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E-Note

A Minimal Model for the Latitudinal Diversity Gradient Suggests a Dominant Role for Ecological Limits

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abstract: The latitudinal diversity gradient (LDG) is one of Earth's most iconic biodiversity patterns and still one of the most debated. Explanations for the LDG are often categorized into three broad pathways in which the diversity gradient is created by (1) differential diversification rates, (2) differential carrying capacities (ecological limits), or (3) differential time to accumulate species across latitude. Support for these pathways has, however, been mostly verbally expressed. Here, we present a minimal model to clarify the essential assumptions of the three pathways and explore the sensitivity of diversity dynamics to these pathways. We find that an LDG arises most easily from a gradient in ecological limits compared with a gradient in the time for species accumulation or diversification rate in most modeled scenarios. Differential diversification rates create a stronger LDG than ecological limits only when speciation and dispersal rates are low, but then the predicted LDG seems weaker than the observed LDG. Moreover, range dynamics may reduce an LDG created by a gradient in diversification rates or time for species accumulation, but they cannot reduce an LDG induced by differential ecological limits. We conclude that our simple model provides a null prediction for the effectiveness of the three LDG pathways and can thus aid discussions about the causal mechanisms underlying the LDG or motivate more complex models to confirm or falsify our findings.

Keywords: latitudinal diversity gradient, ecological limits, diversification, speciation, extinction, dispersal.

Introduction

Across most groups of organisms, species diversity increases dramatically from the poles to the tropics (Hillebrand 2004; Kinlock et al. 2018). For example, a 100-km^2 grid square in Ecuador may contain more than 900 bird species, whereas in Greenland we find only a few. Thirty years ago, Ricklefs referred to this latitudinal diversity gradient (LDG) as "the major, unexplained pattern in natural history" and one that "mocks our ignorance" (Ricklefs in Lewin 1989). Since then, progress has been made on the description of the pattern itself: fine-scale descriptions of richness gradients for many taxa are increasingly available, and extensive empirical efforts and methodological advances have been made, testing predictions from many hypotheses against data in particular clades (e.g., Stephens and Wiens 2003; Wiens and Donoghue 2004; Hawkins et al. 2006) and generalizing patterns across taxa (Jansson et al. 2013). Theoretically, the field has also advanced by suggesting many different explanations for the LDG (Mittelbach et al. 2007; Fine 2015; Lomolino et al. 2016), by exploring their implications (e.g., for conservation, see Willig and Presley 2018), and by proposing ways to synthesize and test these (Pontarp et al. 2019). However, a consensus on the dominant underlying processes for the LDG (Lamanna et al. 2014; Rolland et al. 2015; Jablonski et al. 2017) has not been reached.

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The different hypotheses devised to explain the LDG (Lomolino et al. 2016) can be divided into three broad categories relating to a gradient in ecological limits to diversity, diversification rates, or time for species accumulation (Mittelbach et al. 2007). The assumption of hypotheses based on ecological limits is that the LDG arises due to competition for limited resources, which constrains the number of species that can occur together in any given location (e.g., Mittelbach et al. 2007; Rabosky 2009; with earlier antecedents in the ecological and paleontological literatures: e.g., MacArthur and Wilson 1967; Raup 1972). Diversification rate hypotheses invoke variable speciation or extinction rates due to, for example, higher mutation rates and faster generation times in the tropics (Rohde 1992; Allen et al. 2006) or harsher environmental conditions in temperate regions (Weir and Schluter 2007), respectively. Time for species accumulation hypotheses assume nonequilibrial diversity dynamics, so that regions that were colonized first may have higher richness because diversification has been going on longer (Stephens and Wiens 2003). In this category, we include glacial cycles that would "reset" temperate diversity. There is a fourth type of hypothesis that we found difficult to fit into one of these categories: differential dispersal rates up or down the latitudinal gradient due to, for example, niche conservatism (Wiens et al. 2010). We will simply refer to these as dispersal hypotheses. From here on we will refer to these four categories as pathways through which the LDG may arise.

Various attempts have been made to formalize these main pathways for the emergence of the LDG in mathematical models or computer simulations (reviewed in Gotelli et al. 2009; Pontarp et al. 2019). Hurlbert and Stegen (2014*a*, 2014*b*) showed with a simulation model that any of the original pathways (ecological limits, diversification rates, and time) can produce the LDG, but each pathway predicts different secondary diversity patterns. Moreover, Pontarp and Wiens (2017) explored how several pathways can act together to create more complex primary and secondary LDG patterns. Such studies exemplify the complexity with which LDG patterns are shaped, but they also highlight the multitude of modeling decisions that have to be made to create models that explain the emergence of the LDG from basic ecological processes.

Here, we take a step back from such complex simulation models and develop a minimal model that uses only the high-level processes of speciation, extinction, and range shifts, with the goal of determining how sensitive the LDG is to the existence of the proposed pathways. The model assumes a simplified world with only two spatial locations: the tropical zone and the temperate zone. A key assumption of our model is diversity dependence in species origination (i.e., speciation and colonization) or extinction (Walker and Valentine 1984; Etienne et al. 2012; Valente et al. 2015). This assumption is necessary to accommodate ecological limits, which inherently is an equilibrial explanation. We accommodate nonequilibrial explanations such as time for species accumulation by considering diversity dynamics within our model during the phase before equilibrium richness values are reached. We show that a substantial latitudinal gradient in diversity is generated more easily with a gradient in ecological limits in a much wider range of conditions than with a gradient in either speciation/extinction rate or time for species accumulation.

Model and Methods

For our model, we assume that biodiversity dynamics in any given region can be described by three processes: speciation, extinction, and range shifts (e.g., Goldberg et al. 2011; Schluter and Pennell 2017). We define these processes at the metacommunity level, but they are analogous to the basic population dynamics' processes of birth, death, and emigration/immigration. Analogous to a population's carrying capacity, we assume a limit to diversity (here, "ecological limits") to avoid exponential diversification. This limit is a ceiling to the number of species that can coexist in a region, but the actual number of species can be much lower if extinction or emigration is high. Figure 1 presents a diagram to show these processes schematically. We use this diagram to illustrate how five representative hypotheses for the LDG can be addressed by changing values of particular parameters of the proposed model. The speciation rate hypothesis posits that speciation rates are higher in the tropics. The extinction rate hypothesis states that extinction rates are lower in the tropics. These are clearly diversification rate hypotheses. The ecological limits hypothesis argues that the limit to the number of species that can coexist is higher in the tropics. We interpret this as a limit to origination (speciation plus immigration) or to extinction. For the species accumulation time hypothesis, we assume that the ancestral species originates in the tropics where it can diversify and disperse to the temperate region, which thus starts diversifying later, so tropical regions have a longer period to accumulate species. It is related to the tropical niche conservatism hypothesis, but this hypothesis is a combination of niche conservatism (leading to a strong reduction in dispersal from any climatic zone or settlement success in any other zone) and the requirement that (A) this conservatism is particularly strong in the tropics and/or (B) the ancestral species is tropical (Wiens and Donoghue 2004; Hawkins and DeVries 2009; Löwenberg-Neto et al. 2011; Stevens 2011; Kerkhoff et al. 2014). Version A of the tropical niche conservatism hypothesis can be accommodated by our model by assuming that dispersal out of the tropics is smaller than dispersal into the tropics. We call this scenario "into the tropics," as it obviously implies a higher

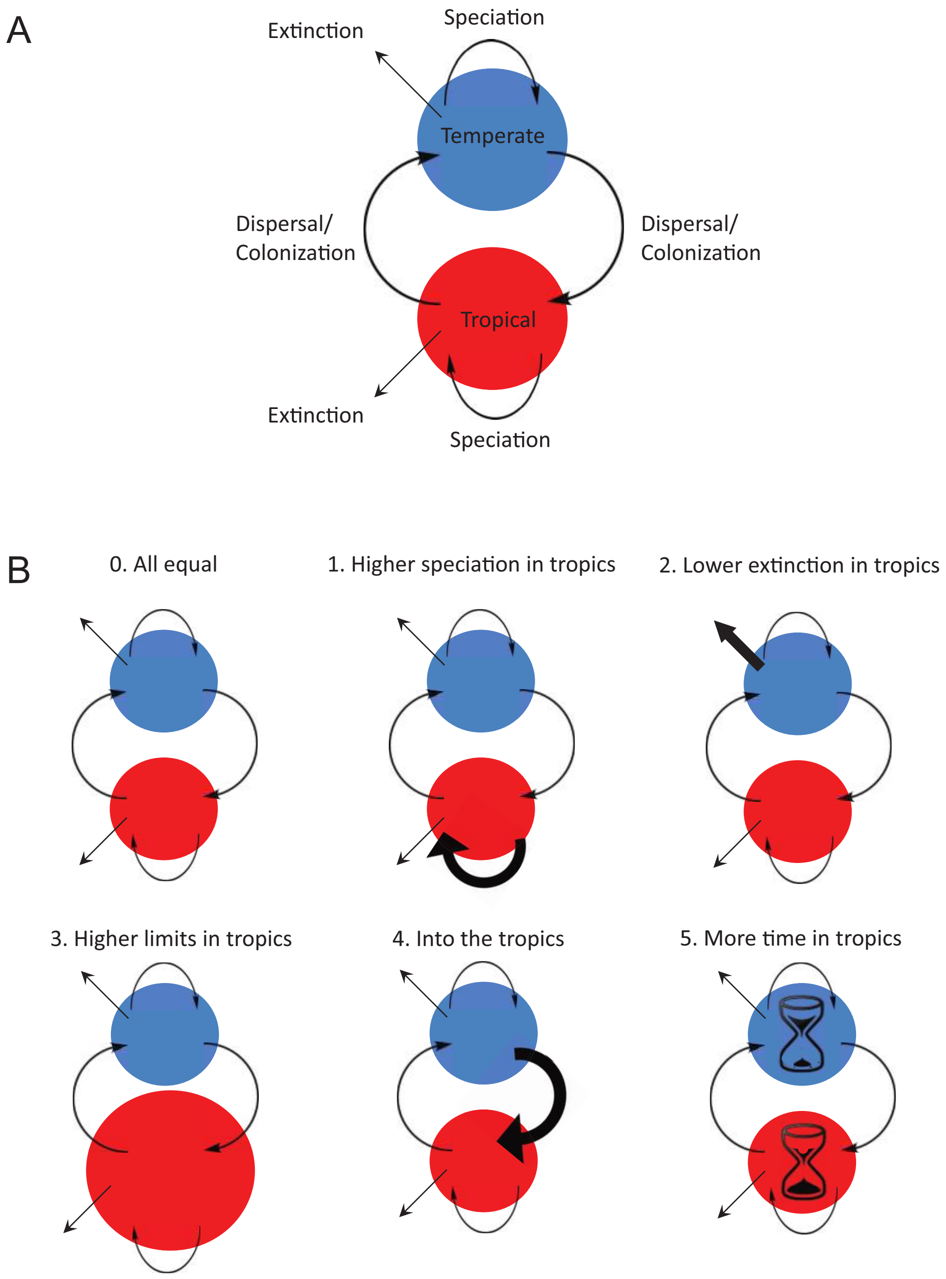

Figure 1: *A*, Conceptual diagram of the processes determining the latitudinal diversity gradient. *B*, Adjustment of this conceptual diagram for five hypotheses explaining the latitudinal diversity gradient. "All equal" corresponds to the null scenario of equal rates for both regions, resulting in no difference in species richness. "Higher speciation in tropics" assumes a higher speciation rate in the tropics than in the temperate zone. "Lower extinction in tropics" assumes a higher extinction rate in the temperate region than in the tropics. "Higher limits in tropics" assumes higher ecological limits in the tropics than in the temperate zone. "Into the tropics" assumes a smaller colonization rate out of the tropics because of niche conservatism in the tropics (species may disperse but cannot establish because of their mismatch with the temperate climate). "More time in tropics" assumes that the temperate zone starts empty and needs to wait for species to arrive from the tropics.

per-species flow into the tropics than out of the tropics. It can be categorized as a dispersal hypothesis. Version B of the tropical niche conservatism hypothesis falls under the explanation invoking differential time for species accumulation, with low dispersal rates between tropical and temperate zones, and we have therefore called it "more time in tropics."

The processes in figure 1 can be captured in three equations, one for the number of species endemic to the temperate zone (S_{high}), one for the number of species endemic to the tropics (S_{low}), and one for the number of species present in both regions (S_{global}), where "high" and "low" refer to latitudes. We denote the speciation rate by λ, the extinction rate by μ, and the dispersal or colonization rate by γ. To incorporate ecological limits, we assume that speciation and colonization are diversity dependent with a linear decline in speciation and colonization rates with diversity (in the destination patch), describing the increased difficulty to establish a new species as diversity increases (e.g., Valente et al. 2015):

$$\begin{aligned}\lambda(\lambda_0, S, K) &= \begin{cases}\lambda_0\left(1-\dfrac{S}{K}\right) & \text{for } S \le K,\\ 0 & \text{for } S > K;\end{cases}\\ \gamma(\gamma_0, S, K) &= \begin{cases}\gamma_0\left(1-\dfrac{S}{K}\right) & \text{for } S \le K,\\ 0 & \text{for } S > K.\end{cases}\end{aligned} \tag{1}$$

Here, S is the number of species in the focal patch, K is the maximum number of species at which no further speciation or immigration is possible, and λ_0 and γ_0 are the intrinsic speciation and immigration rates, respectively, that may depend on environmental factors (e.g., temperature) or properties of the taxon involved (e.g., generation time). We could easily consider other forms of the diversity dependence term $(1 - \mathrm{S/K})$ as well, but in the absence of better information, we find a linear decline a sensible assumption. For completeness, we also explored diversity dependence in the extinction rate according to $\mu = \mu_0/(1 - \mathrm{S/K})$ but this gave qualitatively similar results (see "Results" and figs. S2, S4; figs. S1–S4 are available online).

We now write the diversity dynamics for the diversity in each region by considering the dynamics of the number of endemic species in each region and the number of species present in both. We replace the subscript 0 in equation (1) by the latitude for speciation, either low or high, and by direction for dispersal, either from low to high latitude or from high to low latitude. We furthermore introduce a parameter, α, that measures the effect that dispersal has on the region that sends out the migrants. If $\alpha = 1$ the species will expand their range, whereas if $\alpha = 0$ they will leave the region of origin (i.e., range shift). We write the rate of change in the diversity levels of tropical, temperate, and global species by bookkeeping of the input (by speciation λ and immigration γ) and output (by extinction μ and emigration γ when $\alpha = 0$) in the following three equations:

$$\begin{aligned}\frac{dS_{\mathrm{low}}}{dt} &= -\mu_{\mathrm{low}}S_{\mathrm{low}} + \mu_{\mathrm{high}}S_{\mathrm{global}}\\ &\quad - \gamma(\gamma_{\mathrm{low}\to\mathrm{high}}, S_{\mathrm{high}} + S_{\mathrm{global}}, K_{\mathrm{high}})S_{\mathrm{low}}\\ &\quad + \lambda(\lambda_{\mathrm{low}}, S_{\mathrm{low}} + S_{\mathrm{global}}, K_{\mathrm{low}})(S_{\mathrm{low}} + S_{\mathrm{global}})\\ &\quad + (1 - \alpha_{\mathrm{high}})\\ &\quad \times \gamma(\gamma_{\mathrm{high}\to\mathrm{low}}, S_{\mathrm{low}} + S_{\mathrm{global}}, K_{\mathrm{low}})S_{\mathrm{high}},\\ \frac{dS_{\mathrm{high}}}{dt} &= -\mu_{\mathrm{high}}S_{\mathrm{high}} + \mu_{\mathrm{low}}S_{\mathrm{global}}\\ &\quad - \gamma(\gamma_{\mathrm{high}\to\mathrm{low}}, S_{\mathrm{low}} + S_{\mathrm{global}}, K_{\mathrm{low}})S_{\mathrm{high}}\\ &\quad + \lambda(\lambda_{\mathrm{high}}, S_{\mathrm{high}} + S_{\mathrm{global}}, K_{\mathrm{high}})\\ &\quad + (1 - \alpha_{\mathrm{low}})\\ &\quad \times \gamma(\gamma_{\mathrm{low}\to\mathrm{high}}, S_{\mathrm{high}} + S_{\mathrm{global}}, K_{\mathrm{high}})S_{\mathrm{low}},\\ \frac{dS_{\mathrm{global}}}{dt} &= -(\mu_{\mathrm{low}} + \mu_{\mathrm{high}})S_{\mathrm{global}}\\ &\quad + \alpha_{\mathrm{high}}\gamma(\gamma_{\mathrm{high}\to\mathrm{low}}, S_{\mathrm{low}} + S_{\mathrm{global}}, K_{\mathrm{low}})S_{\mathrm{high}}\\ &\quad + \alpha_{\mathrm{low}}\gamma(\gamma_{\mathrm{low}\to\mathrm{high}}, S_{\mathrm{high}} + S_{\mathrm{global}}, K_{\mathrm{high}})S_{\mathrm{low}}.\end{aligned} \tag{2}$$

These equations are easily solved numerically to obtain the number of species in the temperate zone ($S_{\mathrm{high}} + S_{\mathrm{global}}$) and the tropics ($S_{\mathrm{low}} + S_{\mathrm{global}}$) as a function of time. We invite readers to explore the effect of different initial conditions and parameter values with a Shiny app online at https://seldig.shinyapps.io/RBM-ODE/ or locally on their computers via the code provided in a zip file, available online.[1]

We explore the first four scenarios of figure 1*B* with a threefold gradient in the focal parameter creating the gradient. Specifically, in the scenario with higher speciation rates in the topics, we assumed $\lambda_{\mathrm{low}} = 3 \cdot \lambda_{\mathrm{high}}$. In the scenario with a higher extinction rate in the temperate zone, we assumed $\mu_{\mathrm{high}} = 3 \cdot \mu_{\mathrm{low}}$. In the scenario with higher limits in the tropics, we assumed $K_{\mathrm{low}} = 3 \cdot K_{\mathrm{high}}$. For the into the tropics scenario, we assumed $\gamma_{\mathrm{high}\to\mathrm{low}} = 3 \cdot \gamma_{\mathrm{low}\to\mathrm{high}}$. In all of these scenarios, both zones were initialized with one species each. In the last scenario, the time for species accumulation scenario, we assumed that the temperate zone starts empty and the tropical zone starts with 10 species ($S_{\mathrm{low}}(t = 0) = 10 > S_{\mathrm{high}}(t = 0) = 0$). The default parameter set, chosen to create reasonable diversity levels in all scenarios, is $\lambda_{\mathrm{high}} = 1.5$, $\mu_{\mathrm{low}} = 0.1$, $K_{\mathrm{high}} = 75$, $\gamma_{\mathrm{low}\to\mathrm{high}} = 0.3$, and $\alpha = 0$ (range shift). We also looked at the effect of changing α to 1 (range expansion).

Results

In all scenarios, a latitudinal gradient in diversity is formed, as expected, even though the gradient is sometimes very weak. Our key result is that the gradient in diversity between temperate and tropical zones is most sensitive to a gradient in ecological limits rather than to a gradient in diversification rates or time for species accumulation. When we assume a threefold difference in the underlying gradient for the hypotheses of figure 1 or a 10 to 0 advantage in initial number of species for the tropics, we observe a much larger effect for ecological limits than for the other scenarios (fig. 2).

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[1] Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.

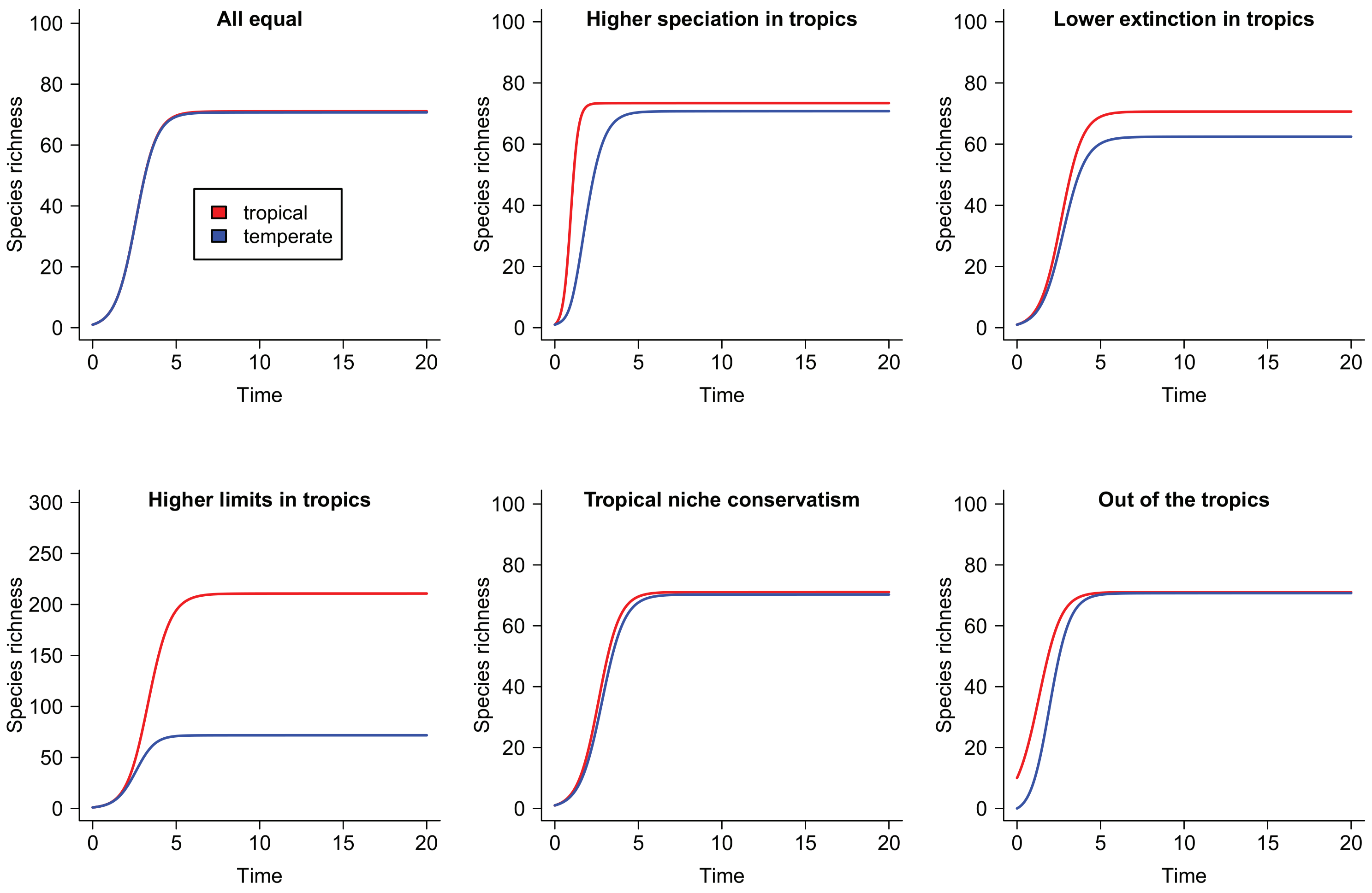

Figure 2: Total number of species (endemics plus shared) in the tropics (red) and the temperate zone (blue) as a function of time according to the set of equations (1), starting with one species in each zone. The first panel corresponds to equal rates for both regions, resulting in no difference in species richness. The second panel assumes a higher speciation rate in the tropics than in the temperate zone ($\lambda_{\mathrm{low}} = 3 \cdot \lambda_{\mathrm{high}}$). The third panel assumes a higher extinction rate in the temperate region than in the tropics ($\mu_{\mathrm{high}} = 3 \cdot \mu_{\mathrm{low}}$). The fourth panel assumes higher ecological limits in the tropics than in the temperate zone ($K_{\mathrm{low}} = 3 \cdot K_{\mathrm{high}}$). The fifth panel assumes a smaller colonization rate from the tropics to the temperate zone than vice versa ($\gamma_{\mathrm{high}\rightarrow\mathrm{low}} = 3 \cdot \gamma_{\mathrm{low}\rightarrow\mathrm{high}}$). The sixth panel assumes that the temperate zone starts empty ($S_{\mathrm{low}}(t = 0) = 10 > S_{\mathrm{high}}(t = 0) = 0$). In all panels, dispersal means range expansion ($\alpha = 1$) and the parameters are $\lambda_{\mathrm{high}} = 1.5$, $\mu_{\mathrm{low}} = 0.1$, and $K_{\mathrm{high}} = 75$, and $\gamma_{\mathrm{low}\rightarrow\mathrm{high}} = 0.3$. The largest difference between red (tropical zone) and blue (temperate zone) curves is obtained in the “higher limits in tropics” scenario.

This result is rather insensitive to whether species shift or expand their range, that is, whether $\alpha = 0$ or $\alpha = 1$, respectively (compare figs. 2, S1*A* with fig. S3*A*), and to whether diversity dependence is in speciation plus immigration or in extinction (compare figs. 2, S1*A* with fig. S2*A*). The results are qualitatively the same when we increase the overall limits (figs. S1*H*, S2*H*, S3*H*, S4*H*) or decrease the dispersal rate to allow more independence between tropical and temperate zones (figs. S1*C*, S2*C*, S3*C*, S4*C*). Only when we decrease the intrinsic speciation rate do we start to observe that a gradient in speciation rate or extinction rate can explain the LDG better than any of the other hypotheses (fig. 3; see also figs. S1*B*, S2*B*, S3*B*, S4*B*). This is because time until equilibrium is increased, and hence the larger limits in the tropics have not yet yielded any advantage. Increasing the intrinsic speciation rate again toward the original value shows that the effect is indeed temporary and that the temperate zone catches up with the tropics given enough time (fig. 4; see also figs. S1*F*, S2*F*, S3*F*, S4*F*). The loss of dominance of ecological limits in shaping the LDG is stronger for low dispersal rate, but this is not due to sensitivity of ecological limits to dispersal rate but occurs because gradients in intrinsic speciation rate or extinction rate gain much impact on the LDG for low dispersal rate (figs. S1*D*, S2*D*, S3*D*, S4*D*). We note, however, that although differential ecological limits play a subordinate role in shaping the LDG under low speciation rate and low dispersal rate, low speciation rate does not yield a strong LDG in the first place, suggesting that the observed substantial LDG is unlikely to arise in this scenario.

Apart from this general pattern, we note a few interesting observations. First, tropical niche conservatism, in our model interpreted as a lower dispersal rate out of the tropics than into the tropics, is unlikely to cause a substantial latitudinal gradient in diversity even before equilibrium is reached (see all supplemental figures). Second, while a lower dispersal rate creates a stronger LDG under the diversification rate and time for species accumulation pathway (higher speciation rate or lower extinction rate in the tropics and out of the tropics), it has the opposite effect under the ecological limits pathway when dispersal is modeled as range expansion, whereas it has no effect under the ecological limits pathway when dispersal is modeled as range shift. Third, whether dispersal is modeled as range expansion or as range shift generally has a small effect, except for the tropical niche conservatism hypothesis and the out of the tropics hypothesis when dispersal rate is sufficiently high (compare fig. S1*D* with fig. S3*D* and fig. S2*D* with fig. S4*D*).

Discussion

The LDG and Proposed Explanations

In this study, we developed a minimal model for the LDG, based only on high-level processes of speciation, extinction, and dispersal, and explored its emergent properties. While we did not aim to resolve "the major, unexplained pattern in natural history" that "mocks our ignorance" (Ricklefs in Lewin 1989), we focused on exploring the general functioning of the overarching pathways that have been identified as explanations for the LDG (diversification rates, ecological limits, time for species accumulation, and dispersal). Our main finding suggests that the LDG is most sensitive to a gradient in the pathway via ecological limits rather than the other pathways. In our model, the ecological limits pathway loses its primary role in having the strongest effect on the LDG only under particular conditions that keep the system far away from equilibrium, here obtained by low speciation rate. It could also arise when perturbance prevents the system from reaching equilibrium, something we did not model here. This latter case might be relevant if considering environmental dynamics (i.e., changes in the model parameters over time) and disturbances (i.e., increases in extinction rates or setting back species richness). While the high sensitivity of the LDG to ecological limits is reduced for low speciation rate, we emphasize that this high sensitivity remains high when changing other parameters. Moreover, in scenarios where the LDG is more sensitive to other, non-limits-related pathways, the LDG pattern is not very strong, making it less likely that the non-limits-related pathways are responsible for the observed LDG.

That the ecological limits pathway seems most effective in creating an LDG is suggestive of its importance for creating this pattern, but it is by no means proof that this pathway is the only or even the main cause of the LDG. Other pathways or their combination can in principle create results that are compatible with the observed data. However, our results show that this requires fine-tuning of parameters and combining pathways. Hence, the higher effectivity of the ecological limits pathway combined with general parsimony considerations (which would discourage this fine-tuning) shifts the evidence in favor of ecological limits playing an important role for the LDG, possibly in conjunction with other mechanisms. This view is consistent with another recent study that finds support for biotic processes and range dynamics controlling the LDG (Henriques-Silva et al. 2019).

Our results provide a general context for the way ecologists and evolutionary biologists should think about the current hypotheses and the way they interpret LDG patterns. Factors other than ecological limits may have the largest influence only if the dynamics are far from equilibrium (fig. 2). Our model thus reconciles the fact that some empirical studies support the time for speciation accumulation effect while others do not. Time for species accumulation may have an effect over shorter timescales if equilibrium has not been reached (Rabosky 2009; Wiens 2011; Manceau et al. 2015; Pontarp and Wiens 2017), while over

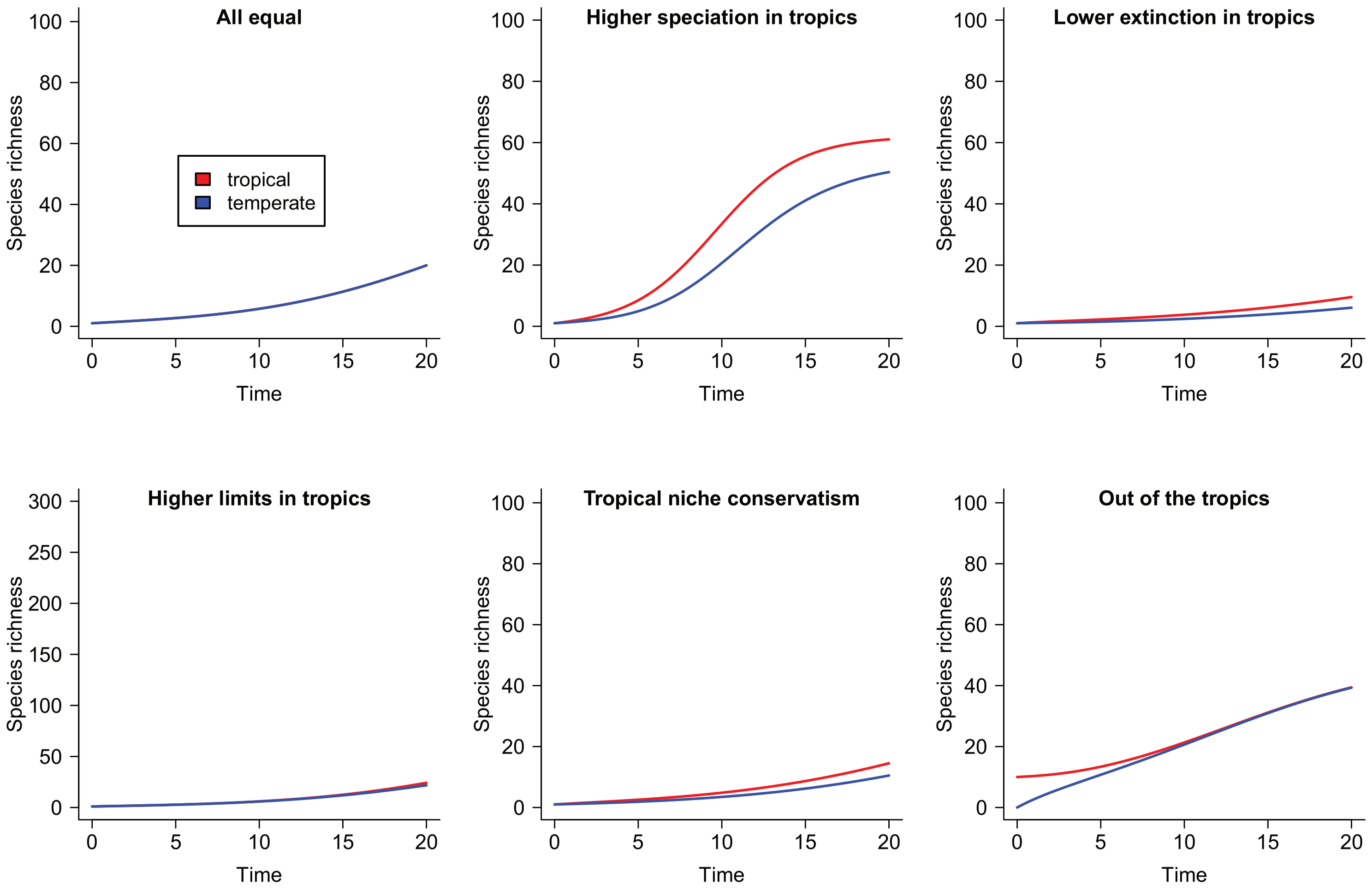

Figure 3: Same as figure 2 except that the default speciation rate has been set to a low value of 0.15. The large difference between red (tropical zone) and blue (temperate zone) in the "higher limits in tropics" scenario in figure 2 has now almost disappeared, and instead the "higher speciation in tropics" scenario now shows the largest difference.

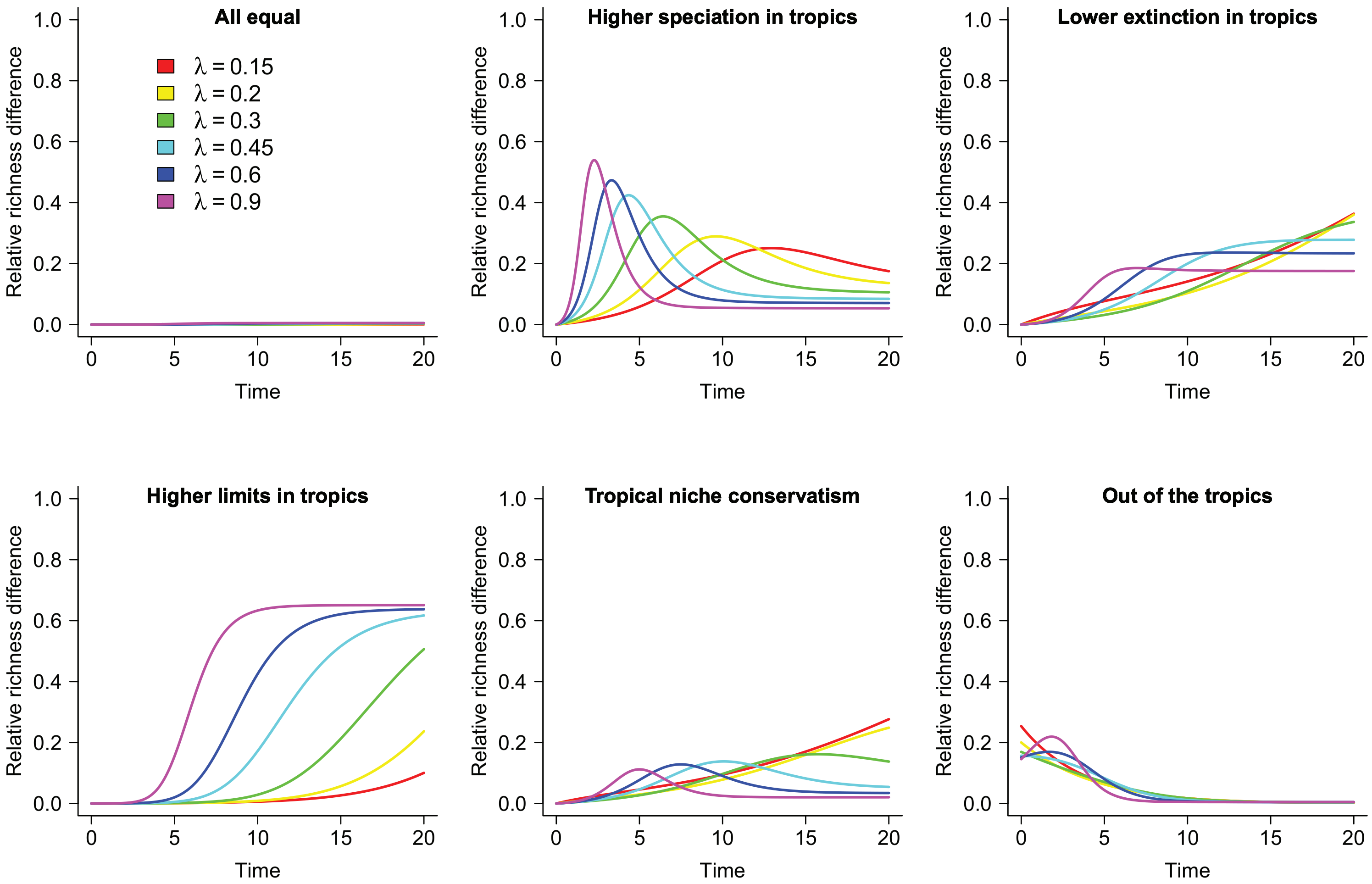

Figure 4: Sensitivity of the relative ratio between the species richness in the tropical zone versus the temperate zone to the intrinsic speciation rate in various scenarios. All parameters except for the varying speciation rate (see legend) are as in figure 2. The relative species richness difference increases in many scenarios but becomes small again, except in the "lower extinction in tropics" and "higher limits in tropics" scenarios.

longer timescales, when equilibrium is approached, the ecological limits effect is more likely. Weir and Schluter (2007) argued that the LDG was due to an underlying gradient in both speciation and extinction rate, where high latitudes had faster turnover than low latitudes. Our model suggests that this explanation for the LDG would be plausible if speciation rates are relatively low (fig. 3).

Our analysis also highlights the role of range dynamics for reducing the LDG as well as the importance of these dynamics for facilitating the convergence of biodiversity dynamics to equilibrium: any gradient in speciation rate, extinction rate, or time to accumulate species can be eroded away by range dynamics, leaving only a gradient in ecological limits to create a latitudinal gradient in diversity. Furthermore, spatial diversity patterns generally depend on phylogenetic scale, so that the patterns for younger or smaller clades often strongly deviate from the universal LDG (Hurlbert and Stegen 2014*b*; Graham et al. 2018), which can be interpreted via insufficient time to reach equilibrium in such clades (Pontarp and Wiens 2017; Machac et al. 2018). An LDG in low-dispersal taxonomic groups also seems most likely caused by a difference in intrinsic speciation rate or time for species accumulation, which may explain the LDG in ants (Economo et al. 2018).

Model Properties and Limitations

Our model is deliberately simple, excluding the lower-level mechanisms that underpin each of the modeled processes, similar to the philosophy of the theory of global biodiversity recently laid out by Worm and Tittensor (2018). This may seem to go against current calls for higher (individual-based) mechanistic complexity (e.g., Cabral et al. 2017; Descombes et al. 2018; Pontarp et al. 2019), including several of the models cited throughout this article. We certainly do not dismiss these calls for more complex mechanistic models, but we believe that parallel to detailed process-based models there is a value of considering only high-level processes in a minimal model to gain a general overview of the sensitivity of the LDG to these explanations. From simple high-level models we can gradually increase model complexity (Getz 1998) or understand the results of existing complex mechanistic models better. For example, while we show that ecological limits may have a pivotal role in creating the LDG, this can be further explored by more complex models that are more explicit about the mechanisms by which ecological limits influence biodiversity, such as competition for limited area and/or resources; we refer the reader to the extensive literature on the topic (for reviews, see, e.g., Rabosky 2013; Hurlbert and Stegen 2014*b*; Storch et al. 2018). Alternatively, one can explore other simple models. For example, the relatively simple but individual-level model of Worm and Tittensor (2018) also identifies ecological limits as a main driver of the LDG, along with a gradient in speciation rate.

In our model, we treat ecological limits as hard upper limits on the maximum number of species that can live in a given environment, either because no more species can speciate or immigrate or because extinction will immediately occur if the upper limit is exceeded. This would correspond to a hard ceiling to the available niches in an environment. However, considering that ecological niches emerge from intrinsic trade-offs of species, it seems unlikely that their maximum would be given only by the environment, independently of the existing species and their properties in a community. More realistic is that total energy available (e.g., total ecosystem net primary productivity) is determined by the environment, and this limits the total biomass or number of individuals. But even in such a case, the number of species would be determined not only by energy or total biomass but also by the rate at which this given biomass (or total number of individuals) is divided into species. The equilibrium diversity would then be determined by the interaction of energetic limits with the rates of species origination and extinction (Storch et al. 2018; Storch and Okie 2019). The rates are in this case involved in generating the equilibrium number of species, and their role in limiting species richness cannot be taken separately from the role of energy availability. This does not necessarily disagree with our finding that the LDG is more sensitive to a gradient in the limits than to gradients in the other factors; instead, it only opens the possibility that rates of speciation and extinction partially drive the limits on species richness in a given environment.

More mechanistic explanations may be useful in modeling the processes of speciation and extinction as well. Interestingly, Weir and Schluter (2007) implicitly modeled speciation as a protracted process, suggesting that differential speciation completion rates may cause the LDG. It will be interesting to study a model of protracted speciation similar to the model we have considered here. This is not trivial, however, because one has to decide how dispersal between zones will affect speciation completion. This is beyond the scope of the current article, which aimed to provide the simplest possible model. For the same reason we have not chosen to extend the model in other relatively straightforward ways—for example, to multiple latitudinal zones or even continuous space—because our model with only two spatial locations allows us to capture the essence of a gradient in one of the underlying processes and to assess the key groups of explanations offered for the LDG.

Conclusions and Perspectives

With a simple model of speciation, extinction, dispersal, and ecological limits to speciation and colonization, we explored the effectiveness of the main LDG hypotheses in affecting this global diversity pattern. Our model shows that a realistic LDG can most easily be created by a gradient in ecological limits. This, together with general parsimony arguments, supports the idea that ecological limits are important for creating the LDG. We note that we draw no conclusions whatsoever about the existence of the other pathways but only about their effect on the LDG. For instance, it may well be that other pathways (e.g., lower extinction rates in the tropics) have been active during ecological history but without creating a substantial effect on the LDG.

The emergent diversity patterns are always contingent on the parameter values. Which parameter values apply must be inferred from empirical data. Brodie (2019) suggests that gradients in ecological limits are ubiquitous among mammals. Because parameters will vary across taxonomic groups, the LDG may have different explanations across these groups (Hillebrand 2004; Graham et al. 2018). Similarly, parameters may vary across time, which then would explain why studies of younger clades often fail to find a latitudinal gradient in diversification rates whereas analyses of older clades do. Such results are, for example, found in comparisons between studies of frog families (Wiens et al. 2006, 2009) and families across amphibians (Pyron and Wiens 2013) and in studies within mammal genera (Soria-Carrasco and Castresana 2012) and across mammals (Rolland et al. 2014). Reconciling these different empirical patterns may require fine-tuning parameter values. It may also require combining multiple gradients in the model parameters. Our results are based on changing only one parameter at a time. If we allowed for differential speciation rates as well as extinction rates and a head start for the tropics in accumulation of species, then perhaps these gradients could together overrule the effect of ecological limits. Our simple model can accommodate all of these explorations, and we have provided a web-based graphical user interface to facilitate further exploration of the model. We hope it will also aid further extensions of the model, for example, including more than just two regions (after all, a gradient is a continuous change rather than a single step) or distinguishing between the Southern Hemisphere and the Northern Hemisphere. When such changes are made, some of the conclusions of this study may have to be modified or changed. This is exactly what we hope for: to provide a starting point for a fresh and more mechanistic perspective on the LDG debate and to provide a reference (sensu null expectation) that should be tested and challenged with other, more complex models so that we can learn from discrepancies but also highlight stable insights about the relative merit of competing ideas about the emergence of global biodiversity.

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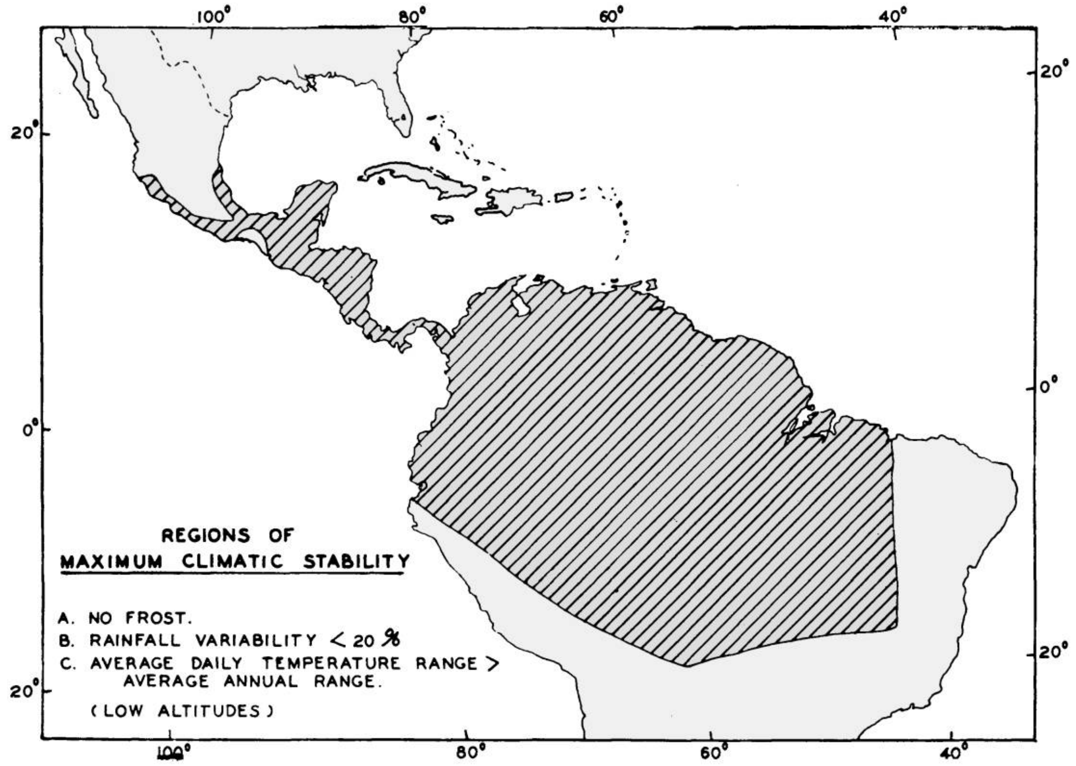

Regions of maximum climatic stability. After figure 1 in “On the Causes of Tropical Species Diversity: Niche Overlap” by Peter H. Klopfer and R. H. MacArthur (*The American Naturalist*, 1961, 95:223–226).