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Spatial and temporal patterns of species diversity in montane mammal communities of western North America

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ABSTRACT

We present the results of the first analysis of distributional patterns of the same taxa across thousands of kilometres and thousands of years, which demonstrate that the exponents for the power relationships in space and time are similar. In both space and time, the distribution of mammalian taxa of the Great Basin and Rocky Mountains follows a 'nested subset' pattern. We conclude that species identities and their relative abundances are non-random properties of communities that persist over long periods of ecological time and across geographic space. This is consistent with species abundance contributing heavily to evolutionary patterns, and allows predictions of how species within communities will respond to future global change.

Keywords: biogeography, Holocene, nestedness, nested subset, palaeontology.

INTRODUCTION

It has long been known that the number of species found in a discrete patch of habitat such as an island increases with the area of the patch (MacArthur and Wilson, 1967; Rosenzweig, 1995). Furthermore, the number of species counted in a community increases with the length of time over which sampling occurs, number of sites that are sampled and number of specimens in a sample (Preston, 1960; Hansen, 1980; Rosenzweig, 1995, 1998; Gaston, 1996; McKinney and Frederick, 1999). A relationship between patterns of species accumulation in time and in space (Preston, 1960) has been suspected, but no clear explanation has materialized (Rosenzweig, 1998). The common pattern of species identities associated with species–area relationships is the 'nested subsets' pattern. This pattern arises when species that appear on few islands occur only on the islands with the most species, while only the most widespread species are found on the islands with few species (Wright *et al.*, 1998).

The nested subset pattern arises because species differ in their distributions across space. Some species use a wider range of resources or persist across a wider range of habitats than

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others (Brown, 1984; Brown *et al.*, 1996; Hanski and Gyllenberg, 1997). Generally, species that use a wide range of resources or tolerate a variety of abiotic conditions can establish more populations in more places than comparable species with relatively narrow niches (Brown, 1995; Cook and Quinn, 1995). Differences in the ability of species to distribute themselves across space have distinct consequences for the structure of communities. Sites that encompass a greater area tend to have more species (Rosenzweig, 1995). This is because large areas include a subset of species not found elsewhere. Therefore, the nested subset pattern of species distribution in space is thought to reflect the gradient in abundance among species (Gaston, 1996; Leitner and Rosenzweig, 1997; Maurer, 1999). Consequently, a relationship emerges between the patterns of distribution and abundance of species in space and the power function describing the species–area relationship (Hanski and Gyllenberg, 1997; Harte *et al.*, 1999; Maurer, 1999).

Assuming that the ecological characteristics that determine a species' distribution in space are conservative over evolutionary time (Peterson *et al.*, 1999), the distribution of a species in space should reflect its ability to persist over time (Jackson, 1974; Boucot, 1979; McKinney, 1997). Species that are widespread and abundant during most of their time on earth should tend to persist over a long period of geological time, whereas species that have relatively narrow ecological tolerances should persist for shorter periods of time. When a series of geological strata randomly sample the same ecological community repeatedly, species that are most abundant should have higher probabilities of appearing in any given stratum, while rare species should appear with lower frequencies (Koch, 1987; Collins and Benning, 1996).

If the distribution and abundance of multiple species in geographic space affect their distribution and abundance through time, one expects to see a relationship between the structure of species assemblages in space and time. In particular, the power function describing a species–area relationship should be similar to that describing the species–time relationship when both samples are drawn from the same regional species pool. The nested subset patterns underlying the species–area and species–time relationships should also be similar. Although palaeontological data sets are consistent with this postulate, it has been difficult to link temporal and spatial patterns quantitatively because few opportunities exist to compare the same species in both space and time. The data presented in this study provide an unprecedented opportunity to examine simultaneously the spatial and temporal distributions of species from the same regional species pool.

METHODS

In the Great Basin of North America (427,000 km^2, 36–41° N), many mountain ranges have isolated islands of boreal vegetation at high elevations (> 2300 m) (Brown, 1971). The mammalian taxa that occupy these 19 mountaintops show the expected species–area and nested distributional patterns typical of such insular habitats (MacArthur and Wilson, 1967; Rosenzweig, 1995; Wright *et al.*, 1998). This same set of boreal mammals inhabits the Yellowstone ecosystem in northwestern Wyoming, USA. A recent analysis of fossiliferous deposits found in Lamar Cave (1900 m, at 45°N), Yellowstone National Park, showed that these same species have co-existed in that ecosystem for the past 3000 years (Hadly, 1996). Lamar Cave has 16 strata of organic deposits that accumulated over varying temporal periods, providing 'islands in time' analogous to the spatial samples represented by the 19 Great Basin mountaintop islands. Similar species have also been documented in Quaternary archaeological and palaeontological deposits of the Great Basin (Heaton, 1985; Grayson, 2000).

Lamar Cave is a palaeontological site that was excavated in natural stratigraphic units to a depth of 3 m. Calibrated radiocarbon dates span the present (Beta-24418) to 3000 years B.P. (CAMS-20356) at the base of the excavation. Species abundance data are derived from the identification of approximately 11,000 mostly cranial elements representing 40 mammalian taxa (Hadly, 1996). Bones from Lamar Cave were accumulated by *Neotoma cinerea* (bushy-tailed woodrat), which collects raptor pellets, mammalian carnivore scats and material from carcasses near the cave. The faunal collections in the cave approximate random sampling of the community of mammals in the local environment (Hadly, 1999).

Data on extant distributions of species from the Great Basin are from a comprehensive faunal list of small mammals (< 3 kg) from the 19 mountaintops above 2286 m spanning approximately 5° of latitude (Brown, 1971). The faunal list from Lamar Cave comprises genera and species whenever possible. The data sets were compared at the species level for six species (i.e. *Marmota flaviventris*, *Neotoma cinerea*, *Zapus princeps*, *Mustela erminea*, *Lepus townsendii* and *Ochotona princeps*) and at the genus level for the remaining five taxa (i.e. *Microtus* spp., *Spermophilus* spp., *Tamias* spp., *Sorex* spp. and *Sylvilagus* spp.). Great Basin ground squirrels include *Spermophilus beldingi* and *S. lateralis*; *S. beldingi* is extralocal to the Yellowstone area but is replaced by *S. armatus* in the Lamar Cave sample. *Sorex* spp. from the Great Basin includes *S. vagrans* and *S. palustris*. The Lamar Cave data for *Sorex* spp. include all shrews found in the region (possibly six species) because isolated cranial elements are difficult to identify to species. Although it is possible that *M. longicaudus* is present in the Lamar Cave deposits, most *Microtus* specimens probably represent *M. montanus* with a small percentage of *M. pennsylvanicus* (Hadly, 1996).

The relationship between species abundance and distribution can be represented by a variety of functions, none of which has any preferred theoretical basis. We assumed that the relationship is non-linear (Hanski and Gyllenberg, 1997) and fitted an arbitrary three-parameter model describing an exponential approach to a maximum number of levels in Lamar Cave in which a species might be found. For each taxon, we counted the number of levels containing at least one specimen of the taxon. We then averaged the number of specimens for each taxon across all levels in which at least one specimen was obtained. We then fitted the three-parameter exponential model to the resulting data using non-linear least squares (Conover, 1971).

The relationships between species number and area and time were described using power functions. To fit the parameters for a power function relationship between species number and area of the Great Basin boreal habitats, we log-transformed both variables and calculated parameter estimates and standard errors using simple linear regression (Neter *et al.*, 1985). To estimate the length of time represented by a particular sampling level, we assumed a constant rate of deposition of specimens across the 3000 years over which deposition occurred. Sampling of the bones from the environment has not been interrupted throughout the past 3000 years (Hadly, 1996). The relative abundance of the primary agent of faunal collection, *Neotoma cinerea*, is constant throughout the time spanned by the deposit. Additionally, the radiocarbon chronology follows an exponential regression concordant with compaction with depth and organic decay (Hadly, 1999). The average rate of deposition thus calculated was about 2.3 specimens per year. The total number of specimens deposited in a given level at a constant rate was assumed to be proportional to the length of time over which deposition had taken place. To obtain a power relationship between species number and time, we log-transformed the number of taxa in each level and plotted it against the logarithm of the estimated time span represented by each level. Simple linear regression was used to obtain parameter estimates and standard errors. Because the exponents of a power relationship are scale-independent (Rosenzweig, 1995), we tested for equality of exponents using a two-sample Student's t-test.

To analyse patterns of distribution of all taxa across both space and time for 'nested subset structure' (Wright *et al.*, 1998), we used two different metrics designed to detect such a structure and to test the null hypothesis that the observed distributional pattern was significantly different from a random assignment of species to locations or levels. The first measure describes the degree of disorder of the distributional patterns of a set of species as a 'temperature' (Atmar and Patterson, 1993) scaled to be between 0° and 100°. A perfectly ordered matrix of distributions (species × sites) has a temperature of 0°. Randomization tests were used to compare the observed temperature of matrices obtained from our spatial and temporal samples to those generated by randomly assigning species to sites within the matrix. The second measure is based on the conditional probabilities of species being present on species-rich sites given their presence on species-poor sites (Wright and Reeves, 1992). This measure is standardized so that a value of 0 indicates a randomized distribution of species among sites and a value of 1 indicates perfect nestedness. Means and variances for the distribution of this statistic were calculated under the null hypothesis of randomness; significance tests were constructed using estimates of these statistics. For each taxon, its distribution across space was taken as the number of Great Basin mountaintops on which it was found. A taxon's distribution over time was measured as the number of levels containing at least one specimen in Lamar Cave. We plotted a relationship between these two variables and used Pearson's, Kendall's and Spearman's correlation measures (Conover, 1971) to estimate the strength of the relationship between them. A linear relationship was fitted using simple linear regression (Neter *et al.*, 1985).

RESULTS

In the 16 stratigraphic levels of Lamar Cave, species that are represented on average by many specimens within a given level also are found in the most stratigraphic levels (Fig. 1). Hall (1946) provided verbal descriptions of the relative abundances of these species in Nevada, which generally agree with the quantitative estimates of abundance in Lamar Cave deposits. Additionally, a correlation of rank order abundance between the most abundant Lamar Cave fossils and those from Crystal Ball Cave, a late Pleistocene deposit from the central Great Basin (Heaton, 1985), is significantly positive (Spearman's rho = 0.83; $n = 12$; $P > 0.01$).

In Lamar Cave, depositional layers that accumulated over the longest periods of time had the most species in them (Fig. 2A), as would be expected from sampling considerations. Interestingly, the exponent of the power law that describes the relationship between species number and time is statistically indistinguishable from the analogous exponent obtained from the species–area relationship for the Great Basin (Fig. 2B) and is concordant with predictions made by Preston (1962) for isolated habitat 'islands'. Thus, depositional layers in the Lamar Cave are like 'islands in time', because they sample the diversity of the same community over time in much the same way that islands in space represent samples from a pool of species with geographic ranges overlapping those islands.

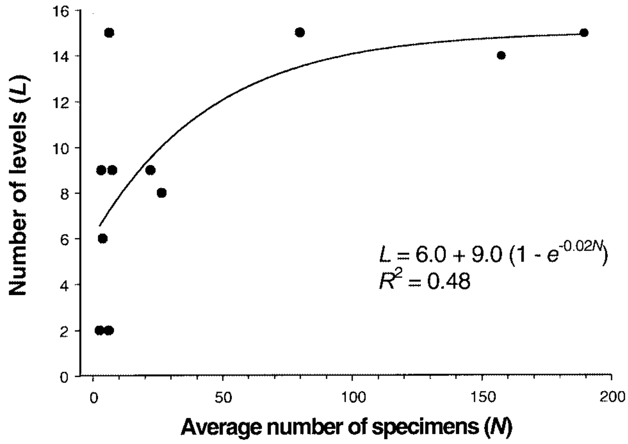

Fig. 1. Relationship between average abundance over depositional layers in which a species was found and the number of layers occupied. Note that this relationship is curvilinear (Hanski and Gyllenberg, 1997). Each point represents a small mammal taxon that occurs both in Yellowstone National Park and on Great Basin mountaintops.

DISCUSSION

The similarity between spatial and temporal islands of small mammals in the Great Basin goes beyond the similarities in the exponents of the power law describing species number. Both sets of data show the same nested subset pattern of distribution. Both nested distributions are statistically distinguishable from a random allocation process that would distribute species indiscriminantly among mountaintops or depositional layers (Table 1). More important, the frequency with which a species is found on mountaintops in the Great Basin is positively correlated with the number of levels it is found in within Lamar Cave (Fig. 3). Thus, communities of small mammals inhabiting boreal habitats in the western United States are non-randomly structured. The temporal and spatial distribution of species is determined by the natural histories of the species involved. Species with life cycles, ecological needs, dispersal abilities and tolerances that allow them to occur at high densities in local ecological communities also dominate the regional species pool. Examples include the woodrat (*Neotoma cinerea*), chipmunks (*Tamias* spp.), marmot (*Marmota flaviventris*), voles (*Microtus* spp.) and ground squirrels (*Spermophilus* spp.).

Table 1. Nestedness calculations of mammalian species from number of mountaintops in the Great Basin and number of levels in Lamar Cave

Nestedness measure	Lamar Cave	Great Basin
Atmar and Patterson (1993) (*T*)	8.26°*	9.02°*
Wright and Reeves (1992) (*C*)	0.69*	0.67*

*Significantly different ($P > 0.001$) from value expected from random allocation of species among samples.

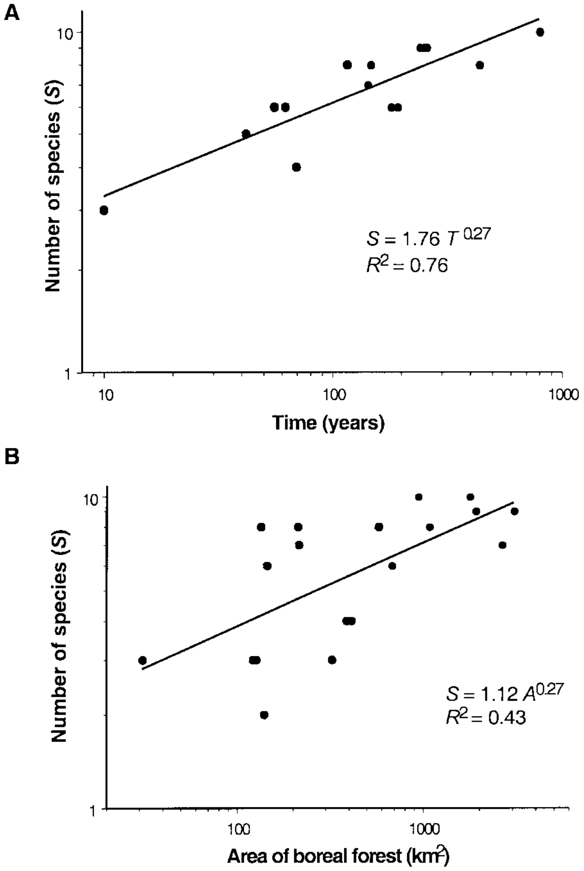

Fig. 2. (A) Relationship between the span of time sampled by a given depositional layer in Lamar Cave and the number of taxa of boreal small mammals. Each point represents a single depositional layer. (B) Relationship between area of boreal habitat on 19 mountaintops of ranges in the Great Basin and the number of boreal small mammal taxa. Each point represents a single Great Basin mountain range. The two slopes are not significantly different ($t_{30} = 0.07$, $P > 0.05$).

Our regional species pool posits that, even in the face of a certain amount of spatial and temporal heterogeneity, species with larger ranges will be found in more places and more time periods than those that have small ranges. We do not believe that the patterns emerge from 'statistical sampling effects'. There are two null models that might be suggested by the phrase 'statistical sampling effects'. First, one could assume that the presence of a species in any particular place or time is completely arbitrary and random. Our nestedness results alone contradict this null model. Second, one could assume that the same community is always present in the time samples, and it is only the length of time that determines the species actually counted. To detect whether the 'same community' null model explains our temporal data, we calculated Fisher's alpha (Rosenzweig, 1995) for each of the depositional layers. In fact, we plotted alphas against length of sampling interval (as in Fig. 2A, but this time with alpha), which results in a positive relationship between alpha and time with a

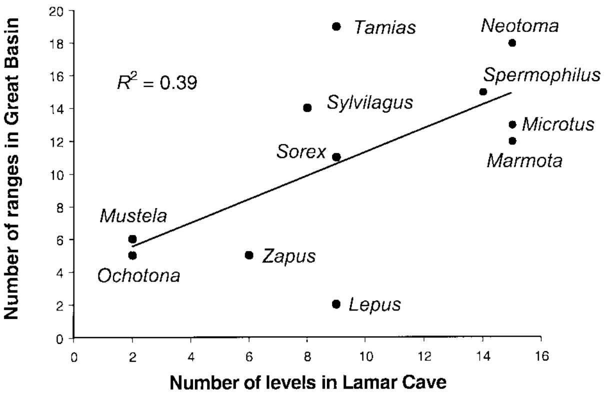

Fig. 3. Nestedness relationship between the number of mountain ranges occupied in the Great Basin and the number of levels containing specimens for 11 taxa of boreal small mammals.

slope of about 0.11 and an r^2 value of 0.27 (much poorer fit). This contradicts the 'same community' null model. It is consistent with the regional species pool model because the concept doesn't require local communities to be the same at different points in time (or space). It does predict, however, that when a species is lost, it will be one that has low abundance (small geographic range).

CONCLUSIONS

The stability of relative abundances of species through the last several thousand years has several important consequences for ecology, evolution and global change. We have demonstrated that only montane communities of sufficient spatial extent and which have been accumulating taxa for an ecologically long period of time can include species with specialized life cycles and low dispersal abilities, such as the western jumping mouse (*Zapus princeps*), pika (*Ochotona princeps*) and ermine (*Mustela erminea*). That the statistical distribution of relative abundance of small mammals has persisted in the Yellowstone ecosystem for 3000 years, despite changes in climatic conditions and local habitat fluctuations, implies that this distribution should be considered a relatively stable attribute of the boreal small mammal community (Riddle, 1998). This spatial and temporal stability in community structure over this time period suggests that 'non-analog' communities, where pairs of species that have non-overlapping contemporary distributions occurred together in the past (Graham, 1986), arose from distributional changes in a few taxa. Species that demonstrate remarkable individual responses to changing climatic conditions do not alter to a large extent the community structure that persists through time if they are a minor component of the local community and of the species pool from which they are drawn. Thus, over ecological time, differential abundance among species produces communities that are more similar than would occur by chance.

Abundance also has a direct influence on evolutionary patterns. If abundance is correlated with geographic range size (Brown and Maurer, 1987), which in turn is correlated with persistence in evolutionary time (Jablonski, 1986; Gaston and Chown, 1999), then abundant species should become extinct less often than rare species. Our quantitative analysis supports this often cited intuitive observation. Abundant species with large geographic ranges thus should give rise to greater numbers of species (Rosenzweig, 1975; Maurer, 1999), which may explain such remarkable radiations as Rodentia. Preliminary data from a middle-Pleistocene montane site, Porcupine Cave, Colorado (E.A.H. and A.D. Barnosky, in prep.), demonstrate support for this contention. The temporal distribution of small mammal taxa tabulated as of 1998 in these deposits demonstrate a significantly nested pattern ($T = 15.9°$) (Atmar and Patterson, 1993). The taxa in Porcupine Cave are comparable to those in Lamar Cave at the generic level. If such patterns are relatively general, then differences in abundance among taxa may lead to taxanomic sorting (Vrba and Gould, 1986) and may, therefore, determine patterns of taxonomic diversity within clades.

Finally, our analyses have important implications for conservation biology. Species diversity has a strong deterministic component that is a consequence of the distribution of abundance among species. Although future global change is likely to bring species together that did not previously co-exist (either directly through species introductions or indirectly through environmental change), we should be able to predict the species most likely to decline based on their commonness and rarity in insulate communities and on their occurrence in temporal records.

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REFERENCES

Atmar, W. and Patterson, B.D. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, **96**: 373–382.

Boucot, A.J. 1979. Community evolution and rates of cladogenesis. *Evol. Biol.*, **11**: 545–636, 647–655.

Brown, J.H. 1971. Mammals on mountaintops: Nonequilibrium insular biogeography. *Am. Nat.*, **105**: 467–478.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. *Am. Nat.*, **124**: 255–279.

Brown, J.H. 1995. *Macroecology*. Chicago, IL: University of Chicago Press.

Brown, J.H. and Maurer, B.A. 1987. Evolution of species assemblages: Effects of energetic constraints and species dynamics on the diversification of North American avifauna. *Am. Nat.*, **138**: 1–17.

Brown, J.H., Stevens, G.C. and Kaufman, D.M. 1996. The geographic range: Size, shape, boundaries, and internal structure. *Ann. Rev. Ecol. Syst.*, **27**: 597–623.

Collins, S.L. and Benning, T.L. 1996. Spatial and temporal patterns in functional diversity. In *Biodiversity: A Biology of Numbers and Differences* (K.J. Gaston, ed.), pp. 253–280. Oxford: Blackwell Scientific.

Conover, W.J. 1971. *Practical Nonparametric Statistics*. New York: Wiley.

Cook, R.R. and Quinn, J.F. 1995. The influence of colonization in nested species subsets. *Oecologia*, **102**: 413–424.

Gaston, K.J. 1996. Species richness: Measure and measurement. In *Biodiversity: A Biology of Numbers and Differences* (K.J. Gaston, ed.), pp. 77–113. Oxford: Blackwell Scientific.

Gaston, K.J. and Chown, S.L. 1999. Geographic range size and speciation. In *Evolution of Biological Diversity* (A.E. Magurran and R.M. May, eds), pp. 236–259. Oxford: Oxford University Press.

Graham, R.W. 1986. Response of mammalian communities to environmental changes during the late Quaternary. In *Community Ecology* (J. Diamond and T.J. Case, eds), pp. 300–313. New York: Harper & Row.

Grayson, D.K. 2000. Mammalian responses to middle Holocene climatic change in the Great Basin of the western United States. *J. Biogeogr.*, **27**: 181–192.

Hadly, E.A. 1996. Influence of late-Holocene climate on northern Rocky Mountain mammals. *Quaternary Res.*, **46**: 298–310.

Hadly, E.A. 1999. Fidelity of terrestrial vertebrate fossils to a modern ecosystem. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **149**: 389–409.

Hall, E.R. 1946. *Mammals of Nevada*. Berkeley, CA: University of California Press.

Hansen, T.A. 1980. Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology*, **6**: 193–207.

Hanski, I. and Gyllenberg, M. 1997. Uniting two general patterns in the distribution of species. *Science*, **272**: 397–400.

Harte, J., Kinzig, A. and Green, J. 1999. Self similarity in the distribution and abundance of species. *Science*, **284**: 334–336.

Heaton, T.H. 1985. Quaternary paleontology and paleoecology of Crystal Ball Cave, Millard County, Utah: With emphasis on mammals and description of a new species of fossil skunk. *Great Basin Nat.*, **45**: 337–390.

Jablonski, D. 1986. Background and mass extinctions: The alternation of macroevolutionary regimes. *Science*, **231**: 129–133.

Jackson, J.B.C. 1974. Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolutionary significance. *Am. Nat.*, **108**: 541–560.

Koch, C.F. 1987. Prediction of sample size effects on the measured temporal and geographic distribution patterns of species. *Paleobiology*, **13**: 100–107.

Leitner, W.A. and Rosenzweig, M.L. 1997. Nested species–area curves and stochastic sampling: A new theory. *Oikos*, **79**: 503–512.

MacArthur, R.H. and Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Maurer, B.A. 1999. *Untangling Ecological Complexity*. Chicago, IL: University of Chicago Press.

McKinney, M.L. 1997. How do rare species avoid extinction? In *The Biology of Rarity* (W.E.. Kunin and K.J. Gaston, eds), pp. 110–129. London: Chapman & Hall.

McKinney, M.L. and Frederick, D.L. 1999. Species–time curves and population extremes: Ecological patterns in the fossil record. *Evol. Ecol. Res.*, **1**: 641–650.

Neter, J., Wasserman, W. and Kutner, M.H. 1985. *Applied Linear Statistical Models*, 2nd edn. Homewood, IL: Irwin.

Peterson, A.T., Soberon, J. and Sanchez-Cordero, V. 1999. Conservatism of ecological niches in evolutionary time. *Science*, **285**: 1265–1267.

Preston, F.W. 1960. Time and space and the variation of species. *Ecology*, **41**: 611–627.

Preston, F.W. 1962. The canonical distribution of commonness and rarity. *Ecology*, **4**: 185–215, 410–432.

Riddle, B.R. 1998. The historical assembly of continental biotas: Late Quaternary range-shifting, areas of endemism, and biogeographic structure in the North American mammal fauna. *Ecography*, **21**: 437–446.

Rosenzweig, M.L. 1975. On continental steady states of species diversity. In *The Ecology and Evolution of Communities* (M. Cody and J. Diamond, eds), pp. 121–140. Cambridge, MA: Harvard University Press.

Rosenzweig, M.L. 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.

Rosenzweig, M.L. 1998. Preston's ergodic conjecture: The accumulation of species in space and time. In *Biodiversity Dynamics* (M.L. McKinney and J.A. Drake, eds), pp. 311–348. New York: Columbia University Press.

Vrba, E.S. and Gould, S.J. 1986. The hierarchical expansion of sorting and selection: Sorting and selection cannot be equated. *Paleobiology*, **12**: 217–228.

Wright, D.H. and Reeves, J.H. 1992. On the meaning and measurement of nestedness of species assemblages. *Oecologia*, **92**: 416–428.

Wright, D.H., Patterson, B.D., Mikkelson, G.M., Cutler, A. and Atmar, W. 1998. A comparative analysis of nested subset patterns of species composition. *Oecologia*, **113**: 1–20.