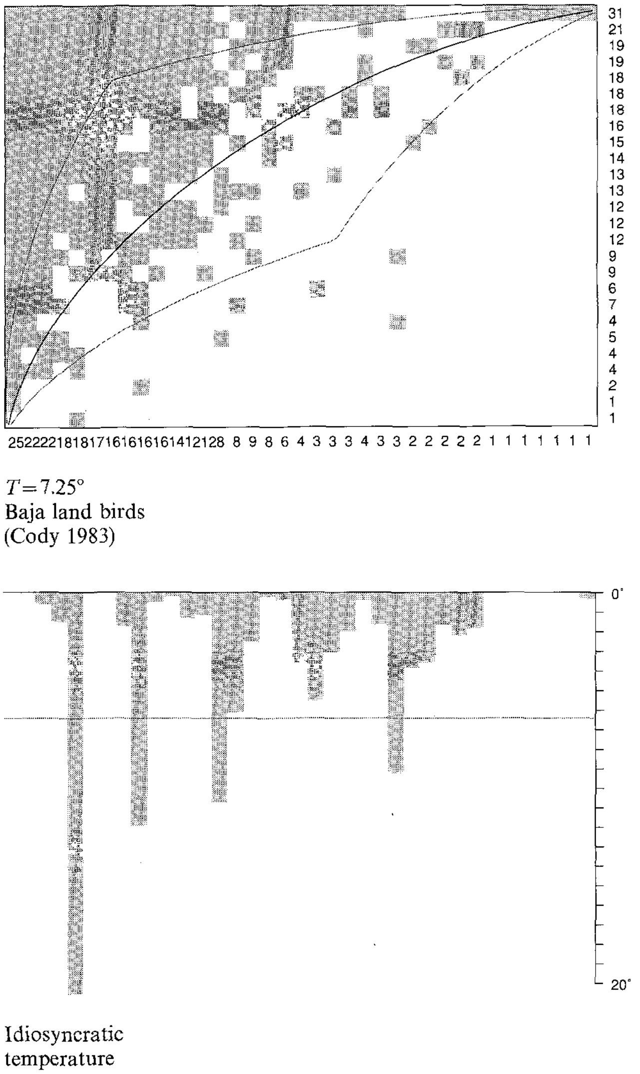


Fig. 6. Idiosyncratic species. Idiosyncratic species may be identified by an idiosyncratic temperature higher than the system temperature of the matrix. System temperature is denoted with a horizontal line. Because the idiosyncratic species elevate the temperature of the matrix as a whole, an idiosyncratic temperature at or greater than system temperature implies that the species is in some manner disconnected from the system-wide biogeography of the archipelago. The species shown are the land birds of the northern and southern islands of the Sea of Cortéz. The majority of species occur in both island sets, but some appear only in one or the other set of islands. That disjunction in species composition creates the idiosyncratic species temperatures shown

exist substantial deviations in $I(j)$, species-to-species, there exist reason to suspect idiosyncratic species histories. In such a case, if $I(j)$ is less than T, then the jth species is likely to have been a member of the original species set on the archipelago. If $I(j)$ is at or greater than T, then the species is quite likely to have been somehow idiosyncratic to the general extinction event that has governed species presences on the archipelago.

Idiosyncratic sites

The inhomogeneity of an archipelago's constituent island sites may similarly be assessed by a row-wise idiosyncratic site temperature, $I(i)$,

$$I(i) = k/n \sum_{j} u_{ij}$$

However, the interpretation of the second measure must be taken with care. Idiosyncratic site temperatures are not generally independent of idiosyncratic species' temperatures. Indeed, often, this second statistic will only recapitulate the idiosyncracies found within the species distributions. The reason for the interdependence of the two measures is clear. Species may be idiosyncratically distributed due to no other factor than the presence of ecogeographical idiosyncracies among the islands themselves. Specific but necessary habitat features may randomly appear on only a subset of the islands. Such intrinsic inhomogeneities among the island sites will influence the distribution of the assemblage's species. Similarly, but quite conversely, islands which are otherwise homogeneous may appear idiosyncratic due to biogeographic factors unconnected with the original insularization event (recent immigrations, competitive exclusions, etc.).

Species distributions on an extinction-dominated archipelago will appear idiosyncratic if one or more of the initial assumptions is substantially violated. While the ultimate cause of the distributional idiosyncracies cannot be determined from a presence-absence matrix without auxiliary information, the causal factors promoting such idiosyncratic distributions are not likely to be obscure. Rather, they may be quite obvious. The value implicit in the measurement of idiosyncratic temperatures is that they offer the possibility of unraveling a portion of the biogeographic history of the archipelago.

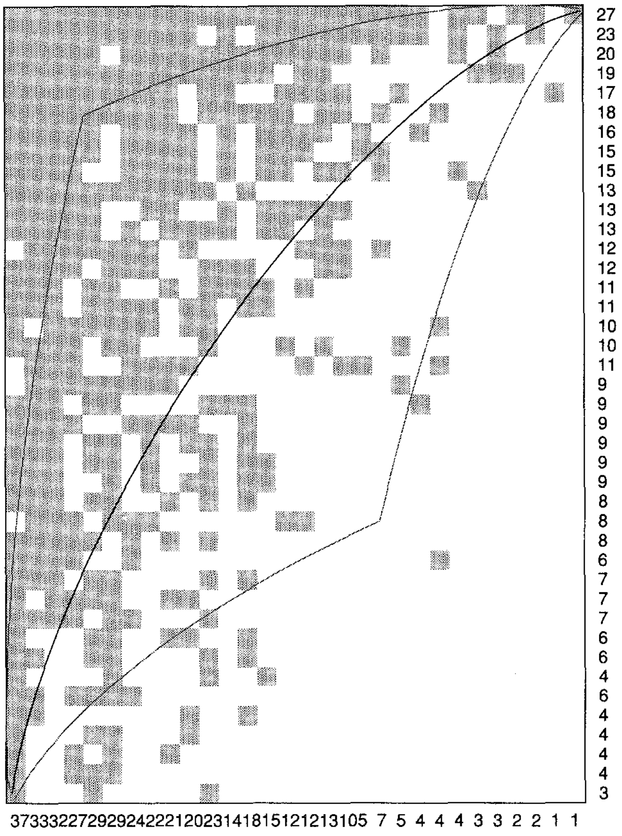
Site population lifetimes

Time is intimately woven into the definitions of temperature and entropy. Under Boltzmann's populational interpretation of entropy, physical temperature is defined as relative particle velocity. The lifetime of a particle at a system state is decreased as the temperature of the system is increased. Biogeographic system temperature cannot logically be different. As the temperature of the matrix is increased, the lifetime of all populations (or absences of a population) must concomitantly decrease. At all $T > 0°$, all populations on all islands possess a finite probability of extinction in the next epoch. But extinction probabilities are not uniformly distributed among all of the cells of a packed matrix. For all T between 0° and 100°, the statistically most stable species' populations will always reside in the upper-left corner of the matrix. Similarly the most stable absences will always appear in the lower-right corner, while the rate of populational turnover will always be greatest on the extinction threshold boundary. Only when the matrix temperature approaches 100° will the mean time-of-residency probability degenerate to a uniform ϕ for all populations on all islands, where ϕ is the matrix fill percentage.

An empirically derived presence-absence data matrix is a snapshot in "now" time. But the matrix is only one frame out of a historical sequence. As the temperature of an island system is increased, the intrinsic rate of populational turnover concomitantly increases. Species' presences will wink on and off at increasingly faster rates with increasing system temperature. That turnover, however, cannot be seen in a single snapshot. The consequence of the inability to view populational turnover over an extended period of time is that all "snapshot" matrices will appear cooler than they actually are. The effect becomes most pronounced at 100°. The matrix pattern for 100° is a uniform gray probability distribution, but probabilities do not exist in a snapshot. Rather, a pattern with some degree of species-island clumping is inevitable in a single time frame, and such a matrix, when packed, will reduce to a substantially cooler "apparent" temperature.

A hot, non-idiosyncratic matrix can reasonably imply only one of two events: either (i) that the order of species extinction was substantially randomized during the initial formation of the archipelago and the isolated populations have not yet relaxed into their stable configurations, or (ii) that species are reimmigrating back onto islands where they were previously absent. This second form of heat is the *noise of species turnover*, as defined by Diamond and Gilpin (1980). In either scenario, short populational lifetimes are strongly implied for species beyond the extinction threshold.

Incompletely isolated, mobile species will increase the overall temperature of a matrix. Species movement between islands ("leakage") allows populations to occasionally appear on islands too small to statistically sustain a local population over an extended period of time. The non-flying small mammal data for the southern Rocky Mountains (Patterson 1984) is among the coldest (most ordered) matrices so far measured ($T = 3.81°$). These small mammal populations are, for the most part, components of the ancestral biota, well insularized, and extinction-driven. However, no set of species can ever be declared to be completely insulated with certainty. Although small mammal species datasets are often cold because of the relatively easy insularization of small mammals, random recolonizations and local extinctions will work to keep small mammal system temperatures elevated above perfect order. Circumstantial evidence suggests that such recolonizations have occurred in certain Rocky Mountain small mammal populations (Davis and Dunford 1987; Lomolino et al. 1989).



$T = 15.87°$
Queen Charlotte
Islands land birds
(Simberloff and Martin 1991)

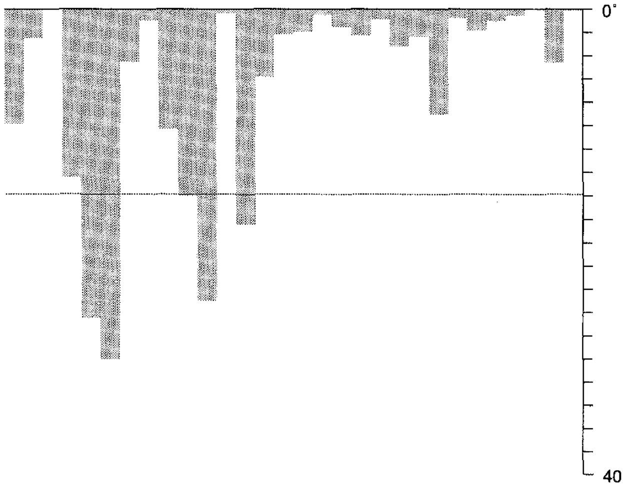


Fig. 7. The hotter matrices of non-insularized species. Because of their inherent mobility, migratory birds will generally exhibit much warmer matrix temperatures than well-insularized species which were part of the ancestral biota. The nested patterns for the birds of the Queen Charlotte Islands are clearly not due to the biogeographic extinction event of the archipelago. Rather, their nestedness undoubtedly reflects the underlying nested structure of suitable habitat. In addition to the intrinsically elevated matrix temperature of the Queen Charlotte birds (see text), six species further exhibit idiosyncratic temperatures near or greater than system temperature. They are (left to right): chestnut-backed chickadee, *Parus rufescens*, song sparrow, *Melospiza melodia*, orange-crowned warbler, *Vermivora celata*, bald eagle, *Haliaeetus leucocephalis*, rufous hummingbird, *Selasphorus rufus*, and the fox sparrow, *Passereillia iliaca*. Competitive exclusion has been proposed as the mechanism promoting the idiosyncratic distributions of the generalist species (Simberloff and Martin 1991), forcing the generalists to appear principally on the smaller islands. However, competitive exclusion is not likely to be an adequate explanation for the idiosyncratic distributions of the bald eagle or the rufous hummingbird

The presence-absence matrices for migratory birds are intrinsically warmer. Figure 7 is the presence-absence matrix ($T=15.87°$) for the land birds of the Queen Charlotte Islands, British Columbia (Simberloff and Martin 1991). The majority of the species represented do not overwinter on the islands. The nestedness that appears in such matrices is not due to the birds themselves but to the underlying nested structure of appropriate habitat on the islands. The yearly-redefined presences and absences of the birds add some (to much) uncertainty to the matrix, elevating its apparent temperature.

Two additional, calculated lines are drawn on each of the matrices in Figs. 5–7. These lines are the points of $\pm 2\sigma$ deviation, appropriately scaled to the length of the unexpectedness diagonal running through all species-island coordinates. Populations above the -2σ line are suggested by the data to be statistically stable and are at (or slightly above) their minimum requirements for long-term survival. Populations on or near the extinction threshold boundary are at risk of extinction/reappearance in the next epoch. Populations below the $+2\sigma$ line must somehow be either extraordinary, idiosyncratic, or at extreme risk of near-term extinction.

Species conservation implications

Fundamental to the design of natural refuges is the salvation of a particular species or group of species which would not otherwise be conserved (Simberloff 1988). At the core of the debate surrounding refuge design remains the persistent question of SLOSS (a single large reserve or several small ones). Brown (1986), after reviewing the highly deterministic order of extinctions implied by nested subsets, concluded that the controversy has now been "largely resolved" in favor of the single large reserve. Yet there is good empirical evidence to suggest that several small reserves often contain more species than a single large reserve of equivalent area (e.g., Simberloff and Gotelli 1984; Quinn and Harrison 1988).

Much of the confusion surrounding proper refuge design arises because there is a middle range in the empirical data where both points of view overlap and either perspective can be argued forcefully. However, that middle range exists only in a moderately warm matrix. As matrix temperature cools, the decision becomes increasingly indisputable in favor of the single large reserve. Indeed, in the case of perfect nestedness ($T=0°$), all doubt is removed. A set of small islands, equal in area to one large island, would each independently "relax" to a single common set of species, without variation, island-to-island. The result would be a clear depauperization of the original species diversity.

But in a warm matrix, species presences are no longer certain. If a presence-absence matrix is sufficiently large and the biogeographic system temperature is warm enough, a large number of possible microstates (species-island combinations) come to exist for a given temperature. Area has proven repeatedly to be a good predictor of species richness, expressed traditionally as

$$S = CA^z$$

where S is species count, A area, C a constant, and z a regression exponent (Arrhenius 1921; Preston 1960, 1962). Because z is less than 1 (typically, 0.15 to 0.4), species counts accumulate at substantially slower rates than does area. The current confusion arises because it is possible to sum the species counts in the low-area islands (the bottom rows of a nested matrix) and demonstrate a species count greater than an equivalently sized area would support at the same system temperature. The effect can be seen in the warm matrices of Figs. 5–7.

But a simple summation is misleading. In an equilibrial circumstance, hot matrices are indicative of short populational lifetimes and highly probable re-colonizations. It is not the area nor the number of islands that elevates species diversity. Rather, it is the probability of high rates of sustained, random recolonizations in the face of relatively quick local extinctions. Whatever barriers exist between the islands, they are not absolute. The question for any refuge designer contemplating a number of small refuges thus becomes: how does the continued fragmentation of the original source area by human encroachment affect the probabilities of recolonization? It is, by definition, an attribute that is beyond the control of the refuge designer. The intervening areas have been ceded to human development.

The simplest method to cool a species-island matrix is to (i) significantly diminish the probability of species recolonizations, and (ii) allow sufficient time for the marginally stable populations to fall away. If the archipelago thus modified is not idiosyncratic in some fundamental manner, the end result of such newly increased isolation must inevitably be (potentially significant) species loss from the smaller islands.

The US Forest Service is currently mandated by US Department of Agriculture regulations, in accordance with the National Forest Management Act of 1976, to determine minimum sustainable population sizes for the species inhabitating lands under its jurisdiction. Although easily stated, no practical ecological task is more formidable to accomplish by direct measurement. But if the governing assumptions hold, even approximately, these questions can be readily answered by the contextual information available in a presence-absence matrix. The statistics outlined here should identify populations of immediate interest and concern.

The key to the long-term survival of any species is the maintenance of a minimum area of suitable habitat. Populations residing near the upper-left -2σ line should accurately define a species' long-term minimum sustainable population size. While minimally-sustainable population sizes are very difficult to assess in a reasonable time scale by direct assessment, the area of appropriate habitat is not particularly difficult to measure. If minimum sustainable population sizes are as tightly linked to minimum habitat area as currently believed, then given a moderately well-defined extinction matrix, the determination of the habitat area alone may prove to be not only a far more easily achievable measure of minimally stable populations than direct demographic measurement, but more accurate as well. A single density measurement, even if correct, has little value without a sense of the long-term statistical variation of the species' populations. A measure of that variation is implicit in a minimized matrix and is present solely because of the profundity of the natural experiment that has been conducted by the process of habitat fragmentation.

No single summary statistic can be of complete value in making refuge design decisions; accurate autecological information will always be necessary. But an ordered presence-absence matrix contains specific system-comprehensive information that would be very difficult to obtain by any other means. Matrix temperature is at once an empirical measure of the degree of uncertainty in species extinction order and an indication of the relative stability of the constituent populations. Because temperature is directly comparable matrix-to-matrix, a specific system temperature implies a specific level of disorder. Much of the non-idiosyncratic disorder in an extinction-dominated archipelago of habitat fragments appears to be attributable to species movements between islands. Idiosyncratic species temperatures further suggest the historical coherence of the species set. But it is a species' position within the matrix that is of the greatest potential conservation value. Position in a minimized unexpectedness matrix is determined by the most fundamental of ecological processes. In that, the presence-absence matrix makes strong implicit suggestions as to the probability of success of species management efforts at specific sites. An unexpected species presence that lies significantly beyond the extinction threshold may be prohibitively expensive to maintain and protect, and its matrix position suggests that those efforts may well prove to be ultimately futile, even on the short-term. In contrast, a highly unexpected, non-idiosyncratic absence offers the high probability of success should a species reintroduction be attempted.

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References

Arrhenius O (1921) Species and area. J Ecol 9: 95–99

Bolger DT, Alberts AC, Soulé ME (1991) Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. Am Nat 137: 155–166

Boltzmann L (1872) Weitere studien über das wärmegleichgewicht unter gasmolekülen. Wien Ber 66: 275–370

Boltzmann L (1905) Populäre schriften. Leipzig. (English translation: Reidel, Dordrecht/Boston. 1974).

Brown JH (1971) Mammals on mountaintops: nonequilibrium insular biogeography. Am Nat 105: 467–478

Brown JH (1986) Two decades of interaction between the Mac-Arthur-Wilson model and the complexities of mammalian distributions. Biol J Linnean Soc 28: 231–251

Brown JH, Gibson AC (1983) Biogeography. Mosby, St. Louis.

Case TJ, Cody ML (1983) Synthesis: pattern and process in island biogeography. In: Case TJ, Cody ML (eds) Island Biogeography in the Sea of Cortéz, Univ of California Press, Berkeley, pp 307–341

Clausius R (1865) Ueber verschiedene für die anwendung begueme formen der hauptgleichungen der mechanischen wärmetheorie. Ann Physik 125: 353–400

Cody ML (1983) The land birds. In: Case TJ, Cody ML (eds) Island Biogeography in the Sea of Cortéz, Univ of California Press, Berkeley, pp 210–245

Connor EF, McCoy ED (1979) The statistics and biology of the species-area relationship. Am Nat 113: 792–833

Cutler A (1991) Nested faunas and extinction in fragmented habitats. Conserv Biol 5: 496–505

Davis R, Dunford C (1987) An example of contemporary colonization of montane islands by small, nonflying mammals in the American Southwest. Am Nat 129: 398–406

Diamond JM (1975) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biol Conserv 7: 129–146

Diamond JM (1984) "Normal" extinctions of isolated populations. In: Nitecki MH (ed) Extinctions. Univ of Chicago Press, Chicago, pp 191–246

Diamond JM, Gilpin ME (1980) Turnover noise: contribution to variance in species number and prediction from immigration and extinction curves. Am Nat 115: 884–889

Fano RM (1961) Transmission of information. MIT Press and John Wiley and Sons, New York

Gleason HA (1922) On the relation between species and area. Ecology 3: 158–162

Gleason HA (1925) Species and area. Ecology 6: 66–74

Lomolino MV, Brown JH, Davis R (1989) Island biogeography of montane forest mammals in the American Southwest. Ecology 70: 180–194

Lowe C (1992) Amphibians and reptiles of the Chiricahua Mountains, a sky island in the Madrean Archipelago. In: Barton AM, Sloane SA (eds) Proc Chiricahua Mountains Research Symp, Southwest Parks and Monuments Assoc, Tucson, pp 62–65

Murphy RW (1983) The reptiles: origins and evolution. In: Case TJ, Cody ML (eds) Island Biogeography in the Sea of Cortéz, Univ of California Press, Berkeley, pp 131–158

Patterson BD (1984) Mammalian extinction and biogeography in the Southern Rocky Mountains. In: Nitecki MH (ed) Extinctions. Univ of Chicago Press, Chicago, pp 247–293

Patterson BD (1987) The principle of nested subsets and its implications for biological conservation. Conserv Biol 1: 323–334

Patterson BD (1990) On the temporal development of nested subset patterns of species composition. Oikos 59: 330–342

Patterson BD, Atmar W (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. In: Heaney LR, Patterson BD (eds) Island biogeography of mammals. Academic Press, London, pp 65–82

Preston FW (1960) Time and space and the variation of species. Ecology 41: 611–627

Preston FW (1962) The canonical distribution of commonness and rarity. Ecology 43: 185–215

Prigogine I (1980) From being to becoming. Time and complexity in the physical sciences. WH Freeman and Co., San Francisco

Quinn JF, Harrison SP (1988) Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. Oecologia 75: 132–140

Ryti RT, Gilpin ME (1987) The comparative analysis of species occurrence patterns on archipelagoes. Oecologia 73: 282–287

Schoener TW, Schoener A (1983) Distribution of vertebrates on some very small islands I. Occurrence sequences of individual species. J Animal Ecol 52: 209–235

Shannon CE (1948) A mathematical theory of communication. Bell Sys Tech J 27: 379–656 (in four parts)

Shannon CE, Weaver W (1949) The mathematical theory of communication. Univ Illinois Press, Urbana

Simberloff D (1988) The contribution of population and community biology to conservation science. Ann Rev Ecol Syst 19: 473–511

Simberloff D, Gotelli N (1984) Effects of insularization on plant species richness in the prairie-forest ecotone. Biol Conserv 29: 27–46

Simberloff D, Levin B (1985) Predictable sequences of species loss with decreasing island area land birds in two archipelagoes. New Zealand J Ecol 8: 11–20

Simberloff D, Martin J-L (1991) Nestedness of insular avifaunas: simple summary statistics masking complex species patterns. Ornis Fennica 68: 178–192

Soulé ME, Alberts AC, Bolger DT (1992) The effects of habitat fragmentation on chaparral plants and vertebrates. Oikos 63: 39–47

Wright DH, Reeves JH (1992) On the meaning and measurement of nestedness of species assemblages. Oecologia 92: 416–428

Yeaton RI, Cody ML (1974) Competitive release in island song sparrow populations. Theor Pop Biol 5: 42–58