

If not one, then all: Is incomplete support for any hypothesis support for all hypotheses?

ARIANNA STOKES



WRITER'S COMMENT: The latitudinal diversity gradient is an ecologist's term for something you are already familiar with. Pause for a moment to imagine the earth's equator versus its poles. If you conjure images of a landscape abundant with life for the former but a rather lifeless landscape for the latter, then you have captured the essence of the latitudinal diversity gradient: species richness is highest at lower latitudes and lowest at higher latitudes. Intriguingly, the cause of the latitudinal diversity gradient remains largely unidentified. Quite in contrast to our uncanny ability to extinguish biodiversity, our ability to identify the origins of biodiversity on a global scale has proved limited. This essay, written for Professor Shapiro's Tropical Ecology (EVE 138) course, is an attempt to sort through the many hypotheses that have been proposed to identify the cause of the earth's gradient in biodiversity. Because I am fond of the way Professor Shapiro steeps his course material in the history of science, I have attempted to approach the essay by giving historical and current perspectives on the efforts made to explain global biodiversity.

INSTRUCTOR'S COMMENT: I've had the pleasure of reading Arianna's writing in two courses—EVE 141 (Principles of Systematics, Spring 2017) and EVE 138 (Tropical Ecology, Spring 2018). Both are highly demanding, synthetic courses involving a great deal of reading and writing. She received an A+ in 141 and a mere A in 138. In 141 she received 8 A+ grades and 2 mere As. My comments on her essays included "Outstanding paper both intellectually and technically," "You write exceedingly well and I tip my hat to you," and "Excellent

and very sophisticated essay.” Her two papers in 138 both received 100 out of a possible 100 points. She is one of the best undergraduate essayists I have encountered in nearly 50 years of teaching. That is a very powerful comment given my own history as a writer and editor in various capacities, not all of them scientific. She is superb at integrating different streams of thought to produce convincing syntheses. In biology classes I rarely encounter students who, like Arianna, seem equally comfortable with Wittgenstein and multivariate statistics!

—Arthur Shapiro, Department of Evolution and Ecology

An opening by Pianka

Any serious discussion of the causes of the latitudinal gradient of biodiversity begins in the same place: with reference to Eric Pianka’s 1966 paper, “Latitudinal Gradients in Species Diversity: A Review of Concepts.” Pianka’s now classic piece is considered the first review to be written on the hypothesized causes for why the earth is species-rich at its equator and species-poor at its poles. Looking back at his heavily utilized paper which gave organization to a growing body of literature, a much older Pianka remarks, “I was a mere graduate student, wet behind the ears, only twenty-five years old, when I wrote it.” If the symbolic birth of the exploration of the latitudinal biodiversity gradient is formally marked by Pianka’s 1966 paper, then the field, which has attracted the minds of many great ecologists, has just passed its fiftieth anniversary. Given that ecologists have been working for half a century to identify the driving forces behind global diversity patterns, what would wet-behind-the-ears students of today be able to say about the latitudinal trends in diversity?

Without doubt they would be able to say a great deal; the number of hypotheses on the determinants of biodiversity has only grown since Pianka’s publication. By 1999, ecologists were woefully observing that the lists of hypotheses attempting to explain biodiversity “grows ever longer: Pianka (1966) presented six hypotheses, Currie (1991) eight, Rohde (1992) twenty-three and Palmer (1994) one hundred and twenty” (Currie, Francis, and Kerr, 1999). However, today’s students certainly have a lot to *say* about latitudinal diversity gradient hypotheses, they don’t

have nearly as much to *conclude*. This is because, stated starkly, ecologists have repeatedly failed to formulate a single conclusive explanation for the latitudinal biodiversity trend, which continues to loom large in the field of ecology and evolution.

What does it take to be the one?

How global biodiversity patterns could remain unexplained despite countless hypotheses put forth on the topic certainly warrants exploration. Important to any such exploration is the identification of criteria that must be fulfilled by an acceptable hypothesis.

One obvious implication of the latitudinal biodiversity gradient is that there are more species in some parts of the world than others. As Wiens forcefully reminded the field in 2011, there are only three processes that act directly upon the number of species in a particular area: speciation, extinction, and dispersal.¹ Therefore, hypotheses concerning the global pattern of biodiversity must make some statement about speciation, extinction, and/or dispersal.

Further criteria for strong hypotheses were laid out nicely by Rohde in his 1992 review. Rohde (1992) diagnosed the body of global biodiversity hypotheses with two ailments: frequent use of circular logic and a failure of theoretical conjectures to be supported by empirical data. Addressing the first ailment, Rohde (1992) pointed out that hypotheses which give biotic interactions as the mechanism driving biodiversity patterns employ circular reasoning if the efficacy of the biotic interactions to drive increased species diversity relies on the pre-established diversity of some, if not all, biotic groups. Rohde (1992) went on to cite twelve of his colleagues' hypotheses that, if presented independently, could be swiftly rejected because they were guilty of employing circular reasoning. Clearly, a hypothesis is useful only if it can explain both the maintenance of biodiversity *and* its initiation. (However, it seems unnecessary that

¹ A fourth process contentiously argued by some to directly determine species numbers is the inherent ecological limit of environments. Wiens (2011) successfully argues that ecological limits do not represent a process that can directly affect the number of species populating an area. He instead asserts that ecological limits act indirectly upon species tallies by affecting the processes of speciation, extinction and dispersal.

the factors responsible for initiating biodiversity be the same as the factors which maintain biodiversity.) Rohde's (1992) second criticism of his colleagues' hypotheses was that empirical evidence failed to support them. This intuitive point, that theoretical hypotheses must not be contradictory to empirical data if and when such data become available, has taken on more importance in the recent decade: advancements in the field of phylogenetics has allowed the evaluation of once untouchable hypotheses (such as those that deal with evolutionary processes) (Schemske and Mittelbach, 2017). Of course, the power of empirical evidence must be considered cautiously. Because many of the factors drawn upon to explain the biodiversity gradient correlate with latitude and covary with each other, few empirical observations can definitively provide support for one factor at the exclusion of the others. This renders many hypotheses unfalsifiable.

In summary, strong hypotheses will use variance in speciation, extinction, and dispersal rates or histories to explain biodiversity, will account for initiation and maintenance of biodiversity, will be testable, and will supported by empirical evidence.

A common explanation with multiple causality?

Acknowledging that only three processes are directly responsible for species' existences does not bring one much closer to solving the mystery of global patterns of biodiversity; a multitude of factors influence how and when speciation, extinction, and dispersal occur. Attempting to narrow down the factors responsible for affecting these three processes in such a way that causes more species to "end up" at lower latitudes than higher latitudes is a hefty task. One helpful assumption to make is that "a common gradient is likely to have a common cause" (Rohde, 1992). The latitudinal biodiversity gradient occurs over such a large scale that it begs an explanation in which the determinants of species-richness at one location are the same determinants of species-richness at another location. However, while the latitudinal biodiversity gradient requires that a single set of determinants be used to explain global biodiversity, there is no particular limit to the number of determinants that may be embraced in that "single set." Indeed, ecologists working to explain the latitudinal gradient in biodiversity have long realized that the pattern is "seriously complicated by multiple causality" (Pianka, 1989).

With the issue of multiple causality in mind, and acknowledging that no single hypothesis has achieved universal acceptance, might we conclude that the inability thus far to explain global biodiversity trends is due not to a failure to identify the right causes but, rather, to a failure to combine causes in the right way? Is it possible that hypotheses already put forth in the literature have enough strength, when brought together, to explain the global trends in biodiversity? The remainder of the paper will be devoted to exploring how the ideas in the six hypotheses found in Pianka's 1966 review have evolved or been recycled into "newer" hypotheses (as presented in Fine 2015). An attempt will also be made to evaluate how, if at all, the leading hypotheses of today may be combined with one another to form the most robust explanation for why the tropics boast such a high number of species.

Pianka's big six

Pianka, first in his famous review and then in papers published afterwards, admitted that the true cause of the latitudinal biodiversity trend was likely due to multiple mechanisms "acting in concert or in series." In 1966, however, the young Pianka believed that the nascent field would be better off by first "consider[ing] and assess[ing] each of the components of control of diversity in isolation before attempting various mixtures." Because of this viewpoint, and most likely because of a general lack of collected data, the six hypotheses that Pianka summarizes appear to be blissfully simple relative to more recent hypotheses. Pianka's reviewed hypotheses include the time theory, the theory of spatial heterogeneity, the predation hypothesis, the competition hypothesis, the theory of climatic stability, and the productivity hypothesis. As Schemske and Mittelbach (2017) thoughtfully point out, four² of these six hypotheses are, at their core, purely ecological explanations (as opposed to evolutionary explanations). The great importance that early ecologists placed on processes of species interactions is evidenced in Pianka's own framing of the issue of global biodiversity as a matter of identifying "the factors that cause ecological coexistence of more species at low latitudes" (1966). Of course, accounting for factors causing the ecological coexistence

² The theory of spatial heterogeneity, the predation hypothesis, the competition hypothesis, and the productivity hypothesis.

of species, which may also be conceptualized as accounting for factors that prevent extinction of pre-specified and simultaneously occurring species, is a valid and necessary exercise. However, the inclination to view biodiversity as merely a matter of species coexistence may lead an undue amount of emphasis to be placed on the processes that maintain—as oppose to cause—species diversity. And as mentioned previously, such an approach runs the risk of presupposing species diversity and employing circular reasoning. Sure enough two³ of the four hypotheses drawing on ecological explanations for biodiversity were later to be found on Rohde's list of "circular 'explanations' of latitudinal gradients of species diversity."

Modern day renditions of hypotheses

How have Pianka's six hypotheses fared over time? A recent review (see Fine 2015) on the hypothesized drivers of the latitudinal biodiversity gradient offered a brief exploration of the status of hypotheses currently found in the field. This review is noteworthy because it attempts to combine older and simpler hypotheses into stronger and broader hypotheses with more explanatory power. Fine (2015) presents fifteen hypotheses, rejects three of them, and ultimately integrates twelve into five broad hypotheses. Of the six hypothesized diversity drivers reviewed by Pianka, all but one are found to be incorporated into the five modern hypotheses given by Fine 2015. (The one hypothesis that does not resurface in Fine 2015 is the time hypothesis. Fine (2015) and others find sufficient evidence to reject the assertion that a longer period of time since the most recent major disturbance in the tropics is the driving cause of high tropical diversity. Notably, however, the passage of time does remain an important element in at least one of Fine's (2015) five hypotheses.) Fine's five hypotheses include time-integrated area and energy and tropical conservatism, climate stability, temperature and evolutionary speed, biotic interactions and speciation rate, and finally biotic interactions and finer niches.

Evaluating these five hypotheses against the criteria for a strong hypothesis (established above), we find that all five hypotheses include a mechanism for influencing the probability of speciation and/or extinction. Only three, however, are free of circular logic; the two

³ The predation hypothesis and the competition hypothesis.

hypotheses dealing with biotic interactions must be eliminated from further discussion on the origin of high tropical biodiversity. Of the remaining three hypotheses, time-integrated area and energy and tropical conservatism, climate stability, and temperature and evolutionary speed, the latter hypothesis lacks empirical evidence. Major strikes against the idea that temperature is associated with increased speciation include the finding that modern-day speciation rates are faster in extra-tropical environments (Weir, 2015), the observation that frigid deep sea benthic communities are highly diverse, and the lack of evidence for the idea that an increase in mutation rates (due to increased temperature) causes an increase in successful speciation events (Fine 2015). While it seems unnecessary to irrevocably discard the temperature and evolutionary speed hypothesis, it should be recognized that the relative importance of the hypothesis in a multiple causality common explanation for the global diversity gradient is likely minimal. Thus, only two hypotheses remain at large: the time-integrated area and tropical conservatism hypothesis and the climate stability hypothesis.

The logic behind the time-integrated area and energy and tropical conservatism hypothesis goes as follows: Lower latitudes contain more of the earth's surface area. Larger areas, over long periods of time, should have larger population sizes. Larger population sizes are less vulnerable to extinction due to random events and more prone to speciation due to the ease with which they may be divided by a barrier. Furthermore, more physical heterogeneity and more geographic features (which act as connectivity barriers) are to be expected over areas of greater size. Therefore, not only should geographic barriers and physical heterogeneity affect larger populations more severely than smaller populations, but the large area of the tropics (where larger populations are expected under this hypothesis) also boasts more geographic features with the potential to divide populations (Fine 2015).

The climate stability hypothesis found in Fine 2015 remains largely unchanged from the rendition found in Pianka's 1966 review. The climate stability hypothesis reasons that low latitude regions have less yearly variation in temperature and precipitation. Less long-term variation is also expected because the effects of the Milankovitch cycles are dampened at lower latitudes. Reduced yearly climatic variation allows for specialization because less energy must be invested in tolerance of a wide range of environmental conditions. Reduced long-term climate

variation works to lower extinction rates and preserve already speciated specialists (Fine, 2015).

How do the time-integrated area and tropical conservatism hypothesis and the climate stability hypothesis interact with each other? The climate stability hypothesis seems to strengthen the outcome predicted by the time-integrated area and tropical conservatism hypothesis: time and area allow for high occurrences of interrupted gene flow while climatic stability allows for high frequencies of very divergent evolution. Together, the two hypotheses are stronger.

The two hypotheses also grow more robust when evaluated in the context of inferences made about tectonic history and paleoclimatic conditions. During the Neogene (the period directly preceding the Quaternary), it is inferred that landmasses (particularly the American continents) had high levels of tectonic activity (Rull, 2011). The Quaternary, on the other hand, is notable for its climatic activity: parts of the earth experienced intermittent glaciation while the majority of the tropics, though significantly cooler than they are today, enjoyed a moderate level of climatic stability (Rull, 2011). Interestingly, estimations of the age of clade diversification events for extant Neotropical species and crown groups suggest that the majority of Neotropical clades likely began their diversification in the Neogene and roughly half of Neotropical clades continued this diversification into the Quaternary (Rull, 2011). These diversification patterns are consistent with a narrative that goes as follows: vicariance of large populations in the tropics was induced by the geological activity of the Neogene resulting in speciation and incipient speciation. The following period of climate stability completed these incipient speciation events (as well as caused further speciation) while simultaneously lowering tropical extinction rates. Such a sequence of events, mediated by the mechanisms provided by the time-integrated area and tropical conservatism hypothesis and the climate stability hypothesis, would be able to establish elevated species richness in tropical areas. Once a certain degree of species richness had been achieved, additional processes may have supplemented or replaced the processes that initiated the original species enrichment. Biotic interactions (such as competition, predation, and biotic spatial heterogeneity) are likely to represent processes responsible for maintaining and strengthening the presently seen latitudinal biodiversity trend after its establishment in the Neogene and Quaternary.

Conclusions

Since Pianka published his 1966 review, work on the latitudinal biodiversity gradient has greatly expanded; the field grapples with an overwhelming number of hypothesized drivers for global diversity patterns. And while technological and statistical progress has allowed hypotheses to be tested, the outcomes of hypothesis tests have seemed only to reveal weaknesses in all hypotheses as opposed to provide exclusive support for any one hypothesis. With this being true, it seems necessary to consider several hypothesized drivers of diversity as working in synergy and/or in succession to each other. Fine (2015) identifies older hypotheses and integrates them into five broader hypotheses (which retain many of the basic ideas presented in Pianka 1966). Further integration of Fine's hypotheses, considered in tandem with inferences of earth's prehistoric conditions, allows for the strongest explanation of the latitudinal biodiversity gradient. The integration of multiple factors capable of driving diversity is the only way to tackle a global pattern in biology because, as Karl Popper states in his last published work, "natural phenomena are influenced by webs of interactions far too complex to untangle" (Currie, Francis, and Kerr, 1999). The multiple causality of the latitudinal biodiversity gradient should be embraced; ecologists should give up attempts to untangle this problem with individual hypotheses and start considering the interplay of hypotheses.

References

- Currie DJ, Francis AP, Kerr JT. 1999. Some general propositions about the study of spatial patterns of species richness. *Ecoscience*. 6: 392-399.
- Fine P. V. A. 2015. Ecological and evolutionary drivers of geographic variation in species diversity. *Annual Review of Ecology, Evolution, and Systematics* 46:369–392.
- Pianka ER. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100:33–46.
- Pianka ER. 1989. Latitudinal gradients in species diversity. *Trends in*

- Eco. and Evo. 4:223.
- Rohde K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65:514–27.
- Rull V. 2011. Neotropical biodiversity: timing and potential drivers *Trends in Eco. and Evo.* 26:508-513.
- Schemske DW, Mittelbach GG. 2017. Latitudinal gradients in species diversity”: reflections on Pianka’s 1966 article and a look forward. *American Naturalist.* 189:599-603.
- Weir JT. 2014. Environmental harshness, latitude and incipient speciation. *Molecular Ecology.* 23:251–253.
- Wiens JJ. 2011. The causes of species richness patterns across space, time, and clades and the role of “ecological limits.” *Q. Rev. Biol.* 86:75–96.