

The Latitudinal Gradient of Diversity: Synthesis of Pattern and Process

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Summary

The latitudinal gradient of species diversity is a nearly universal pattern (Brown 1995) and latitude has been said to have the "boldest signature" with respect to the spatial distribution of biodiversity (Lewin 1989, Gaston 1996). In fact, the inverse relationship between species richness and latitude is known from a diverse set of taxa, including vertebrates (mammals--Simpson 1964, Kaufman and Willig *in press*; birds--Cook 1969, Blackburn and Gaston 1996; herptiles--Kiestler 1971, Rosenzweig 1995; fish--Macpherson and Duarte 1994, Oberdorff et al. 1995), non-vertebrate chordates (tunicates--Fischer 1960), invertebrates (ants--Brenner and Ruggiero 1994, papilionid butterflies--Scriber 1973, termites--Collins 1989, crayfish--France 1992, amphipods--France 1992, gastropods--Rex et al. 1993, coral--Fischer 1960), protozoans (fossil foraminiferans--Stehli et al. 1969) and plants (columnar cacti--Mourelle and Ezcurra 1997, fossil angiosperms--Crane and Lidgard 1989, trees--Currie and Paquin 1987, orchids--Dressler 1981). Although many studies appear each year on this topic, progress to ascertain a convincing general underlying mechanism has been stymied. The current ecological approach to research on the latitudinal gradient suffers from a lack of rigor and creativity in the examination of the pattern and in the quest for the process (detailed below). In addition, progress should be enhanced by capitalizing on new technologies to handle large datasets and perform comparative research across taxa to search for generalities.

Problem Statement

Although the latitudinal gradient of species diversity is pervasive, 30 years of intensive research has yielded no general explanation for the pattern. I propose to address four problems that I see in current approaches to research on the latitudinal gradient. The first two issues relate to the pattern itself: shape and components. First, the latitudinal gradient usually is characterized only as a simple relationship between species richness and latitude; little attention is paid to the mathematical form of the relationship. Second, the latitudinal gradient is typically characterized simply as a pattern of species richness; there is little exploration of other related latitudinal patterns. One exception is Rapoport's rule, the positive

relationship between geographic range size and latitude (Stevens 1989), although this relationship has been challenged of late (e.g., Gaston et al. *in press*). The final two issues relate to the elucidation of the causal process itself: generality and testability. Third, the simplest starting point is the idea that the ubiquity of the latitudinal pattern of diversity is due to a common mechanism. However, many of the hypothesized explanations apply only to a restricted set of places, times, or taxa. Fourth, current hypotheses (see Rohde 1992) predict only the inverse relationship between species richness and latitude that is already known to exist; predictions unique to a hypothesis or set of hypotheses must be devised and tested to narrow the possible field of causal mechanisms. With recent advances in geographic information systems, it is possible to address these issues in a quantitatively rigorous manner, including development of theoretical models and evaluation via empirical tests.

Description of the Latitudinal Pattern: I propose to compile data on the distributions of a number of taxa to be incorporated into a GIS for use in spatially explicit analyses. I have compiled distributions for all mainland New World mammals (~1500 species) that are ready to be digitized into GIS. In addition, other organismal datasets are available for examination (e.g., North American Breeding Bird Survey, Cogger 1994, Turner et al. 1995). Rigorous quantitative analyses of various vertebrate, invertebrate, and plant groups will provide a comprehensive examination of the pattern and allow me to look for generalities (such as the mathematical form or the existence of corollary patterns such as Rapoport's rule). Specific questions include the following, to be addressed for each individual taxonomic group and compared amongst groups to reveal any general phenomena.

What is the form of the relationship between species richness and latitude? Is there a single linear gradient, a different relationship within and outside the tropics, or no gradient at all?

Do significant latitudinal patterns occur consistently across all levels of diversity (alpha--local richness, beta--species turnover, gamma--regional richness)?

Are there significant latitudinal patterns in variables other than species richness, such as geographic range (Rapoport's rule), numerical dominance in communities, or smoothness of range edges?

Are there differences in patterns between animals and plants, endotherms and ectotherms, marine and terrestrial organisms, flying and nonvolant animals?

Evaluation of Possible Underlying Processes: It is difficult to determine the ecologically significant effects of "latitude" and this is the crux of the problem in discerning the causes for the latitudinal diversity gradient. Too many times latitude is dismissed as not being a real variable. Remember that, although latitudinal parallels are a human construct, they do reflect physical features of geography. Latitude characterizes the rotation of the earth on its axis, the tilt of the earth

relative to the sun, and the input of solar energy. (Only areas between the Tropics of Cancer and Capricorn--the tropics--ever receive solar radiation which falls perpendicularly on the earth; this produces the most intensive heating of the earth's surface. Within the Arctic or Antarctic Circle, sunlight is delivered at a low angle and heating is minimal.) So, is latitude primarily a variable that quantifies input of solar radiation to the earth's surface? Or, is it a more complex variable that encapsulates global patterns of temperature, precipitation, and productivity? Does it incorporate a multiplicity of interacting factors that would not be as meaningful if considered individually? To address these issues, solar input will be modeled in a realistic manner across geographic space, incorporating digital elevation models, cloud cover patterns, etc. This will enable me to examine the relationship between latitude and the input of solar radiation or other environmental variables to see how these variables relate to species patterns and if they quantitatively capture latitude through statistical explanation of organismal patterns.

Use of GIS will allow me to analyze environmental data (such as temperature, precipitation, productivity, etc.) in a spatially and geographically explicit context in order to characterize the environmental template on which species distributions are overlain. There are practical and conceptual questions about how species are affected by their environment. For example, what environmental conditions are most important to the organism (likely to be taxon-specific): mean conditions, general variability, extremes, or threshold conditions? What metrics best encapsulate the ecological influences of the environment? To assess the direct importance of the abiotic factors, I will evaluate taxonomic groups to see if richness patterns have tight and consistent links to specific environmental variables. In addition, I would like to assess how biotic interactions among species may affect species richness and may be related to latitude. Measuring biotic interactions is difficult and we have little information how they vary over geographic space. One possibility for measuring interaction involves parasitism. I currently am attempting to obtain data on the relationship between latitude and the number of parasite species within single host species. The discovery of an inverse relationship would supply a biotic mechanism by which species packing, and thus the number of species, is increased in the tropics.

Further, research such as Connell's (1961) intertidal study of the interaction between abiotic and biotic effects on species distribution establish what might be a parallel to the latitudinal gradient (Brown et al. 1996). To test this possibility, I will evaluate an abiotic-biotic hypothesis that invokes a combination of abiotic and species-interaction mechanisms as causes for the latitudinal pattern. Briefly, Kaufman (1995) proposed that abiotic factors are most limiting at high latitudes and decrease in importance toward the tropics, whereas biotic interactions are most limiting in the tropics and decrease in importance as abiotic factors become limiting. Abiotic factors limit the number of

species directly through increased physiological stress and indirectly through decreased productivity. In contrast, biotic interactions, within constraints set by productivity, limit the local abundance (or dominance in the community) and distribution of species, and thus provide opportunities for more species to coexist. Further, abiotic and biotic factors affect the distributions of individual species, with abiotic conditions tending to set the high-latitude range boundary, whereas biotic interactions set the low-latitude range boundary. This abiotic-biotic mechanism predicts several other phenomena to vary in concert with latitude: species' range size (positive; Rapoport's rule), level of dominance of the most common species (positive), and range characteristics such as the variability of the edge (negative).

Development of Theory and Conceptual Approaches: To address the questions elaborated above, I will develop new statistical approaches or incorporate those of others presently being developed. The current body of statistics does not deal with many aspects of testing for pattern in large-scale statistical distributions. Many ecological questions are not properly addressed by regression and correlation (which are appropriate for a single controlling factor) but require statistics sensitive to multiple interacting variables, each of which may be necessary but not sufficient or limiting but not controlling. For such research, it is important to establish rigorously any breakpoints or boundaries for distributions of points (Blackburn et al. 1992, Thomson et al. 1996). In addition, geostatistics provides techniques for analysis of spatial patterns and dynamics, and is ripe for application to ecology (Rossi et al. 1992, Liebhold et al. 1993, Villard and Maurer 1996). Randomization techniques also can provide a powerful tool to distinguish between deterministic patterns and random (null) distributions.

Rationale for NCEAS Support

This postdoctoral project combines theoretical modeling with empirical testing. In addition, the proposed work would help advance statistical methods for application to large-scale spatial ecology. Synthesis will occur both through quantitative analyses of latitudinal patterns for different taxa and empirical testing for a consistent link of environmental variables and theoretical mechanisms of proposed causes. The Center seeks to support novel approaches to address pertinent ecological issues; my project certainly falls under this objective. This research is data-intensive and requires the type of state-of-the-art GIS facilities that the Center provides. In addition, I foresee collaboration with those at the National Center for Geographic Information and Analysis. Finally, this research complements that of the "Ecological and Evolutionary Dynamics of Species' Borders" working group, as both research agendas require us to confront issues dealing with distributions and their edges, statistical and

modeling issues, and related spatial aspects in their application. As a postdoctoral associate, my performance as a member of the Species' Borders working group would be enhanced and vice versa.

Proposed Activities and Timetable

I propose to begin this postdoctoral research 1 September 1998, with a 2-year total duration for the project. The initial 6 months will be spent gathering relevant datasets and scanning or digitizing organismal distributions as well as coverages for relevant environmental data. The next year will be spent analyzing data, exploring statistical approaches, and following up on results. In part, my results will be my guide, as each question answered will certainly outline new questions. In this time period, I will write papers on results from taxa that merit address in and of themselves. During the final six months, I will draw together significant results (both positive and negative) to be published as synthetic papers addressing relevant issues of the latitudinal gradient.

Anticipated Results and Beneficiaries

Why are there so many organisms in the tropics? This fundamental question of diversity has been asked repeatedly. I seek to make substantial progress in this area of ecology by forging a deeper understanding of the dynamics which lead to the pattern of distributions of species and by advancing statistical methodology as applied to large-scale and spatial ecological questions. I foresee writing several synthetic papers from this project, in addition to presenting the results at such meetings as those of the Ecological Society of America. I hope that this work, and interactions that it will foster, will help to integrate such sciences as ecology, geography, environmental science, and conservation biology.

Literature Cited

- Blackburn, T. M., and K. J. Gaston. 1996. Spatial patterns in the species richness of birds in the New World. *Ecography* **19**:369-376.
- Blackburn, T. M., J. H. Lawton, and J. N. Perry. 1992. A method of estimating the slope of upper bounds of plots of body size and abundance in natural animal assemblages. *Oikos* **65**:107-112.
- Brener, A. G. F., and A. Ruggiero. 1994. Leaf-cutting ants (*Atta* and *Acromyrmex*) inhabiting Argentina: patterns in species richness and geographical range sizes. *Journal of Biogeography* **21**:391-399.
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago, Illinois, USA.

- Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* **27**:597-623.
- Cogger, H. G. 1994. *Reptiles and amphibians of Australia*. Cornell University Press, Ithaca, New York, USA.
- Collins, N. M. 1989. Termites. Pages 455-471 in H. Lieth and M. J. A. Werger, editors. *Tropical rain forest ecosystems: biogeographical and ecological studies*. Ecosystems of the World Volume 14B. Elsevier, Amsterdam, Netherlands.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42**:710-723.
- Cook, R. E. 1969. Variation in species density of North American birds. *Systematic Zoology* **18**:63-84.
- Crane, P. R., and S. Lidgard. 1989. Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. *Science* **246**:675-678.
- Currie, D. J., and V. Paquin. 1987. Large-scale biogeographical patterns of species richness of trees. *Nature* **329**:326-327.
- Dressler, R. L. 1981. *The orchids, natural history and classification*. Harvard University Press, Cambridge, Massachusetts, USA.
- Fischer, A. G. 1960. Latitudinal variations in organic diversity. *Evolution* **14**:64-81.
- France, R. 1992. The North America latitudinal gradient is species richness and geographical range of freshwater crayfish and amphipods. *American Naturalist* **139**:342-354.
- Gaston, K. J. 1996. Biodiversity: latitudinal gradients. *Progress in Physical Geography* **20**:466-476.
- Gaston, K. J., T. M. Blackburn, and J. I. Spicer *In press*. Rapoport's rule: time for an epitaph? *Trends in Ecology and Evolution*.
- Kaufman, D. M. 1995. Diversity of New World mammals: universality of the latitudinal gradients of species and bauplans. *Journal of Mammalogy* **76**:322-334.
- Kaufman, D. M., and M. R. Willig. *In press*. Latitudinal patterns of mammalian species richness in the New World: the effects of sampling method and faunal group. *Journal of Biogeography*.

- Kiester, A. R. 1971. Species density of North American amphibians and reptiles. *Systematic Zoology* **20**:127-137.
- Lewin, R. 1989. Biologists disagree over bold signature of nature. *Science* **244**:527-528.
- Liebhold, A. M., R. E. Rossi, and W. P. Kemp. 1993. Geostatistics and geographic information systems in applied insect ecology. *Annual Review of Entomology* **38**:303-327.
- Macpherson, E., and C. M. Duarte. 1994. Patterns in species richness, size, and latitudinal range of East Atlantic fishes. *Ecography* **17**:242-248.
- Mourelle, C., and E. Ezcurra. 1997. Rapoport's rule: a comparative analysis between South and North American columnar cacti. *American Naturalist* **150**:131-142.
- Oberdorff, T., J.-F. Guégan, and B. Huguény. 1995. Global scale patterns of fish species richness in rivers. *Ecography* **18**:345-352.
- Rex, M. A., C. T. Stuart, R. R. Hessler, J. A. Allen, H. L. Sanders, and G. D. F. Wilson. 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* **365**:636-639.
- Rohde, K. 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 University Press, Cambridge, UK.
- Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Monographs* **62**:277-314.
- Scriber, J. M. 1973. Latitudinal gradients in larval feeding specialization of the world Papilionidae (Lepidoptera). *Psyche* **80**:355-373.

- Simpson, G. G. 1964. Species density of North American Recent mammals. *Systematic Zoology* **13**:57-73.
- Stehli, F. G., R. G. Douglas, and N. D. Newell. 1969. Generation and maintenance of gradients in taxonomic diversity. *Science* **164**:947-949.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* **133**:240-256.
- Thomson, J. D., G. Weiblen, B. A. Thomson, S. Alfaro, and P. Legendre. 1996. Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology* **77**:1698-1715.
- Turner, R. M., J. E. Bowers, and T. L. Burgess. 1995. *Sonoran Desert plants: an ecological atlas*. University of Arizona Press, Tucson, Arizona, USA.
- Villard, M.-A., and B. A. Maurer. 1996. Geostatistics as a tool for examining hypothesized declines in migratory songbirds. *Ecology* **77**:59-68.

Proposal Keywords - please indicate keywords that apply to your proposal as instructed for each category below

1. Organizational Focus
(pick 1)

- Global
 Ecosystem
 Community
 Meta-population
 Population
 Organismal
 Cellular
 Molecular

2. Regional Focus
(pick all that apply)

- California
 United States
 Southwest
 Northwest
 Southcentral
 Northcentral
 Southeast
 Northeast
 Africa
 Antarctic
 Arctic
 Asia
 Australia/NZ
 Canada
 Central America
 Europe
 South America
 Global

3. Ecological Theme
(rank up to 3)

- amensalism
 biodiversity
 biogeography
 commensalism
 community dynamics
 competition
 complex systems
 dispersal
 disturbance
 ecological economics
 evolution
 genetics
 global change
 methodological innovation
 microclimate
 mutualism
 nutrient cycling

4. Taxonomic Group
(pick all that apply)

- Plants
 Invertebrates
 insects
 other terr. inverts
 marine inverts
 aquatic inverts
 Vertebrates
 mammals
 birds
 reptiles/amphibians
 fish
 Microbes
 Fungi

5. Methods
(pick all that apply)

- Statistical modeling
 Numerical Analysis
 Simulation model
 Visualization
 Meta-analysis
 Classification and Mapping
 Other GIS, geostatistics

6. Research Application
(rank up to 3)

- acid rain
 agriculture
 aquaculture
 coastal resources
 conservation
 ecosystem management
 energy
 environmental policy
 fisheries
 forestry
 global warming
 human population
 land management
 ozone
 pollution
 reserve siting/design
 restoration
 toxicology
 Other _____

7. Biomes
(pick all that apply)

- paleoecology
- plant-animal interactions
- population dynamics
- predator-prey interactions
- primary production
- soil processes
- succession
- parasitism
- symbiosis
- Other _____

-
- Marine
 - Benthic
 - Pelagic
 - Intertidal
 - Terrestrial
 - Forest
 - Grassland
 - Desert
 - Wetlands