

ORIGINS AND MAINTENANCE OF TROPICAL BIODIVERSITY

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Keywords: arctic zone, biodiversity patterns, biogeography, geographical, latitudinal diversity gradient, macroecology, plant diversity, polar zone, species diversity, species richness, temperate zone, tropics.

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Summary

The increase in biological diversity of some groups from the poles toward the equator is one of the most fundamental patterns of life on earth. Currently more than 30 different mechanisms and factors have been proposed and debated to explain the latitudinal gradient in species diversity. Although known for about two centuries, this pattern still lacks a general consensus, which makes it probably as one of the great modern challenges of macroecology. Here, we present 15 several hypotheses that have been proposed to explain why the tropics harbor more species than temperate habitats.

1. Introduction

The increase in biological diversity of some groups from the poles toward the equator is one of the most fundamental patterns of life on earth. This gradient pattern, often referred to as the latitudinal gradient in species diversity, was initially documented by Alexander von Humboldt in 1807, when he stated: “*The nearer we approach the tropics, the greater the increase in the variety of structure, grace of form, and mixture of colors, as also in perpetual youth and vigor of organic life*”. Ever since the first hypothesis, the number of explanatory hypotheses for why this gradient exists, has increased, and currently more than 30 different mechanisms and factors have been proposed and debated to explain it. Although known for about two centuries, this pattern still lacks a general consensus, which makes it probably as one of the great modern challenges of macroecology. In general the pattern predicts that when moving from high to low latitudes the average species richness increases, this pattern has been well documented for a wide spectrum of taxonomic groups (e.g., mammals, fishes, insects, and plants). However, there are notable exceptions to this general pattern of high biodiversity in the tropics. For example, neither wasps (Ichneumonidae: Hymenoptera), aquatic plants, ectoparasites in fish, birds, nor mammals seem to exhibit species richness in relation to decreasing latitudinal gradients. Thusly, the latitudinal gradient in species richness might be more complex than initially observed by Humboldt and others. Consequently, all hypotheses which attempt to explain this phenomena should be based on biotic, abiotic, historical, geographical, and biogeographic factors, environmental stability, habitat heterogeneity, productivity, stochastic forces, ecological and evolutionary time, species ranges, environmental gradients, interspecific interactions and many others mechanisms. Many of the current hypotheses, found in the literature, are not mutually exclusive, and others merely offer different levels of explanation. To account fully for a latitudinal gradient in species richness, in this chapter, we examine the ecological and evolutionary outcomes of the origins and maintenance of tropical biodiversity to try to understand “*why tropic regions have the highest biodiversity?*” We begin by summarizing the differences between tropic, temperate, and polar regions, and then turn to the pattern of biodiversity, “*why are there so many different kinds of organisms in the tropics?*” and finally to latitudinal gradients in species richness diversity and their hypotheses.

2. Tropics: Description, Climate and Ecosystems

The word “*tropic*” comes from the Greek word “*tropos*” meaning “*turning towards*”, depicting the oscillation of the sun between the two tropics. The tropics are geographic region of the Earth where the sun is centered on the equator and limited in latitude by the Tropic of Cancer in the northern hemisphere (23° 26' 22"N) and the Tropic of Capricorn in the southern hemisphere (23° 26' 22"S). Consequently, to the north and south of the tropics are located the temperate and arctic zones. The Earth has eight different climatic zones in the northern and southern hemispheres, like two polar zones, two boreal, two temperate, two subtropical and two tropical zones. Much of the Earth's global mean temperature variability originates in the tropics. Solar radiation is the primary factor that determines the Earth's climate. Because of the spherical shape of the Earth, with increasing latitude a reduction of solar radiation occurs, therefore, tropical regions around the equator receive the greatest amount of solar radiation during the solar year. This latitudinal difference in solar radiation results in higher temperature in

the tropics, especially near the equator, than it does in temperate and arctic zones. Consequently, many species show ecological and evolutionary adaptations because temperature variation is greater nearer to the poles than at the equator, and seasonal differences in temperature also occur in higher latitudes (i.e., spring, summer, fall, winter).

Tropical ecosystems exist in a large diversity of habitat types such as rainforests, dry forests, savannas, deserts and others. They also contain particularly high biodiversity, and especially high numbers of endemic species. In fact, tropical habitats represent an important component in all Earth's life diversity, because great part of the 34 biodiversity hotspots (areas of high numbers of endemic species) are tropical ecosystems.

3. Earth's Biodiversity

Biodiversity is defined as the variety of all forms of life, from genes to species, through to the broad scale of ecosystems. Biodiversity varies widely over the surface of the earth. Although an approximate estimate of species numbers on Earth cannot be given, some patterns are well established, such as the fact that the warmer tropics harbor many more species than colder environments. For most of the main groups of large organisms on earth, like plants and animals, the number of species increases markedly toward the equator. It is estimated that tropical forests contain more than half the species on Earth. The tropics represent a remarkable biodiversity, including plants, birds, insects like especially ants, beetles, butterflies and termites; amphibians, mammals, and other organism groups. Species richness is generally related to variations in the physical environment and many large-scale species richness in different groups of organism are often related geographically. One of the most striking differences between temperate and tropical forests is the number of plant species. To determine why tropic regions have the highest biodiversity constitutes an important and intriguing challenge for ecologists and biogeographers. For decades, scientists have conducted a large variety of studies of geographical and broad-scale patterns of biodiversity, seeking to explain and explore their implications. But the question still persists, "*Why are there more species in the tropics than in temperate regions?*" Recently this long-standing question has been addressed primarily by seeking environmental correlates of diversity. But to understand the causes of these diversity patterns, this question must be examined by evolutionary and biogeographic processes that directly change species numbers (i.e., speciation, extinction, and dispersal). The literature shows several examples of diversity factors affecting species distribution (e.g., Krebs 1994). Charles J. Krebs (1994) discussed that tropical-to-polar gradients in species richness may be produced by up to eight causal factors: history, spatial heterogeneity, competition, predation, climate, climatic variability, productivity, and disturbance, all of which can interact over evolutionary and ecological time.

4. Why are there so Many Different Kinds of Organisms in the Tropics?

The tropical regions are part of a larger pattern of increasing biodiversity with

decreasing latitude worldwide. This global biodiversity pattern holds for almost all groups of organisms on Earth, even shallow water, open sea and bottom-dwelling marine organisms follow this same trend. As stated previously, for a long time, biologists, ecologists and biogeographers have developed a large number of hypotheses to explain latitudinal diversity trends, these hypotheses including climate, available solar radiation, habitat variability, predation, pathogens, length of area, level of environmental disturbance, among others. One theory for high species richness in the Tropics is the “time hypothesis”. This theory proposes that tropical areas appeared earlier than colder environments on Earth. Thus, in tropical habitats, the biodiversity increases are a result of this longer time period. The Tropics also had a large time for the evolution of a greater variety of organisms and also to accumulate these new species. This “time hypothesis” is an old theory, which it was fully stated in 1878 by the English naturalist Alfred Russel Wallace, co-discoverer with Darwin of the theory of evolution by natural selection.

5. Latitudinal Gradients in Species Richness and Their Hypotheses

The latitudinal gradient of species diversity is one of the most striking and robust global patterns in biogeography on Earth. This pattern is one of the most and oldest primary trends concerning life's species on earth. It is evident that an increase in biological diversity occurs from the polar to equatorial regions. Specifically, in relation to the gradient in species richness, there is a negative relationship between number of species and latitude. This strong trend is seen in the great majority of taxonomic groups, such as: plants, birds, mammals, reptiles, amphibians, fishes, arthropods, fungi and many others organisms. However, there are few exceptions that occur inside of specific and small taxonomic groups. For instance, the diversity of birds shows the same latitudinal pattern, nevertheless, subgroups such as penguins do not. Recently, an evaluation of almost 600 studies documented this trend's remarkable consistency across space, scale, habitat and taxonomic group showing that species richness of most taxonomic taxa increases towards the equator and this trend is substantially stronger at regional than local scales. This trend is strongly related to northern and southern hemispheres, to marine and terrestrial groups, to active and passive dispersers, and to ectothermic and endothermic taxa.

Surprisingly though, after decades of study, a universally accepted explanation for the latitudinal diversity gradient remains elusive. Several hypotheses have been proposed but until now ecological ones have predominated over half a century. According to Charles J. Krebs (1994), there are three main groups of proposed hypotheses that contributed to the development of an overarching latitudinal diversity gradient hypothesis: (1) *Ecological hypotheses*. This group of hypotheses is centered on mechanisms of coexistence and maintenance of species diversity; (2) *Evolutionary hypotheses*. This group of hypotheses is centered on rates of diversification of species, and (3) *Historical hypotheses*. This group of hypotheses is centered on the duration and extent of environmental events in Earth's history. Recently, M. R. Willig and collaborating (2003) showed that there are over 30 quantitative and qualitative hypotheses concerning the latitudinal gradient of richness in which species richness should increase with decreasing latitude. Moreover, they argue that many of the mechanistic factors associated with different hypotheses are shared or correlated; as a

result, indirect tests can be problematic and controversial. Therefore, we present 15 several hypotheses that have been proposed to explain why the tropics harbor more species than temperate or arctic zones.

5.1. History Factor

According to this hypothesis, proposed by zoogeographers and paleontologists, species richness increases with an ecological or an evolutionary time scale. Then, the tropics diversify more rapidly than those in the temperate and polar regions because of stable and favorable environmental conditions, without climatic disasters like glacier slides and avalanches. Another factor is an uninterrupted length of time through which the species can develop, as the diversity increases with the time; the tropics consequently have more species than younger regions. Comparatively, the tropics display examples of mature biodiversity evolution, whereas temperate and polar regions are immature.

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Bibliography

Collin, P.H. (2004). Dictionary of environment & ecology. Fifth edition. Bloomsbury Publishing [A dictionary of environmental and ecological sciences]

Cotgreave, P. & Forseth, I. (2002). Introductory Ecology. The Blackwell. 288 pages [A textbook introducing students to the basic principles of ecological science]

Denslow, J.S. (1987). Tropical rainforest gaps and tree species diversity. *Annu. Rev. Ecol. Syst.* 18: 431-451 [A comprehensive review on plant species diversity in tropical rainforest]

Gaston, K.J. (2000). Global patterns in biodiversity. *Nature* 405: 220-27 [A comprehensive discussion on global patterns in biological species diversity]

Givnish, T.J. (1999). On the causes of gradients in tropical tree diversity. *Journal of Ecology* 87: 193-210 [A comprehensive discussion on several diversity hypotheses of woody species in tropical forests]

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American Naturalist* 163: 192-211 [A comprehensive discussion on the decline of biodiversity with latitude using nearly 600 latitudinal gradients assembled from the literature]

Krebs, C.J. (1994) *Ecology: The experimental analysis of distribution and abundance*. Fourth edition. Benjamin Cummings. 686 pages [A textbook introducing students to the basic principles of ecological science]

Krohne, D.T. (2000). *General Ecology*. Second edition. Wadsworth publishing Company, Belmont, CA. 512 pages [A textbook introducing students to the basic principles of ecological science]

Mittelbach, G.G.; Schemske, D.W.; Cornell, H.V.; Allen, A.P.; Brown, J.M.; Bush, M.B.; Harrison, S.P.; Hurlbert, A.H.; Knowlton, N.; Lessios, H.A.; McCain, C.M.; McCune, A.R.; McDade, L.A.; McPeck, M.A.; Near, T.J.; Price, T.D.; Ricklefs, R.E.; Roy, K.; Sax, D.F.; Schluter, D.; Sobel, J.M. & Turelli, M.

(2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* 10: 315-331 [A comprehensive review on two major hypotheses for the origin of the latitudinal diversity gradient]

Molino, J.F. & Sabatier, D. (2001). Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science* 294: 1702-1704 [This is a case study reporting on intermediate disturbance hypothesis in a tropical rain forests]

Ricklefs, R.E. (2001). *The Economy of Nature*. Fifth Edition. W.H. Freeman and Company. England [A textbook introducing students to the basic principles of ecological science]

Rohde, K. (1992). Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65: 514-527 [A comprehensive review on hypotheses that attempt to explain latitudinal gradients in species diversity]

Willig, M.R.; Kaufman, D.M. & Stevens, R.D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* 34: 273-309 [A comprehensive review on over 30 hypotheses advanced to account for the latitudinal gradient]

Biographical Sketches

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