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
shrink. 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 disorder and will be defined to vary from $0^\circ$ (completely replicable extinction order) to $100^\circ$ (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 de-pauperate 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 x 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 $i$th 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