

The latitudinal diversity gradient

Key concepts

- The latitudinal diversity gradient
- Mid-domain effect
- Niche conservatism and niche evolution
- Biotic theories

Introduction

We've already encountered several ideas aimed at explaining patterns of species richness. They cover a range of spatial scales, from the relatively small (e.g. the Janzen-Connell effect) to the relatively large (e.g. species-area relationships). One pattern at a very large scale has been debated for decades and refers to a latitudinal gradient. If we were to take a planetary transect from pole to pole, we would find that species richness tends to be greatest at low (equatorial) latitudes and tapers off towards the poles (Fig. 2). Hillebrand (2004) established that this was true regardless of hemisphere or taxonomic group. There are many theories offered to explain these observations, and the goal of this chapter is to explore and critique some of the leading candidates.

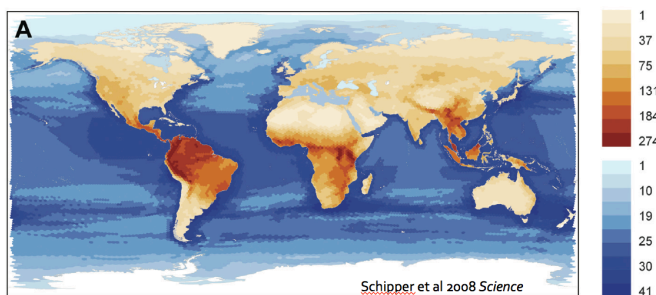


Figure 1: New World birds, including hummingbirds, exhibit higher species richness in tropical latitudes

Figure 2: Species richness for terrestrial and freshwater (brown) and marine (blue) mammals, from Schipper et al. 2008, Science.

The mid-domain effect

Continuous land masses such as Africa and the Americas occupy equatorial latitudes as well as regions in both the southern and northern hemispheres. Consider a domain represented as a line that is split into three equal zones (northern, central and southern). If species occupied random continuous latitudinal ranges (segments of that line) then we would expect to find approximately 55% of species in each of the northern and southern zones, and approximately 80% of species in the central zone, with many species in more than one zone (Fig. 3).

Simulation results based on this principle have led some ecologists to conclude that there doesn't need to be any important differences between temperate and tropical regions to account for a latitudinal species gradient, while others contend that mid-domain effects serve as useful null models against which to compare other explanations. Relying exclusively on this effect to explain patterns of species richness has been criticized for reasons including

- species and population ranges are not determined randomly
- the mid-domain effect fails to capture some empirical patterns of species richness
- evolutionary history (phylogeny is ignored)

For some sets of species, especially wide-ranging species, the mid-domain effect is consistent with patterns in data.

Historical or evolutionary hypotheses

Species-energy hypothesis

Tropical regions are often characterized as having plenty of sunlight and rain, with associated high primary productivity. Such ecosystems have the capacity to support a large number of individuals. Ecologists have argued that the large population sizes both increase the potential for speciation (Fig. 4, top panel) and lower the extinction rates leading to more species in the tropics. Bivalve data suggest that many more genera have gone extinct in non-tropical versus tropical regions (Jablonski et al., 2006), though in general it is methodologically challenging to ascertain extinction rates reliably. Evidence for higher diversification rates, measured in various taxonomic groups, is equivocal but certainly exhibited in some groups including New World birds (Fig. 5, Cardillo et al. 2005). However it is less clear that these species richness patterns over broad spatial scales are necessarily linked to population sizes and primary productivity.

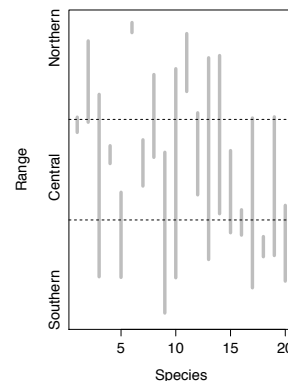


Figure 3: Randomly selected species ranges along a hypothetical southern-northern interval. By chance alone, species are expected to be observed in the central region more commonly.

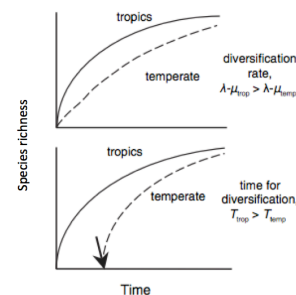


Figure 4: Over evolutionary time, tropical regions may have acquired a relatively high species richness due to a higher diversification rate (top panel) or by virtue of being an effectively older biome (bottom panel). Adapted from Mittelbach et al. 2007

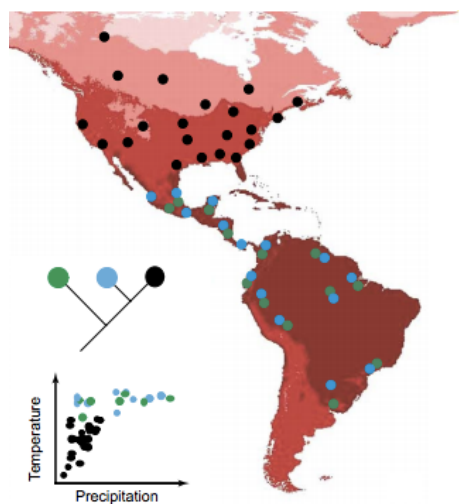
Metabolic hypothesis: Warmer temperatures can impact an organism's metabolic rate, and metabolic rates are positively associated with mutation rates. Consequently, scientists have argued that organisms in the tropics may have higher mutation rates, increasing the population-level genetic variance that natural selection can act on.

Specialization in predictable biomes

From geologic time scales to inter-annual periods, tropical biomes are more predictable than temperate biomes. Temperate regions have experienced several glaciation events and within a year, temperate regions exhibit dramatic seasonal changes. By contrast, the tropics are more predictable. This observation has led some ecologists to argue that tropical populations have had a longer time in which to specialize to their predictable environment (Fig. 4, bottom panel). In turn, focusing in on a narrow niche, can then facilitate speciation.

Scientists have argued that, at least in some ecological dimensions such as rainfall, the tropics can also represent a dynamically changing environment, interrupting the ability of species to evolve narrow niche specialism.

Limited dispersal from the tropics



If tropical regions are generating more species than temperate regions, there must additionally be limited or slow dispersal of these species into temperate regions to account for the disparity in species richness estimates. One of the main mechanisms for this is niche conservatism (Fig. 6). Some clades of species are unable to evolve tolerances to the environmental conditions associated with temperate regions and remain geographically constrained.

Biotic hypotheses

Interspecific interactions can promote species richness. However, in seeking to explain latitudinal species richness gradients, interactions such as competition and predation assume that interaction strength

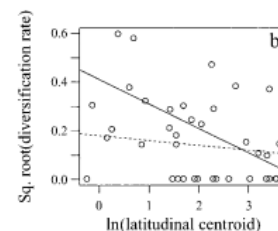


Figure 5: Diversification rate (measured as $\ln[\text{number of species}]/10^6\text{yr}$) as a function of latitude in young (solid line) and old (dashed line) clades of New World birds. From Cardillo et al. 2005

Figure 6: Hypothetical example illustrating niche conservatism and niche evolution. Different colored dots on the map and graph indicate localities for members of three clades. Lighter shades of red indicate colder yearly minimum temperatures. Two of the clades (blue and green) exhibit niche conservatism. Species in these clades are confined to tropical climates and fail to invade other regions despite their geographical proximity. The third clade (black dots) exhibits niche evolution, invading temperate regions (presumably by evolving tolerance to freezing winter temperatures) and no longer occurs in the ancestral tropical region. Adapted from Wiens and Donoghue, 2004.

Counter examples: The generality of mechanisms acting alone or together to explain the trend of increased species richness in the tropics, needs to be appraised along with examples where taxonomic groups have higher species richness in the temperate regions. These include the groups associated with sawflies, aphids, and certain ichneumonids and aquatic macrophytes. Niche evolution potentially has a role to play in explaining such patterns (Fig. 6, black dots).

is higher in the tropics (Fig. 7). This makes them largely *proximal* mechanisms, since the theory does not necessarily explain why the interactions would be stronger.

Competition

Competition drives species to have smaller and smaller niches (as doing so relieves the pressure of competition which has a negative effect on fitness). This in turn promotes diversification and speciation.

Predation

Strong predation can regulate competition (ensuring no one species at a lower trophic level will dominate). Predation could be stronger in tropical regions as conditions can allow year round activity (versus seasonal activity in temperate/boreal/arctic regions).

Mutualism

Predictable conditions associated with tropical regions appear to promote co-evolutionary interactions such as mutualisms (e.g. plant pollination by insects and birds is common, rather than wind dispersal).

Spatial heterogeneity

From coral reefs to rain forests, tropical regions typically contain a more extensive spatial matrix, facilitating coexistence of species. For example, the variation in foliage height in tropical forests is thought to contribute to supporting a relatively high bird species richness. Again, this is proximal since the theory does not speak directly to why the complex spatial matrix (tropical forest plant species richness) exists.

Geographical area

Some ecologists claim that the tropical biome is one of the geographically largest, and that area itself can explain high species richness through a simple species-area relationship. However, the underlying assumption that the tropical biome is disproportionately large is contested.

Concluding remarks

The pattern of increasing species richness in moving from pole to equator is very robust. There are numerous theories offered to explain this pattern. They all contribute to explaining some of the pattern, but all of them have limitations. It is likely that multiple mechanisms

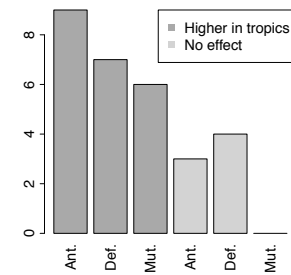


Figure 7: Schemske et al. 2009, identified several types of antagonistic agents (Ant., n=12), antagonistic defenses (Def., n=11) and mutualisms (Mut., n=6). The effects were predominantly stronger in the tropics (occasionally the same in tropical and temperate regions and never stronger in temperate regions).

are occurring together and no one theory may explain this fascinating global pattern.

Test yourself

- How would you summarize the relationship between species richness and latitude? What are some of the compelling pieces of evidence?
- Can you articulate four separate theories for the latitudinal species richness gradient? What are the associated limitations of these theories?

Further reading

- J. Schipper et al. 2008 “The Status of the World’s Land and Marine Mammals: Diversity, Threat, and Knowledge”, *Science*
- H. Hillebrand 2004 “On the Generality of the Latitudinal Diversity Gradient”, *American Naturalist*
- G.G. Mittelbach et al. 2007 “Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography”, *Ecology Letters*
- D. Jablonski et al. 2006 “Out of the Tropics: Evolutionary Dynamics of the Latitudinal Diversity Gradient”, *Science*
- M. Cardillo et al. 2005 “Testing for Latitudinal Bias in Diversification Rates: an Example using New World Birds”, *Ecology*
- D.W. Schemske et al. 2009 “Is there a latitudinal gradient in the importance of biotic interactions?” *Ann. Rev. Ecol. Evol. Sys.*

Homework

1. Without referring back to notes, sketch the relationship between species richness and time in a tropic and temperate region (i.e. two separate lines) to illustrate (a) the effect of diversification rate (b) the effect of a biome's effective age.
2. Using primary literature (research papers identified by searching, for example, google scholar) find a graphical example not mentioned in this chapter which demonstrates the classic relationship between species richness and latitude (over a range including tropical and temperate regions).