

## “Latitudinal Gradients in Species Diversity”: Reflections on Pianka’s 1966 Article and a Look Forward

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I was a mere graduate student, wet behind the ears, only 25 years old, when I wrote it. I don’t usually re-read my own papers—but now, five decades later, I am pleased to find it cerebral and fairly well written. (Eric Pianka, 2016)

Just as the 1960s were marked by revolutionary changes in music, culture, and politics, so too were they foundational for the emergence of modern ecology, with classical observational approaches giving way to mathematical theory and experiments. The University of Washington was a crucible for this movement in the 1960s, with young faculty such as Bob Paine, Gordon Orians, and Alan Kohn working in close collaboration with a number of exceptionally creative graduate students, including Henry Horn, Eric Pianka, Christopher Smith, Jared Verner, and Mary Willson. Collectively, this group pioneered a new way of thinking about ecological problems and was instrumental in defining the discipline of evolutionary ecology, a union of ecological and evolutionary perspectives that mirrors the goals of the American Society of Naturalists: “to advance and to diffuse knowledge of organic evolution and other broad biological principles.”

Of the many notable contributions by the Washington group, Eric Pianka’s 1966 article “Latitudinal Gradients in Species Diversity: A Review of Concepts” is emblematic of the creative energy at work during this era to address big problems in ecology and evolution. The paper was the first chapter of Eric’s PhD dissertation (1965), “Species Diversity and Ecology of Flatland Desert Western North America,” which (like many graduate students at the time) he painstakingly typed himself (fig. 1).

Eric’s influential paper (as of February 2017: 1,536 citations, Google Scholar; 967 citations, Web of Science) pro-

vided the first synthesis of the major hypotheses for the latitudinal diversity gradient (LDG) and stimulated the research trajectories of legions of naturalists. It has been reprinted in three different volumes of classic papers, including tropical ecology (Jordan 1981), tropical forest biology (Chazdon and Whitmore 2002), and biogeography (Lomolino et al. 2004), and thus it continues to serve as a foundational reference for the study of geographic patterns of biodiversity.

In reviewing previous studies, Pianka compiled six hypotheses that addressed possible causes of the LDG (table 1). For each, he provided a rationale for the biological processes involved. He did not evaluate the validity of the hypotheses or identify those he considered most plausible, but where possible, he did identify areas of future research. One important theme he highlighted throughout the paper is the challenge of distinguishing different mechanisms that might generate the same pattern: “Obviously, there is room for considerable overlap between these different hypotheses, and several may be acting in concert or in series in any particular situation” (Pianka 1966, p. 42). Below we briefly summarize Pianka’s six hypotheses.

**HYPOTHESIS 1.** *The time theory* proposes that the species richness of communities increases with time due to ecological (immigration) and evolutionary (speciation) processes. Multiple glaciations in northern latitudes reduced the time available for diversification, while tropical regions remained relatively undisturbed, leading to the LDG.

**HYPOTHESIS 2.** *The theory of spatial heterogeneity* suggests that the LDG results from the greater heterogeneity and/or complexity of physical and biotic factors (e.g., foliage height diversity) in the tropics. This is essentially an argument that the number of available habitats controls the number of species in a community.

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**HYPOTHESIS 3.** *The competition hypothesis* proposes that natural selection in the temperate zone is governed more by abiotic than by biotic factors, and as a result, competition is stronger in the tropics, niches are narrower, and more species can be supported.

**HYPOTHESIS 4.** *The predation hypothesis* is an alternative to the competition hypothesis, suggesting that competition is actually lower in the tropics due to a reduction in population sizes caused by higher predation in tropical environments. Lower competition reduces the likelihood of competitive exclusion and increases species richness.

**HYPOTHESIS 5.** *The theory of climatic stability* predicts that the stable climate in tropical regions leads to greater specialization, narrower niches, and higher species richness.

**HYPOTHESIS 6.** *The productivity hypothesis* suggests that the greater productivity of tropical regions increases species richness, perhaps by allowing narrower niches, tighter species packing, and greater niche overlap.

#### Pianka's Hypotheses Revisited

Pianka's 1966 article synthesized the wide range of ideas regarding the causes of the LDG in hopes of stimulating new research. Fifty years after its publication, there is still no consensus as to the primary mechanisms that contribute to the origin and maintenance of the LDG. Yet the remarkable diversity of life found in the humid tropics is as fascinating to biologists today as it was to Pianka in 1966 or to Wallace and Darwin more than 150 years ago. Here we briefly review how each of the six hypotheses summarized by Pianka has fared over the past 50 years.

The *time* hypothesis, which dates back to A. R. Wallace, is perhaps the oldest and most widely accepted of the six hypotheses. Since Pianka, development of detailed databases on the fossil record and knowledge of paleoclimates has provided a clearer picture of the development of biodiversity through deep time, and this has provided new opportunities for examining the time hypothesis (Jablonski et al. 2017). For example, a time-integrated biogeographic analysis of diversification in forest trees has suggested that tropical environments are older and thus have had more time for diversification (reviewed in Fine 2015), consistent with the time hypothesis. However, empirical tests of this hypothesis are challenging because it is difficult to separate the effects of age and climate (tropical vs. temperate). If tropi-

cal environments are older, historically larger, and more diverse, is the increased diversity due to age, area, climate, or all of the above? A recent approach to this problem examined the joint effects of time, area, and latitude on speciation of endemic fish and found that age, area, and latitude have significant and equivalent effects (Hanly et al. 2017). As one striking example that time per se is not the only factor contributing to fish diversification, consider that Lake Baikal, located at 55.63°N, is the largest by volume and the oldest (>27 million years) lake in the world, yet it has just 52 species of fish, 37 of which are endemic. In comparison, Lake Victoria, located at 1.30°S, is just 18,000 years old, yet it has 566 species, of which 450 are endemic.

The theory of *spatial heterogeneity* has received little attention since Pianka's review, which probably reflects the general opinion that tropical regions do not display greater heterogeneity of the physical environment. However, there is evidence that tropical forests have greater heterogeneity in tree height, which may contribute to the increased diversity of short-statured species in tropical forests (King et al. 2006). The role of biotic interactions in the LDG has expanded beyond the *competition* and *predation* hypotheses that were the focus of Pianka's review to include mutualisms such as pollination, which may promote reproductive isolation of plants and their pollinators. This has led to renewed interest in Dobzhansky's proposal that the greater importance of biotic interactions in the tropics promotes diversification (Dobzhansky 1950). A recent review of latitudinal patterns in the strength of biotic interactions largely confirms Dobzhansky's hypothesis, although more data are needed (Schemske et al. 2009). Although Dobzhansky did



**Figure 1:** Eric Pianka typing his dissertation. Photo courtesy of E. Pianka.

**Table 1:** Pianka’s (1966) six hypotheses and Fine’s (2015) five hypotheses for the latitudinal diversity gradient

Hypothesis	Our interpretation of the main focus
Pianka 1966:	
1. The time theory	Ecology and evolution
2. The theory of spatial heterogeneity	Ecology
3. The competition hypothesis	Ecology
4. The predation hypothesis	Ecology
5. The theory of climatic stability	Ecology and evolution
6. The productivity hypothesis	Ecology
Fine 2015:	
1. Time-integrated area, energy, and tropical niche conservatism	Evolution
2. Climate stability	Evolution
3. Temperature and evolutionary speed	Evolution
4. Biotic interactions and speciation rate	Evolution
5. Biotic interactions and finer niches	Ecology

not provide a mechanism linking biotic interactions to the LDG, a recent extension of his ideas suggests that strong biotic interactions coupled with coevolution lead to faster rates of adaptation and speciation in the tropics (Schemske 2009).

The theory of *climatic stability* remains relatively unexplored, although interest has been renewed in Janzen’s idea that mountains are a greater barrier to gene flow in the tropics than in temperate zones and that this may contribute to diversification. This hypothesis that “mountain passes are higher in tropics” is based on the idea that populations physiologically adapted to cold, high-elevation habitats in the aseasonal tropics are less likely to migrate across warmer valleys than are their temperate counterparts that are adapted to far greater seasonal variation in temperature (Janzen 1967). Finally, although the *productivity* hypothesis has been reviewed extensively, both with respect to geographic patterns in community diversity and to the LDG specifically, a direct mechanism linking productivity to species richness remains elusive.

**Current Hypotheses for the LDG:  
An Emphasis on Evolution**

Pianka’s six hypotheses for the latitudinal diversity gradient (table 1) focus predominantly on mechanisms of species coexistence: “The question of basic ecological interest is . . . what are the factors that allow ecological coexistence of more species at low latitudes?” (Pianka 1966, p. 34). Interestingly, in the more than 50 years since Pianka’s review, explanations for the LDG now place greater emphasis on evolutionary mechanisms (Mittelbach et al. 2007). For example, Fine (2015) reviews five hypotheses for the LDG (table 1), including latitudinal differences in rates of diversification (speciation and/or extinction) and their drivers and

differences in the time and area available for diversification in tropical and temperate biomes (in combination with tropical niche conservatism and available energy). Only one of Fine’s hypotheses is purely ecological.

Understandably, Pianka’s 1966 review focused mainly on ecology. Interspecific competition and species coexistence via niche partitioning formed the foundation of community ecology in the 1960s. These processes were thought to determine the number of species found in most local communities and, by extension, patterns of species diversity at broader spatial scales. Pianka also may have given evolution less emphasis because evolutionary hypotheses were thought untestable at the time. For example, he suggested (Pianka 1966, p. 35) that “the evolutionary time theory is not readily amenable to conclusive tests, and will probably remain more or less unevaluated for some time.” Since Pianka’s review, technological advances on a variety of fronts have made it possible to test evolutionary hypotheses. For example, molecular phylogenies allow the estimation of clade-specific diversification rates in relation to climate, latitude, and other factors. Further, satellite imagery and GIS mapping now provide unprecedented means to characterize global patterns of landform, climate, productivity, and species richness. These and other technological achievements have greatly advanced both paleo- and neontological studies of the LDG (Jablonski et al. 2017).

**The Question of Coexistence Still Matters**

The current emphasis on historical and evolutionary hypotheses for the LDG is a welcome and needed addition to the ecological hypotheses that figured so prominently in Pianka’s early review. However, we should not lose sight of the question of species coexistence. Even if evolution produces more species in the tropics compared to the temper-

ate zone (e.g., due to higher speciation rates and/or a longer evolutionary history), unless interspecific competition is always weak and communities are unsaturated, we still need to explain how more species can coexist at low latitudes than high.

One explanation for why more species are able to coexist in the tropics than in the temperate zone is that primary productivity is higher in the tropics, allowing more individuals to be supported per unit area and, therefore, more species (hypothesis 6 in Pianka's list; table 1). However, for well-documented taxa such as birds and trees, the increase in numbers of individuals per unit area from high latitudes to low latitudes is small compared to the dramatic increase in species richness (Currie et al. 2004; Brown 2014), suggesting that the productivity hypothesis by itself is insufficient. Another long-held hypothesis for enhanced species coexistence in the tropics (included at multiple points by Pianka) is that tropical species have narrower niches, which allows tighter species packing in tropical communities. Indeed, many examples of tropical species with very specialized niches exist, yet results from individual studies and from meta-analyses are mixed. Major obstacles to testing the narrower-niches hypothesis include the poor quality of the data (few studies have collected data specifically to test the hypothesis), the limited geographic scope of studies, and the wide variation in sampling methods. Much more work is needed to better test the narrower-niches hypotheses. Below, we suggest two additional mechanisms (not discussed in Pianka's review) that may promote greater niche diversity and allow more species to coexist in the tropics relative to the temperate zone.

### Species as Niches

Biotic interactions coupled with speciation may greatly expand the available niche space. As suggested by Vermeij (2005), "Every species is potentially a resource on which some other species can in principle specialize or to which another species must adapt." More simply, species can be niches for other species. Consider the army ant *Eciton burchellii*, which forages in large swarms and collects thousands of arthropod prey for the colony in a single day. More than 300 species of insects, birds, and other organisms depend on *E. burchellii* for all or part of their livelihood (e.g., eating prey the ants collect or flush, consuming the waste they discard, living in ant nests, riding on ant bodies, and more). Rettenmeyer et al. (2011) speculate that the more than 300 known associate species of *E. burchellii* are "likely only the tip of the iceberg," with thousands of specimens yet to be described and their associations characterized. Army ants are a spectacular example of how even a single species may create niches for other species. There are many such examples in nature,

and they seem far more common at low latitudes than high, but no studies have attempted to quantify this difference.

### Novel Niches

Price (2008) suggested that "at least 50% of the increase in (bird) species numbers in the tropics is due to the presence of unusual niches." This is likely a "best guess," but there is little doubt that tropical species occupy a variety of novel niches rarely found in the temperate zone. Further, many of these niches are functionally associated with warm temperatures and stable environments and thus may not be possible in a seasonally cold climate. For example, many tropical fish species are herbivorous or frugivorous, but these feeding modes are rare at high latitudes. Other, more unusual, feeding modes such as scale and fin eating have evolved many times in tropical fishes but are essentially absent in temperate fishes. A strong case can be made that herbivory is metabolically feasible only in warm environments for fishes and probably most poikilotherms. However, why other novel niches (e.g., scale eating, parasite cleaning, electrical communication, and predation in fishes; flower piercing, ant following, and herbivory in birds; ant eating, blood feeding in mammals) are common in the tropics but are much rarer in the extra-tropics deserves further study.

### The Next 50 Years?

Pianka's article was a milestone in organizing the myriad hypotheses for the LDG into a manageable framework for future study. What will the next 50 years bring? First, we are hopeful that current and future naturalists will continue to investigate the ecological and evolutionary mechanisms that contribute to the LDG. Second, and perhaps most important, is to ask how much tropical diversity will remain 50 years from now and to explore what can be done to preserve it. At the very time when we are developing the scientific tools to deeply probe and understand the causes of the LDG, that diversity is rapidly disappearing. What will be left for future naturalists to study? This question was largely absent 50 years ago but now demands our attention.

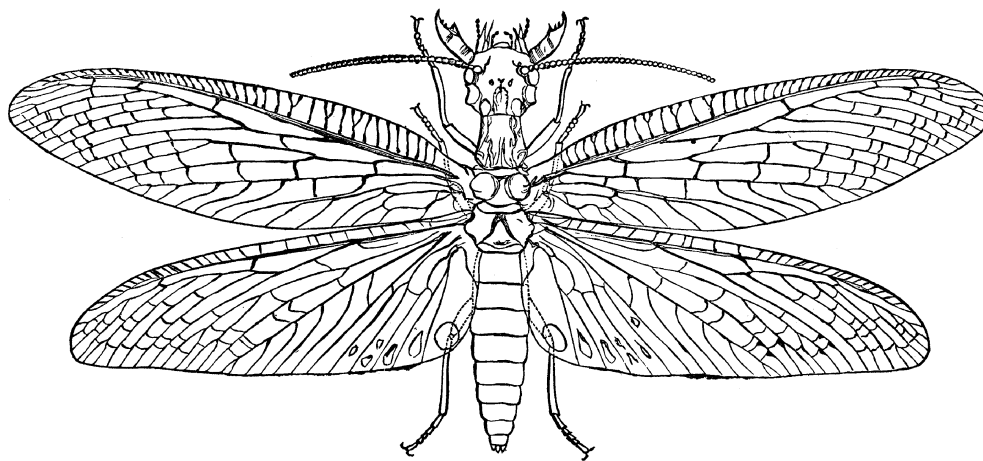
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“One of the largest and most formidable looking, though perfectly harmless, insects we have, is the *Corydalus cornutus*. . . . Insects like this were characteristic of the Coal Period, probably breeding in the marshes and fens of Carboniferous times.” From “Natural history miscellany: zoölogy” (*The American Naturalist*, 1867, 1:434–439).