

Latitudinal gradients in species diversity
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The pattern

The increase in species richness or biodiversity that occurs from the poles to the tropics, often referred to as the latitudinal gradient in species diversity, is one of the most widely recognized patterns in ecology. Put another way, localities at lower latitudes generally have more species than localities at higher latitudes. Explaining the latitudinal diversity gradient is one of the great contemporary challenges of macroecology (Willig et al. 2003, Pimm and Brown 2004, Cardillo et al. 2005). The question “What determines patterns of species diversity?” was among the 25 key research themes for the future identified in 125th Anniversary issue of *Science* (July 2005). There is a lack of consensus among ecologists about the mechanisms underlying the pattern, and many hypotheses have been proposed and debated.

Importance of pattern

Understanding the global distribution of biodiversity is one of the most significant objectives for ecologists and biogeographers. Beyond purely scientific goals and satisfying curiosity, this understanding is essential for applied issues of major concern to humankind, such as the spread of invasive species, the control of diseases and their vectors, and the likely effects of global climate change on the maintenance of biodiversity (Gaston 2000). Tropical areas play a prominent role in the understanding of the distribution of biodiversity, as their rates of habitat degradation and biodiversity loss are exceptionally high.

Hypotheses for pattern

Although many of the hypotheses exploring the latitudinal diversity gradient are closely related and interdependent, most of the major hypotheses can be split into four general categories: spatial/area, energy/climatic, evolutionary/historical, and biotic.

Spatial/Area hypotheses

There are two major hypotheses that depend solely on the spatial and areal characteristics of the tropics.

Mid-domain effect

Using computer simulations, Colwell and Hurtt (1994) and Willig and Lyons (1998) first pointed out that if species' latitudinal ranges were randomly shuffled within the geometric constraints of a bounded biogeographical domain (e.g. the continents of the New World, for terrestrial species), species' ranges would tend to overlap more toward the center of the domain than towards its limits, forcing a mid-domain peak in species richness. Colwell and Lees (2000) called this stochastic phenomenon the mid-domain effect (MDE), presented several alternative analytical formulations for one-dimensional MDE (expanded by Connolly 2005), and suggested the hypothesis that MDE might contribute to the latitudinal gradient in species richness, together with other explanatory factors considered here, including climatic and historical ones. Because "pure" mid-domain models attempt to exclude any direct environmental or evolutionary influences on species richness, they have been claimed to be null models (Colwell et al. 2004, 2005). On this view, if latitudinal gradients of species richness were determined solely by MDE, observed richness patterns at the biogeographic level would not be distinguishable from patterns produced by random placement of observed ranges (Colwell and Lees 2000). Others object that MDE models so far fail to

exclude the role of environment at the population level and in setting domain boundaries, and therefore cannot be considered null models (Hawkins and Diniz-Filho 2002; Hawkins et al. 2005; Zapata et al. 2003, 2005). Mid-domain effects have proven controversial (e.g. Jetz and Rahbek 2001, Koleff and Gaston 2001, Lees and Colwell, 2007, Romdal et al. 2005, Rahbek et al. 2007, Storch et al. 2006; Bokma and Monkkonen 2001, Diniz-Filho et al. 2002, Hawkins and Diniz-Filho 2002, Kerr et al. 2006, Currie and Kerr, 2007). While some studies have found evidence of a potential role for MDE in latitudinal gradients of species richness, particularly for wide-ranging species (e.g. Jetz and Rahbek 2001, Koleff and Gaston 2001, Lees and Colwell, 2007, Romdal et al. 2005, Rahbek et al. 2007, Storch et al. 2006; Dunn et al. 2007) others report little correspondence between predicted and observed latitudinal diversity patterns (Bokma and Monkkonen 2001, Currie and Kerr, 2007, Diniz-Filho et al. 2002, Hawkins and Diniz-Filho 2002, Kerr et al. 2006).

Geographical area hypothesis

Another spatial hypothesis is the geographical area hypothesis (Terborgh 1973). It asserts that the tropics are the largest biome and that large tropical areas can support more species. More area in the tropics allows species to have larger ranges, and consequently larger population sizes. Thus, species with larger ranges are likely to have lower extinction rates (Rosenzweig 2003). Additionally, species with larger ranges may be more likely to undergo allopatric speciation, which would increase rates of speciation (Rosenzweig 2003). The combination of lower extinction rates and high rates of speciation leads to the high levels of species richness in the tropics.

A critique of the geographical area hypothesis is that even if the tropics is the most extensive of the biomes, successive biomes north of the tropics all have about the same area. Thus, if the geographical area hypothesis is correct these regions should all have approximately the same species richness, which is not true, as is referenced by the fact that polar regions fewer species than temperate regions (Gaston and Blackburn 2000). To explain this, (Rosenzweig 1992) suggested that if species with partly tropical distributions were excluded, the richness gradient north of the tropics should disappear. Blackburn and Gaston 1997 tested the effect of removing tropical species on latitudinal patterns in avian species richness in the New World and found there is indeed a relationship between the land area and the species richness of a biome once predominantly tropical species are excluded. Perhaps a more serious flaw in this hypothesis is some biogeographers suggest that the terrestrial tropics are not, in fact, the largest biome, and thus this hypothesis is not a valid explanation for the latitudinal species diversity gradient (Rohde 1997, Hawkins and Porter 2001). In any event, it would be difficult to defend the tropics as a "biome" rather than the geographically diverse and disjunct regions that they truly include.

Energy/Climate hypotheses

Climate is the most often cited explanation of the latitudinal species diversity gradient. Because of the tilt of the earth on its axis, the tropics receive direct solar energy for a greater proportion of the year compared to higher latitudes (temperate and polar zones). Thus, lower latitudes generally have warmer temperatures and less seasonality than higher latitudes.

Species-energy hypothesis

The species energy hypothesis suggests the amount of available energy sets limits to the richness of the system. Thus, increased solar energy (with an abundance of water) at low latitudes causes increased net primary productivity (or photosynthesis). This hypothesis proposes the higher the net primary productivity

the more individuals can be supported and the more individuals the more species there will be in an area. Put another way, this hypothesis suggests that extinction rates are reduced towards the equator as a result of the higher populations sustainable by the greater amount of available energy in the tropics. Lower extinction rates lead to more species in the tropics.

One critique of this hypothesis has been that increased species richness over broad spatial scales is not necessarily linked to increased number of individuals, which in turn is not necessarily related to increased productivity (Cardillo et al. 2005). Additionally, the observed changes in the number of individuals in an area with latitude or productivity are either too small (or in the wrong direction) to account for the observed changes in species richness (Cardillo et al. 2005). The potential mechanisms underlying the species-energy hypothesis, their unique predictions and empirical support have been assessed in a major review by Currie et al. (2004).

Climate harshness hypothesis

Another climate-related hypothesis is the climate harshness hypothesis, which states the latitudinal diversity gradient may exist simply because fewer species can physiologically tolerate conditions at higher latitudes than at low latitudes because higher latitudes are often colder and drier than tropical latitudes. Again, Cardillo et al. (2005) find fault with this hypothesis, stating that although it is clear that climatic tolerance can limit species distributions, it appears that species are often absent from areas whose climate they can tolerate.

Climate stability hypothesis

Similarly to the climate harshness hypothesis, climate stability is suggested to be the reason for the latitudinal diversity gradient. The mechanism for this hypothesis is that while a fluctuating environment may increase the extinction rate or preclude specialization, a constant environment can allow species to specialize on predictable resources, allowing them to have narrower niches and facilitating speciation. The fact that temperate regions are more variable both seasonally and over geological timescales (discussed in more detail below) suggests that temperate regions are thus expected to have less species diversity than the tropics.

Critiques for this hypothesis include the fact that there are many exceptions to the assumption that climate stability means higher species diversity. For example, low species diversity is known to occur often in stable environments such as tropical mountaintops. Additionally, many habitats with high species diversity do experience seasonal climates, including many tropical regions that have highly seasonal rainfall (Brown and Lomolino 1998).

Historical/Evolutionary hypotheses

There are three main hypotheses that are related to historical and evolutionary explanations for the increase of species diversity towards the equator.

The historical perturbation hypothesis

The historical perturbation hypothesis proposes the low species richness of higher latitudes is a consequence of an insufficient time period available for species to colonize or recolonize areas because of historical perturbations such as glaciation (Brown and Lomolino 1998, Gaston and Blackburn 2000). This

hypothesis suggests that diversity in the temperate regions have not yet reached equilibrium, and that the amount of species in temperate areas will continue to increase until saturated (Clarke and Crame 2003).

The evolutionary rate hypothesis

The evolutionary rate hypothesis argues higher evolutionary rates in the tropics have caused higher speciation rates and thus increased diversity at low latitudes (Cardillo et al. 2005). Higher evolutionary rates in the tropics have been attributed to higher ambient temperatures, higher mutation rates, shorter generation time and/or faster physiological processes. More research needs to be done to determine whether or not speciation rates actually are higher in the tropics. Understanding whether extinction rate varies with latitude will also be important to whether or not this hypothesis is supported.

The hypothesis of effective evolutionary time

This hypothesis assumes that diversity is determined by the evolutionary time under which ecosystems have existed under relatively unchanged conditions, and by evolutionary speed directly determined by effects of environmental energy (temperature) on mutation rates, generation times, and speed of selection (Rohde 1992). It differs from most other hypotheses in not postulating an upper limit to species richness set by various abiotic and biotic factors, i.e., it is a nonequilibrium hypothesis assuming a largely non-saturated niche space. It does accept that many other factors may play a role in causing latitudinal gradients in species richness as well. The hypothesis is supported by much recent evidence, in particular the study by Wright et al. (2006).

Biotic hypotheses

Biotic hypotheses claim ecological species interactions such as competition, predation, mutualism, and parasitism are stronger in the tropics and these interactions promote species coexistence and specialization of species, leading to greater speciation in the tropics. These hypotheses are problematic because they cannot be proximate cause of the latitudinal diversity gradient as they beg the question of why species interactions might be stronger in the tropics. An example of one such hypothesis is the greater intensity of predation and more specialized predators in the tropics has contributed to the increase of diversity in the tropics (Pianka 1966). This intense predation could reduce the importance of competition (see competitive exclusion) and permit greater niche overlap and promote higher richness of prey. However, as discussed above, even if predation is more intense in the tropics (which is not certain), as it cannot be the ultimate cause of species diversity in the tropics because it fails to explain what gives rise to the richness of the predators in the tropics.

Several recent studies have failed to observe consistent changes in ecological interactions with latitude (Lambers et al. 2002, Hillebrand 2004). These studies suggest the intensity of species interactions are not correlated with the change in species richness with latitude.

Synthesis and Conclusions

There are many other hypotheses related to the latitudinal diversity gradient, but the above hypotheses are a good overview of the major ones still cited today. It is important to note that many of these hypotheses are similar to and dependent on one another. For example, the evolutionary hypotheses are closely dependent on the historical climate characteristics of the tropics.

The generality of the latitudinal diversity gradient

Recently, Hillebrand (2004) performed an extensive meta-analysis of nearly 600 latitudinal gradients from published literature to determine the generality of the latitudinal diversity gradient across different organismal, habitat and regional characteristics. Hillebrand found the latitudinal gradient occurs in marine, terrestrial, and freshwater ecosystems, in both hemispheres. The gradient is steeper and more pronounced in richer taxa (i.e. taxa with more species), larger organisms, in marine and terrestrial versus freshwater ecosystems, and at regional versus local scales. The gradient steepness (the amount of change in species richness with latitude) is not influenced by dispersal, animal physiology (homeothermic or ectothermic) trophic level, hemisphere, or the latitudinal range of study. The study could not directly falsify or support any of the above hypotheses, however results do suggest a combination of energy/climate and area processes likely contribute to the latitudinal species gradient. Notable exceptions to the trend include the ichneumonidae, shorebirds, penguins, and freshwater zooplankton.

Conclusion

The fundamental macroecological question that the latitudinal diversity gradient depends on is ‘What causes patterns in species richness?’ Species richness ultimately depends on whatever proximate factors are found to affect processes of speciation, extinction, immigration, and emigration. While some ecologists continue to search for the ultimate primary mechanism that causes the latitudinal richness gradient, many ecologists suggest instead this ecological pattern is likely to be generated by several contributory mechanisms (Gaston and Blackburn 2000, Willig et al. 2003, Rahbek et. al 2007). For now the debate over the cause of the latitudinal diversity gradient will continue until a groundbreaking study provides conclusive evidence or there is general consensus that multiple factors contribute to the pattern.

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