

OIKOS

8481DU

OIKOS 81: 000-000. Copenhagen 1998

An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World

Michael R. Willig and S. Kathleen Lyons

Willig, M. R. and Lyons, S. K. 1998. An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World. - *Oikos* 81: 000-000.

Although latitudinal gradients in species richness are well-documented for a plethora of taxa in terrestrial, freshwater, and marine environments, little consensus exists concerning the predominant biological factor that is responsible for the pattern. We produced an analytical null model to assess the degree to which gradients in species richness could be a consequence of the random determination of the limits of species ranges. The model predicts a parabolic increase in species richness toward the middle of a latitudinal domain in the absence of underlying environmental gradients. Our stochastic model accounted for a significant portion of variation in marsupial and bat species richness for each of three different latitudinal domains in the New World: continental limits, the latitudinal extent of each higher taxon, and the smallest latitudinal extent which comprises 95% of the species in the higher taxon. A unique prediction of the stochastic model, which distinguishes it from all other hypotheses, is that parabolic latitudinal gradients in richness should exist for species wholly contained within random latitudinal subsets. Observed gradients for New World marsupials and bats document that this is true. Regardless of taxon or domain, differences between observed and expected species richness (residuals) were not related appreciably to latitudinal band area ($r^2 < 0.15$). The ubiquity and similarity of latitudinal gradients in species richness for different taxa could be a consequence of pervasive stochastic mechanisms rather than a product of a dominant underlying environmental gradient to which all species respond. Application of our null model to other gradients (e.g., depth, productivity, disturbance) may provide insight into mechanisms affecting patterns of species richness in other ecological or biogeographic settings.

Willig, M. R. and Lyons, S. K., *Ecology Program, Dept of Biological Sciences and The Museum, Texas Tech Univ., Lubbock, TX 79409-3131, USA (cmrwr@ttacs.ttu.edu)* (present address of SKL: *Committee on Evolutionary Biology, Univ. of Chicago, 1025 E. 57th St. - Culver Hall 402, Chicago, Illinois 60637-1573, USA*).

Gradients of species diversity have long fascinated biogeographers, ecologists, systematists, and evolutionary biologists (Wallace 1878, Schall and Pianka 1978, Rosenzweig 1995). The greater richness of tropical biotas compared to their temperate and polar counterparts, as well as the latitudinal decline in species richness with increasing latitude, are viewed as almost universal truths that apply to a wide variety of animals and plants in terrestrial, freshwater, and marine environments (Brown

and Gibson 1983, Brown 1988). These same large-scale phenomena frequently are recapitulated at the level of local communities (Fleming 1973, Lacher and Mares 1986). Indeed, the pervasive appearance of latitudinal gradients in species richness has led to the search for a dominant biological process that is indifferent to taxonomic affinity or geographic location and origin (Pianka 1966, Stehli et al. 1969, Rohde 1978, 1992, Ricklefs 1979, Stevens 1989, Kaufman 1994).

Accepted 30 June 1997

Copyright © OIKOS 1998

ISSN 0030-1299

Printed in Ireland - all rights reserved

OIKOS 81:2 (1998)

Explanations for the latitudinal gradient are legion and controversial. In general, they include both historical and equilibrium approaches, comprising 10 classical (evolutionary time, spatial heterogeneity, competition, predation, climatic stability, productivity, ecological time, climatic predictability, stability of primary production, and rarefaction [Pianka 1966, Stehli et al. 1969]) and four recent hypotheses (nonequilibrium interactions among competitors, complex vertical structuring of plant species diversity, Rapoport's Rule of decreasing range size with decreasing latitude, and the positive correlation between rate of evolution and temperature [Huston 1979, Terborgh 1985, Stevens 1989, Rohde 1992]). These hypotheses are not mutually exclusive, and some are circular or unsubstantiated by empirical evidence (Rohde 1992). Although overwhelming support exists for the existence of latitudinal gradients in species richness, no consensus has emerged identifying the causal agent, and notable exceptions to the general pattern have been documented, especially for parasitic taxa (Owen and Owen 1974, Rathke and Price 1976, Janzen 1981). To produce a gradient in species richness, all hypotheses require an underlying latitudinal gradient in the environmental conditions or biological factors which affect species richness. Nonetheless, a latitudinal gradient in species richness recently has been documented for benthic invertebrates inhabiting the North and South Atlantic (Rex et al. 1993), despite the continuity and homogeneity of the deep sea physical environment.

At least in part, the universality of the latitudinal gradient may be a consequence of the bounded nature (e.g., the distribution of New World terrestrial taxa are limited by the northern-most and southern-most extensions of the continents) of global environments (Pielou 1977). To test this supposition, we constructed a simple probabilistic model based on the binomial distribution. It predicts the number of species at each latitude in the absence of environmental heterogeneity or gradients. An analogous simulation approach was developed recently by Colwell and Hurtt (1994), whereas an identical random simulation approach was used by Lyons and Willig (1997) to evaluate patterns of latitudinal range size.

The stochastic model

If the endpoints of the southern and northern latitudinal extremes of a landmass are represented by 0 and 1, respectively (Fig. 1), the latitudinal position of any point (P) may be represented by its proportional distances between endpoints (p from the southern terminus, 0; q from the northern terminus, 1; with the sum of p and q equaling 1). If the distribution of a species is affected by chance alone, then the probability that it includes P is given by:

$$Pr(P) = 1 - p^2 - q^2 = 2pq$$

where p^2 is the probability that a species distribution will exclude P and exclusively occur to the south, and q^2 is the probability that a species distribution will exclude P and exclusively occur to the north. As a consequence, the number of species expected to occur by chance alone at point P is given by $2pqS$, where S is the number of species in the species pool (i.e., the species richness of the landmass).

Fortunately, the variance (V) of $2pq$ is well known as a consequence of extensive work in population genetics (Nei and Roychoudhury 1974, Nei 1975) and is given by

$$V(2pq) = \{2(S-1)/S^3\} \{(3-2S)(p^4) + 2(S-2)p^3 + p^2\}$$

This facilitates calculation of 95% confidence intervals for predicted species richness at P .

All other hypotheses which purport to identify the factors that produce a gradient in species richness only predict a general trend: richness increases toward the tropics. More detailed quantitative predictions concerning the precise form of the increase or the number of species expected at each latitude are not intrinsic to those hypotheses. Consequently, empirical evaluation of each hypothesis or falsification of competing hypotheses in the sense of strong inference (Platt 1964) is difficult. In contrast, our stochastic model produces a symmetrical gradient of species richness (Fig. 1) which attains a maximum ($0.5S$) at the midpoint of the latitudinal bounds (i.e., when $p = q = 0.5$). Therefore, the model provides a quantitative prediction (along with confidence limits) of species richness which can be compared to empirical data for any particular taxon. Clearly the existence of a pattern and its recapitulation above and below the equator does not necessarily require deterministic mechanisms (Colwell and Hurtt 1994, Lyons and Willig 1997). Chance alone can produce patterns with all of the mathematical precision of deterministic mechanisms.

Empirical assessment

We used distributional data for bats (Koopman 1982) and marsupials (Streilein 1982), updated according to information provided by Eisenberg (1989), to test if the predictions from the stochastic model accounted for observed latitudinal gradients in the New World. Both taxa have been shown to exhibit significant gradients of richness in the New World (bats, Willig and Sandlin 1991, Willig and Selcer 1989; marsupials, Willig and Gannon 1997). For this test, we digitized the distribution for each species of bat or marsupial, and tallied the number of species in each taxon that occurred within 1-degree latitudinal bands. The correlation between observed and predicted species richness in each band is a

? J

(?)

? #

? order

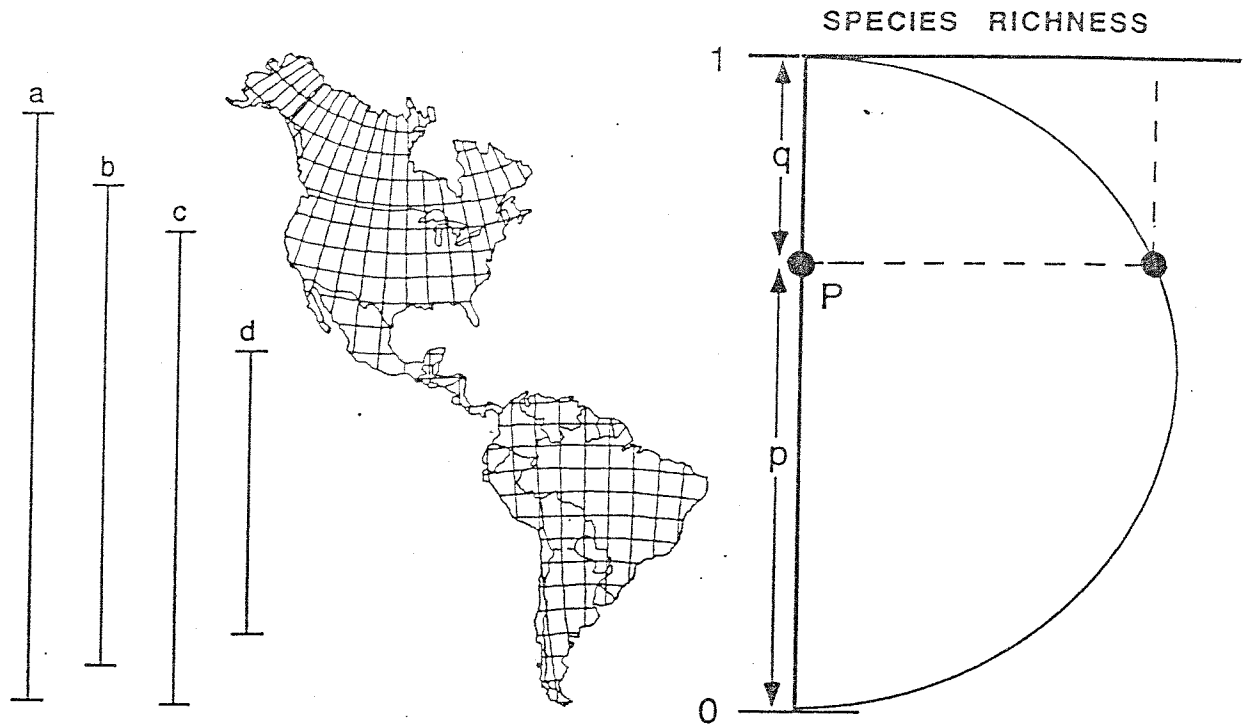


Fig. 1. Illustration of the relationship between actual latitudinal limits of the continental New World and the theoretical prediction of the species richness gradient. The proportional distance of any point P from the southern (p) or northern (q) terminus determines the expected species richness ($2pqS$) at a latitude, where S is the number of species in the biota. As a consequence, the form of the relation between richness and latitude is a parabola that attains its maximum at the midpoint between latitudinal extremes. Similar parabolic gradients in species richness are obtained for each of the other two methods of delimiting latitudinal termini for the model. The latitudinal domain based upon the distributional limits of bats is 66°N to 55°S and is represented by vertical bar a ; whereas that of marsupials is 47°N to 55°S and is represented by vertical bar c . The smallest latitudinal domain that encompasses 95% of all species of bats is 57°N to 43°S and is represented by vertical bar b ; whereas that of marsupials is 26°N to 41°S and is represented by vertical bar d .

quantitative measure of the degree to which actual species richness gradients are a product of random processes or are indistinguishable from patterns generated by stochastic mechanisms.

The latitudinal extent of the landmass used in our analyses is based upon the assumption that expansive bodies of water (e.g., oceans) represent inhospitable habitats (i.e., hard boundaries, sensu Pielou [1977] and Colwell and Hurtt [1994]) for occupation by bats or marsupials. Nonetheless, a variety of other geographic, historical, or ecological attributes of a landmass might limit the distribution of each fauna. A more realistic delineation of hospitable areas for each taxon can be determined empirically from the actual distributional limits of the Chiroptera or Marsupialia. As such, we assessed the efficacy of the simulation model to predict species richness gradients in three fashions. The first is based upon the latitudinal extents of North and South America. The second is based upon the actual distributional limits of the higher taxon in question (i.e., the range of bats [a in Fig. 1] or marsupials [c in Fig. 1]). The third is based upon limits imposed by the smallest latitudinal range which includes 95% of all species in

the higher taxon (b in Fig. 1 for bats; d in Fig. 1 for marsupials). The third approach recognizes that the latitudinal boundaries of a higher taxon are dynamic, expanding and contracting as species expand their geographic range or become locally extinct. Moreover, the latitudinal extent of an entire fauna can be strongly influenced by one or a few species (e.g., *Didelphis virginiana* for the Marsupialia), the third domain minimizes this effect.

The proportion of variation in species richness explained by the stochastic model for marsupials differed greatly, depending upon the latitudinal domain used to delimit distributional boundaries (continental limits, $r^2 = 0.35$; marsupial distributional limits, $r^2 = 0.69$; 95% distributional limits, $r^2 = 0.94$). In contrast, the proportion of variation in species richness explained by the stochastic model for bats differed little with latitudinal domain (continental limits, $r^2 = 0.67$; bat distributional limits, $r^2 = 0.71$; 95% distributional limits, $r^2 = 0.77$). Nonetheless, in all cases, the variation in species richness explained by the stochastic model was significant ($P < 0.05$). Others (Pielou [1977] for benthic marine algae along the Atlantic coast of the New

World; Hughes et al. [1996] for eucalypt species in Australia; Blackburn and Gaston [1996] for New World birds) examining patterns of species richness in entire landmasses have found peaks near latitudinal mid-points as well. Especially noteworthy is the modal pattern of species richness for eucalypts in Australia; the mid-continental peak (30 and 35 degrees S latitude) is not tropical!

Random subsets

If the essence of the latitudinal gradient in species richness is a consequence of stochastic phenomena, then the predictions of the model should hold for any latitudinal subset of a landmass, as long as only species wholly contained within those latitudinal bounds are considered in the analysis. In an incisive manner, this distinguishes the prediction of the stochastic model from those of all other competing hypotheses that suggest that species richness attains a tropical maximum *per se*, rather than a maximum located at the middle of latitudinal boundaries. To test this notion, we randomly generated 20 pairs of northern and southern latitudinal limits for bats and marsupials separately. For both taxa, the simulated latitudinal limits were constrained in two fashions: (1) the limits must span at least 20 degrees of latitude, and (2) the limits must include at least 20 species whose distributions are wholly contained therein. For marsupials, the stochastic model significantly explained variation in species richness for 19 of the 20 simulated boundaries (average r , 0.73; standard error of r , 0.05). Similarly for bats, the stochastic model significantly explained variation in species richness for 20 of the 20 simulated boundaries (average r , 0.77; standard error of r , 0.03).

Deviations from model predictions

Clearly, detection of a latitudinal gradient is enhanced by the degree to which the distributional limits of species in a taxon are affected by stochastic processes. To some extent, the absence of habitable land beyond continental boundaries contributes to this phenomenon. Biogeographic studies in the New World that attribute biological causation to latitudinal gradients of species richness based on a non-random hypothesis must show that the observed gradient is different from that produced by chance alone. If biological processes were to favor tropical diversity, *per se*, then stochastic processes could alter the form or countermand the presence of tropical maxima in species richness on continents in which the tropics is *not* located in the central portion of the land mass.

Like any null hypothesis, our stochastic model provides a foundation for assessing the degree to which deterministic factors modify the form of species richness gradients. Systematic deviations between predicted and observed richness should stimulate formation of hypotheses that describe the observed differences rather than the observed gradient, *per se*. For example, much of the variation in species richness of marsupials and bats in the New World is explained by the stochastic model, yet systematic departures from the predictions exist that are taxon-specific (compare Figs 2 and 3). The stochastic model consistently overestimates species richness at all latitudes for marsupials, whereas tropical richness is underestimated and non-tropical richness overestimated by the model for bats. This suggests that unique evolutionary histories or physiological constraints of marsupials and bats, or any of the other biogeographic models (Pianka 1966, Stehli et al. 1969, Huston 1979, Terborgh 1985, Stevens 1989, Rohde 1992) could interact to modify the general pattern produced by stochastic mechanisms.

Nonrandom factors such as the shape of continents (i.e., the area of latitudinal bands) could affect the marked deviations between observed and expected patterns of species richness. Indeed, a positive relation between species richness and area is a fundamental principle in geographic ecology that has persisted for over 120 years (Rosenzweig 1995, Goetelli and Greaves 1996) and has been deemed "one of ecology's few genuine laws" (Schoener 1974). We evaluated the degree to which deviations from the null model were a consequence of variation in area by saving the differences between observed and expected values (residuals), and measuring the degree to which they are related to variation in the area of latitudinal bands. In all cases, less than 15% of the variation in the magnitude of residuals was due to variation in area. Other biotic or abiotic factors that differ in a quantitative fashion with latitude should be assessed via similar approaches.

Ramifications

Patterns in species richness are not restricted to latitude. For example, they have been well documented with respect to elevation (Whittaker 1956, 1960, 1977, Dressler 1981), depth (Vinogradova 1962), and disturbance (Horn 1975, Connell 1978, Tilman 1982). If the domain over which taxa are distributed is bounded, and if constituent species have continuous distributions in the ecological space of the domain, then the stochastic model may contribute to empirical patterns in species richness. As such, maxima in species richness should occur at the center of elevational gradients and depth gradients; at least for some taxa, this is true (Whittaker 1960, 1977, Vinogradova 1962, Horn 1975, Dressler

1981). By the same reasoning, species richness should be greatest at intermediate levels of disturbance, and this has become increasingly well documented (Horn 1975, Connell 1978, Tilman 1982). Hence, the stochastic model may have far reaching applications beyond those of a biogeographic nature.

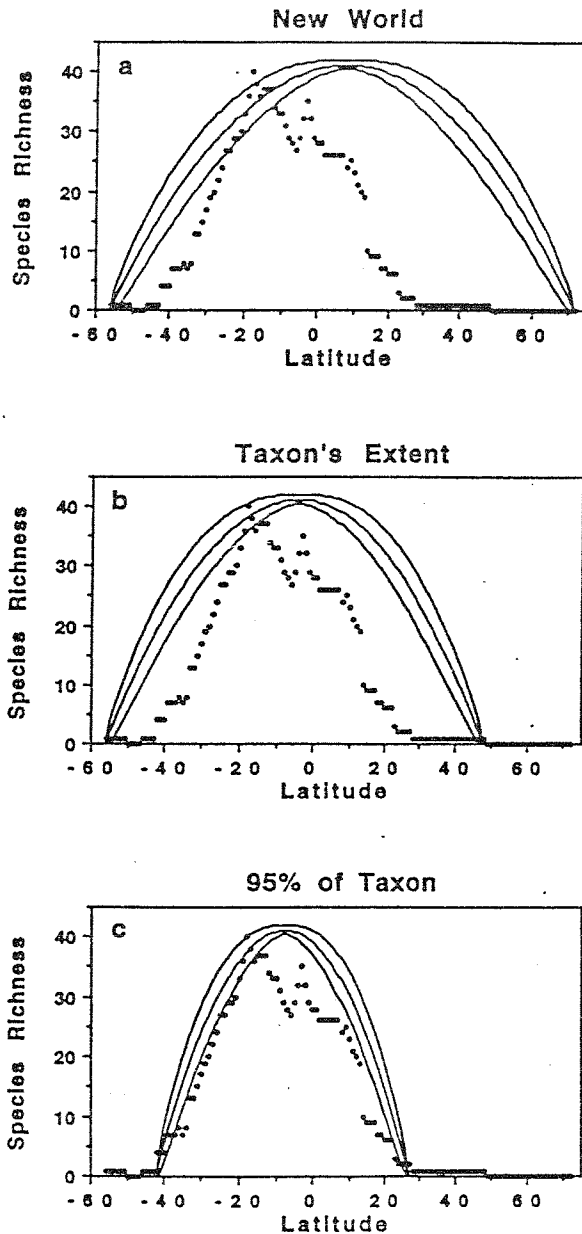


Fig. 2. Comparison of actual species richness gradients for marsupials (solid circles) and those predicted by the stochastic model (inner curve represents actual predictions, outer lines define the 95% confidence bands) for three different latitudinal domains: a, continental New World; b, the distributional limits of all marsupials; c, the smallest distribution within which 95% of all species occurs.

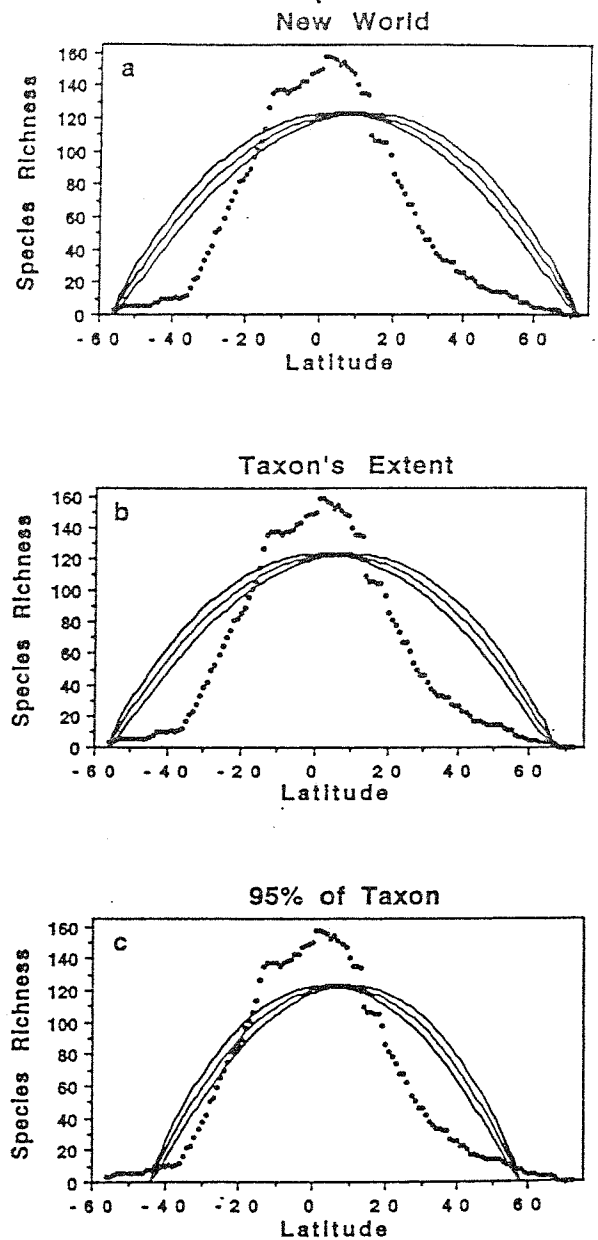


Fig. 3. Comparison of actual species richness gradients for bats (solid circles) and those predicted by the stochastic model (inner curve represents actual predictions, outer lines define the 95% confidence bands) for three different latitudinal domains: a, continental New World; b, the distributional limits of all marsupials; c, the smallest distribution within which 95% of all species occurs.

Acknowledgements - Many contributed to the gestation of ideas represented in this paper. In particular, we thank W. Madison and N. Slade for critical suggestions concerning the model development and evaluation, as well as L. J. Held, T. E. Lacher, Jr., M. A. Mares, M. A. McGinley, D. L. Moorhead, M. L. Rosenzweig, J. Wiens, and M. K. Rylander. We are grateful to B. T. A. Croyle and R. D. Stevens for assistance with data compilation. S. K. Lyons was supported in part by a grant from the Graduate School of Texas Tech University. M. R. Willig was supported by grant BSR-8811902 from the

National Science Foundation to the Terrestrial Ecology Division, University of Puerto Rico, and the International Institute of Tropical Forestry as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest. Additional support was provided by grant number 821671010 from the Environmental Protection Agency and Texas Tech University. Finally, we acknowledge the intellectual stimulation provided by interactions with participants at a workshop entitled "Analysis of Relationships Between Productivity and Diversity Using Experimental Results from the Long-Term Ecological Research Network" sponsored by the National Center for Ecological Analysis and Synthesis.

References

- Blackburn, T. M. and Gaston, K. J. 1996. Spatial patterns in the species richness of birds in the New World. - *Ecography* 19: 369-376.
- Brown, J. H. 1988. Species diversity. - In: Myers, A. and Giller, P. S. (eds), *Analytical biogeography*. Chapman and Hall, London, pp 57-89.
- and Gibson, A. C. 1983. *Biogeography*. - Mosby, St. Louis, MO.
- Colwell, R. K. and Hurtt, G. C. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. - *Am. Nat.* 144: 570-595.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. - *Science* 199: 1302-1310.
- Dressler, R. L. 1981. *The orchids: natural history and classification*. - Harvard Univ. Press, Cambridge, MA.
- Eisenberg, J. F. 1989. *Mammals of the Neotropics: the northern Neotropics*. Vol. 1. Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana. - Univ. of Chicago Press, Chicago.
- Fleming, T. 1973. Numbers of mammal species in North and Central American forest communities. - *Ecology* 54: 555-563.
- Goetelli, N. J. and Graves, G. R. 1996. Null models in ecology. - Smithsonian Inst. Press, Washington, DC.
- Horn, H. S. 1975. Markovian processes of forest succession. - In: Cody, M. L. and Diamond, J. M. (eds), *Ecology and evolution of communities*. Belknap Press of Univ. of Harvard Press, Cambridge, MA, pp. 196-213.
- Hughes, L., Cawsey, E. M. and Westoby, M. 1996. Geographic and climatic range sizes of Australian eucalypts and a test of Rapoport's rule. - *Global Ecol. Biogeogr. News Lett.* 5: 128-142.
- Huston, M. 1979. A general hypothesis of species diversity. - *Am. Nat.* 113: 81-101.
- Janzen, D. H. 1981. The peak in American ichneumonid species richness lies between 38 degrees and 42 degrees north. - *Ecology* 62: 532-537.
- Kaufman, D. M. 1994. Diversity of New World mammals: universality of the latitudinal gradient of species and bauplans. - *J. Mammal.* 76: 322-334.
- Koopman, K. F. 1982. Biogeography of bats of South America. - In: Mares, M. A. and Genoways, H. H. (eds), *Mammalian biology in South America*. Spec. Publ. Ser. 6, Pymatuning Laboratory of Ecology, Univ. of Pittsburgh, pp. 273-302.
- Lacher, Jr., T. E. and Mares, M. A. 1986. The structure of neotropical mammal communities: an appraisal of current knowledge. - *Rev. Chil. Hist. Nat.* 2: 121-134.
- Lyons, S. K. and Willig, M. R. 1997. Latitudinal patterns of range size: methodological concerns and empirical evaluations for New World bats and marsupials. - *Oikos* 80: 292-304.
- Nei, M. 1975. *Molecular population genetics and evolution*. - North-Holland, Amsterdam, The Netherlands.
- and Roychoudhury, A. K. 1974. Sampling variances of heterozygosity and genetic distance. - *Genetics* 76: 379-390.
- Owen, D. F. and Owen, J. 1974. Species diversity in temperate and tropical Ichneumonidae. - *Nature* 249: 583-584.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. - *Am. Nat.* 100: 33-46.
- Pielou, E. C. 1977. The latitudinal spans of seaweed species and their patterns of overlap. - *J. Biogeogr.* 4: 299-311.
- Platt, J. R. 1964. Strong inference. - *Science* 146: 347-352.
- Rathke, B. J. and Price, P. W. 1976. Anomalous diversity of tropical ichneumonid parasitoids: a predation hypothesis. - *Am. Natur.* 110: 889-893.
- Rex, M. A., Stuart, C. T., Hessler, R. R., Allen, J. A., Sanders, H. L. and Wilson, G. D. F. 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. - *Nature* 365: 636-639.
- Ricklefs, R. E. 1979. *Ecology*. - Chiron Press, Concord, MA.
- Rohde, K. 1978. Latitudinal gradients in species diversity and their causes. I. A review of the hypotheses explaining the gradients. - *Biol. Zbl.* 97: 393-403.
- 1992. Latitudinal gradients in species diversity: the search for the primary cause. - *Oikos* 65: 514-527.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. - Cambridge Univ. Press, Cambridge.
- Schall, J. J. and Pianka, E. R. 1978. Geographical trends in numbers of species. - *Science* 201: 679-686.
- Schoener, T. W. 1974. The species-area relationship within archipelagos: models and evidence from island land birds. - In: Firth, H. J. and Calaby, J. H. (eds), *Proceedings of the 16th International Ornithological Congress*, Australian Academy of Science, Canberra, pp. 629-642.
- Stehli, F. G., Douglas, D. G. and Newell, N. D. 1969. Generation and maintenance of gradients of taxonomic diversity. - *Science* 164: 947-949.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. - *Am. Nat.* 133: 240-256.
- Streilein, K. E. 1982. Behavior, ecology and distribution of South American marsupials. - In: Mares, M. A. and Genoways, H. H. (eds), *Mammalian biology in South America*. Spec. Publ. Ser. 6, Pymatuning Laboratory of Ecology, Univ. of Pittsburgh, pp. 231-250.
- Terborgh, J. 1985. The vertical component of plant species diversity in temperate and tropical forests. - *Am. Nat.* 126: 760-776.
- Tilman, D. 1982. Resource competition and community structure. - Princeton Univ. Press, Princeton, NJ.
- Vinogradova, N. G. 1962. Vertical zonation in the distribution of deep-sea benthic fauna in the ocean. - *Deep-Sea Res.* 8: 245-250.
- Wallace, A. R. 1878. *Tropical nature and other essays*. - Macmillan, London.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. - *Ecol. Monogr.* 22: 1-44.
- 1960. Vegetation of the Siskiyou Mountains, Oregon and California. - *Ecol. Monogr.* 30: 279-338.
- 1977. Evolution of species in land communities. - *Evol. Biol.* 10: 1-67.
- Willig, M. R. and Selcer, K. W. 1989. Bat species density gradients in the New World: a statistical assessment. - *J. Biogeogr.* 16: 189-195.
- and Sandlin, E. A. 1991. Gradients of species density and turnover in New World bats: a comparison of quadrat and band methodologies. - In: Mares, M. A. and Schmidly, D. J. (eds), *Latin American mammals: their conservation, ecology and evolution*. University of Oklahoma Press, Norman, pp. 81-96.
- and Gannon, M. R. 1997. Gradients of species density and turnover in marsupials: a hemispheric perspective. - *J. Mammal.* 78: 756-765.