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► **To cite this version:**

Jonathan Rolland, Benjamin G Freeman. The latitudinal diversity gradient. 2022, 10.1093/obo/9780199941728-0144 . hal-03796971

**HAL Id: hal-03796971**

**<https://hal.science/hal-03796971v1>**

Submitted on 4 Oct 2022

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## The latitudinal diversity gradient

Jonathan Rolland<sup>1</sup> and Benjamin G. Freeman<sup>2</sup>

<sup>1</sup>CNRS, UMR5174, Laboratoire Evolution et Diversité Biologique, Université Toulouse 3 Paul Sabatier, Bâtiment 4R1, 118 Route de Narbonne, 31062 Toulouse, France.

<sup>2</sup>Department of Zoology and Biodiversity Research Centre, University of British Columbia, Vancouver, BC, Canada

### Introduction

**The latitudinal diversity gradient describes the decline in the number of species from the tropics to the temperate regions. The latitudinal diversity gradient is observed in most clades of animals, plants and microorganisms, and remains one of the oldest and most famous mysteries in ecology. The ubiquity of this pattern suggests the possibility of a single, general explanation for the latitudinal diversity gradient, and scientists since Von Humboldt and Darwin have formulated dozens of hypotheses to explain the causes of this gradient. We review the literature describing the main evolutionary hypotheses related to the three fundamental processes that can explain why some places (like the tropics) have more species than others: speciation, extinction and colonisation (dispersal). The recent advances in global-scale datasets of species distributions, the fossil record, and molecular mega-phylogenies give some hope of determining the primary cause(s) of the latitudinal diversity gradient.**

### General Overview

Alexander von Humboldt was one of the first authors to describe the latitudinal diversity gradient in 1807 (Hawkins 2001). Following his multi-year expedition to the biodiverse tropical Andes in South America (Otté and Bohn 1850), von Humboldt noticed that tropical species (distributed between 23.4° North and 23.4° South) greatly outnumbered temperate species. This pattern, called the latitudinal diversity gradient, is a general pattern that applies to most taxa, such as amphibians (Wiens et al. 2009), birds (Cardillo 2005, Ricklefs 2006), insects (Condamine et al. 2012), mammals (Davies 2008), marine invertebrates (Jablonski 2006), teleost (Rabosky 2008) and micro-organisms (Fuhrman 2008). Hillebrand (2004) reviewed latitudinal patterns of species richness, and formally showed that most taxonomic groups indeed harbour a latitudinal diversity gradient. However, there are exceptions. Some clades have no latitudinal gradient of diversity, or even an inverse gradient where species richness peaks in the temperate zones (for example in lagomorphs and for some bryophytes, fungi and insect groups; e.g. Kouki et al. 1994). There are dozens of hypotheses that attempt to explain the pattern, but until recently, many remained untested. Three processes can contribute to the greater accumulation of lineages in the tropics: higher speciation rate in the tropics, higher extinction rate in the temperate regions (Mittelbach 2007) or higher dispersal rate from high latitude to low latitude (Wiens

and Donoghue 2004, Darlington 1959). Now, the combination of increasingly powerful genomic datasets used to infer species' evolutionary histories and global datasets describing species' distributions at unprecedented scale, has led to exciting tests of hypotheses to explain the latitudinal diversity gradient.

Brown, J. H. 2014. Why are there so many species in the tropics? *Journal of biogeography* 41:8-22.

An important review of the literature summarizing the key hypotheses and literature explaining the latitudinal diversity pattern. In particular it describes the hypotheses related to phylogenetic niche conservatism and ecological productivity and underlines the importance of kinetics and the impact of temperature on evolutionary rates.

Cardillo, M., C. D. L. Orme, and I. P. F. Owens. 2005. Testing for latitudinal bias in diversification rates: an example using New World birds. *Ecology* 86:2278–2287.

One of the first studies using phylogenies to test whether speciation rate varies with latitude; the authors found that speciation is higher in the tropics in a large clade of birds.

Condamine, F. L., F. A. H. Sperling, N. Wahlberg, J. Y. Rasplus and G. J. Kergoat. 2012. What causes latitudinal gradients in species diversity? Evolutionary processes and ecological constraints on swallowtail biodiversity. *Ecology Letters* 15:267–277.

A large scale analysis of butterflies testing different potential drivers of the latitudinal diversity gradient. This work shows a strong role of shifts in species distribution from high to low latitudes related to cooling events, and a possible role of diversification.

Darlington P.J. 1959. Area, climate, and evolution. *Evolution* 13:488–510.

One of the first articles to formalize hypotheses about species dispersal between temperate and tropical regions.

Davies, T. J., S. A. Fritz, R. Grenyer, C. D. L. Orme, J. Bielby, O. R. P. Bininda-Emonds, M. Cardillo, K. E. Jones, J. L. Gittleman, G. M. Mace, and A. Purvis 2008. Phylogenetic trees and the future of mammalian biodiversity. *Proceedings of the National Academy of Sciences of the USA* 105:11556–11563.

This article describes the gradient of species diversity in mammals and proposes causes for the extinction of mammals.

Fuhrman, J. A., J. A. Steele, I. Hewson, M. S. Schwalbach, M. V. Brown, J. L. Green, and J. H. Brown 2008. A latitudinal diversity gradient in planktonic marine bacteria. *Proceedings of the National Academy of Sciences of the USA* 105:7774–7778.

A rare study of the latitudinal diversity of pelagic marine bacteria from 103 samples in coastal and pelagic water. This study confirms a strong latitudinal gradient in the world of oceanic micro-organisms.

Hawkins, B. A. 2001. Ecology's oldest pattern? *Trends in Ecology & Evolution* 16:470.

This article discusses when the latitudinal diversity gradient was first discovered and proposes that Alexander von Humboldt was likely the first scientist to describe this pattern.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. *American Naturalist* 163:192–211.

A highly-cited article studying the slope and the pervasiveness of the latitudinal diversity gradient in many clades.

Jablonski, D., Roy, K. and Valentine, J.W. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314:102–106.

A very important article testing the fundamental hypotheses about the construction of the latitudinal gradient with exceptional fossil data of bivalves. This article suggests that the tropics are both a cradle and museum of biodiversity.

Kouki et al. 1994. Reversed latitudinal gradient in species richness of sawflies (Hymenoptera, Symphyta)

This article describes the example of sawflies, a clade that shows an inverse latitudinal diversity gradient, with higher diversity in the temperate regions.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* 10:315–331.

A classic review of the major hypotheses related to the construction of the latitudinal diversity gradient.

Otté, E. C. and H. B. Bohn translators 1850. Views of Nature: or Contemplations on the Sublime Phenomena of Creation; with Scientific Illustrations, 3rd edn (Alexander von Humboldt), Henry G. Bohn

This is the translation of what could be a first description of the latitudinal diversity gradient according to Hawkins et al. 2001 *Trends Ecol. Evol.*

Ricklefs, RE 2006. Global variation in the diversification rate of passerine birds. *Ecology* 87: 2468–2478.

This article studies the variables, including latitude, that explain diversification rates in birds; it was one of the first studies to show faster diversification in tropical clades.

Wiens, J.J. C. H. Graham, D. S. Moen, S. A. Smith, T. W. Reeder 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *American Naturalist* 168:579–596.

This article tests hypotheses of the origin of the latitudinal diversity gradient in hylid frogs.

Wiens, J. J., J. Sukumaran, R. A. Pyron and R. M. Brown 2009. Evolutionary and biogeographic origins of high tropical diversity in old world frogs (Ranidae). *Evolution* 63:1217–1231.

This article studies the role of diversification and dispersal in a large group of Ranidae frogs.

## Textbooks

To our knowledge no textbooks are focused solely on the latitudinal diversity gradient, but many books focusing on species diversity considered this pattern at great length, such as Rosenzweig 1995. For example, Worm & Tittensor 2018 have described the latitudinal gradients for many clades. General textbooks of macroecology (Gaston & Blackburn 2000), biogeography (Lomolino 2017) and speciation (Price 2008) all include sections covering the latitudinal diversity gradient.

Worm, B., and D. P. Tittensor 2018. *A Theory of Global Biodiversity*. Princeton University Press.

This book focuses on differences of species diversity through space, and provides a large number of examples of patterns for various clades.

Lomolino, M. V., Riddle, B. R., and R. J. Whittaker 2017. *Biogeography*. Sunderland, MA: Oxford University Press.

A classic book describing the grand principles of biogeography, describing the main global patterns of diversity and the major factors affecting them.

Gaston, K. J. and T. M. Blackburn 2000. *Pattern and Process in Macroecology*. Blackwell Science Ltd.

A highly cited book on the ecological causes of patterns of diversity. This book had a particularly strong impact on ecologists studying biogeography.

Coyne, Jerry A., and H. Allen Orr. 2004. *Speciation*. Vol. 37. Sunderland, MA: Sinauer Associates.

A major book for students and researchers interested in the speciation process and the mechanisms of reproductive isolation. Even though it could be updated to include new advances in genomics, this book describes in detail the fine scale process that explain the emergence of large scale patterns of biodiversity.

Price, T. 2008. *Speciation in birds*. Roberts and Co.

A very complete summary of how new species of birds form, and how this process of speciation may be related to global scale diversity patterns.

Rosenzweig, M. L., 1995 *Species diversity in space and time*. Cambridge University Press.

A classic book focusing on the major patterns of diversity such as latitudinal pattern and the species-areas relationship and equilibrium models.

## Journals

Articles investigating the latitudinal diversity gradient appear in ecology and evolution journals such as *The American Naturalist*, *Proceedings of the Royal Society B*, *Ecology Letters*, *Evolution*, *Global Ecology and Biogeography*, *Journal of Biogeography*, and *Nature Ecology and Evolution*. Reviews can be found in journals such as *Trends in Ecology and Evolution*. More generalist journals including *Science*, *Nature*, and *Proceedings of the National Academy of Sciences USA* also regularly publish articles on this subject.

*The American Naturalist*, 1867–. [<http://www.press.uchicago.edu/ucp/journals/journal/an.html>]\*

The journal from the Society of American Naturalists, publishes high quality science in ecology and evolutionary biology and often in rather long format. This journal publishes both theoretical and empirical works.

*Evolution* 1947–. [[http://onlinelibrary.wiley.com/journal/10.1111/\(ISSN\)1558-5646](http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1558-5646)]\*

The original journal from the Society for the Study of Evolution and has been a central journal for publishing research on latitudinal gradients in a phylogenetic context. The journal publishes articles, commentaries, book reviews and perspectives.

*Proceedings of the Royal Society B* 1905–. [<https://royalsocietypublishing.org/journal/rspb>]\*

Old and prestigious journal of the Royal Society, publishes rather short articles in the field of evolutionary biology and ecology. It also publishes short reviews and comments.

*Nature Ecology and Evolution*, 2017–. [<https://www.nature.com/natecolevol/>]\*

A new high profile journal in ecology and evolution. Publishes rather short and broad-impact research articles and reviews.

*Trends in Ecology and Evolution*, 1986–. [<http://www.cell.com/trends/ecology-evolution/>]\*

Publishes mostly rather short reviews on timely topics of research in all fields of evolution and evolutionary biology.

*Proceedings of the National Academy of Sciences USA*, 1915–. [<https://www.pnas.org>]\*

*PNAS* is a very prestigious general journal established by the National Academy of Sciences of the United States of America covering a large spectrum of biology research including ecology and evolution.

*Ecology letters*, 1998–. [<https://onlinelibrary.wiley.com/journal/14610248>]\*

This journal publishes high impact and rather short articles. It has been one of the leading journals specializing in the ecological and evolutionary drivers of diversity patterns in the last decade.

Nature, 1869–. [<https://www.nature.com>]\*

The two big general journals - *Nature* and *Science* - often publish articles of exceptional importance in global analyses of species distribution including some functional, phylogenetic or phylogenomic components.

Science, 1880–. [<https://www.science.org>]\*

With *Nature*, *Science* is the leading journal for publishing very short high impact articles in all fields of sciences, including evolution and ecology.

### **Latitudinal diversity patterns are dynamic through time**

Most studies of the latitudinal diversity gradient examine the diversity of life on Earth today. However, an important question is the degree to which this pattern has remained the same through time. Studies of the fossil record have found that the relative shape of the latitudinal diversity gradient has changed over time, and that these changes are associated with large shifts in Earth's climate (Crame 2011, Mannion et al. 2014). The gradient was relatively flat during 'greenhouse' warm periods in Earth's history, for example at the end of the Cretaceous. In contrast, the gradient was steeper during 'coldhouse' periods, such as the end of the Cenozoic. For example, Song et al. 2020 reported a flat latitudinal diversity gradient after the Permian–Triassic extinction for invertebrates and Rose et al. 2011 showed that during the Paleocene the latitudinal gradient of North American mammals was flat. Attempts to reconstruct the latitudinal diversity gradient in the deep past are complicated by geographic biases in bedrock availability and fossil sampling (Jones et al. 2021). Notwithstanding these difficulties, variation over time in the shape of the gradient offers an interesting way to test hypotheses about the factors generating the latitudinal diversity gradient, and suggests that overall climate strongly shapes latitudinal patterns of diversity. These changes over time may even be occurring at present: it has recently been suggested that anthropogenic climate change is altering the latitudinal diversity gradient for marine life (Chaudhary et al. 2021).

Crame, J. A. 2001. Taxonomic diversity gradients through geological time. *Diversity and Distribution*. 7: 175–189.

One of the first studies to detail latitudinal diversity patterns for bivalves clades at different periods in Earth's history. The study finds an equatorial peak of diversity during the Carboniferous (Visean and Tournaisien, 358-330 Myrs) but a peak at mid latitude during the end of the Cretaceous (72-66 Myrs), which suggests that the latitudinal gradient may be flatter in warm periods.

Rose, P. J., D. L. Fox, J. Marcot, C. Badgley 2011. Flat latitudinal gradient in Paleocene mammal richness suggests decoupling of climate and biodiversity. *Geology*. 39:163:166.

An important article showing that the latitudinal diversity gradient for North American mammals was flat at the beginning of the Cenozoic; this dataset is arguably the most complete fossil record available for mammals. This also suggests that the current steep latitudinal diversity gradient has been created recently.

Mannion, P. D., P. Upchurch, R. B. Benson and A. Goswami. 2014. The latitudinal biodiversity gradient through deep time. *Trends in ecology & evolution*. 29:42-50.

An insightful review of the past literature on the paleontological evidence for variations in the past latitudinal biodiversity gradients.

Jones L. A., C. D. Dean, P. D. Mannion, A. Farnsworth and P. A. Allison. 2021. Spatial sampling heterogeneity limits the detectability of deep time latitudinal biodiversity gradients. *Proceedings of the royal society B*. 288: 20202762.

A first attempt to distinguish whether the latitudinal diversity gradient can be accurately reconstructed from paleontological data alone. The article uses simulations to test whether bedrock availability for each geological period will be sufficient to reconstruct latitudinal gradient. Their results suggest that it may be difficult to reconstruct latitudinal diversity patterns with confidence for some periods.

Chaudhary, C., A. Richardson, D. Schoeman and M. J. Costello. 2021. Global warming is causing a more pronounced dip in marine species richness around the equator. *Proceedings of the National Academy of Science of the U.S.A.* 18:e2015094118

This article suggests for the first time that there might be a decline in marine tropical diversity since the 1950s. The article presents a global scale analysis of nearly 50,000 marine species, and proposes that the latitudinal gradient may have shifted in the last decades from an equatorial position to mid-latitudes (due to this tropical decline). If these results are confirmed, it may suggest that large-scale shifts of distribution of major biodiversity gradients can be exceptionally fast.

Song, H., S. Huang, E. Jia, X. Dai, B. M. Paull, and A. M. Dunhill 2020. Flat latitudinal diversity gradient caused by the Permian–Triassic mass extinction. *Proceedings of the National Academy of Science of the U.S.A.* 117:17578–17583.

A case study showing that the slope of the latitudinal diversity gradient of bivalves flattened after the Permian-Triassic extinction. This result confirms the results of Sun et al. 2012 in *Science* and provides further evidence that the latitudinal gradient may be flattened by the extinction of species in tropical regions when climate is extremely warm. See also the commentary of Mannion in the same issue.

### **Major explanations for the pattern**



The number of hypotheses to explain the latitudinal diversity gradient has consistently grown over time. Some of the classic articles reviewing these hypotheses include the work of Pianka (1966), Rohde et al. (1992), Willig et al. (2003), Mittelbach et al. (2007) and Brown (2014). We can mainly distinguish two types of hypotheses: hypotheses related to rates of diversification (speciation and extinction) and hypotheses related to dispersal of lineages (history). The first type of hypothesis proposes that rates of speciation should be higher (“cradle hypothesis”) and extinction rate lower (“museum hypothesis”) in the tropics compared to temperate regions. The second type of hypothesis proposes that species have mainly shifted their distributions from high latitudes to low latitudes over geologic time, leading to the disproportionate accumulation of species in the tropics (Wiens and Donoghue 2004). This hypothesis implies that niche conservatism was strong (Wiens and Graham 2005) as most species have failed to colonize the temperate regions, but instead have followed their preferred temperature towards equator during the global cooling in the last 40 million years (Saupe et al. 2019, Rolland et al. 2018). This hypothesis also relates to the fact that, at the beginning of the Cenozoic, there were already fewer species in the temperate regions, as the temperate biome was representing a small fraction of the area on earth. Note that there are many more hypotheses; we summarize some of these in the section “Other hypotheses”.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, C. M. McCain, A. R. McCune, L. A. McDade, M. A. McPeck, T. J. Near, T. D. Price, R. E. Ricklefs, K. Roy, D. F. Sax, D. Schluter, J. M. Sobel and M. Turelli, 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* 10: 315–331

A major review presenting evolutionary hypotheses to explain the latitudinal diversity gradient. Hypotheses related to diversification and time for speciation are detailed with schematics.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100:33–46.

One of the first major efforts detailing the main hypotheses to explain the latitudinal diversity gradient. Many modern hypotheses are built on the ideas presented in this article.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65:514–527.

More recent than Pianka et al. 1966, this article gave a nearly-exhaustive view of the main hypotheses in the literature in the early 1990s.

Zachos, J. C., G. R. Dickens and R. E. Zeebe. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451:279–283.

A highly cited analysis reconstructing global temperature during the Cenozoic based on the carbon isotopes of foraminifera shells obtained from deep marine cores.

Rosenzweig, M. L. 1992. Species diversity gradients: we know more and less than we thought. *Journal of Mammalogy* 73:715-730

A classic article investigating the causes of richness gradients; in particular it details the hypothesis that larger areas can promote diversification.

Saupe, E. E., Farnsworth, A., Lunt, D. J., Sagoo, N., Pham, K. V., & Field, D. J. 2019. Climatic shifts drove major contractions in avian latitudinal distributions throughout the Cenozoic. *Proceedings of the National Academy of Sciences of the USA* 116:12895-12900.

A recent test of tropical niche conservatism based on reconstruction of past distribution of species matching the distribution of fossils.

Wiens, J. J., & Graham, C. H. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review in Ecology Evolution and Systematics* 36:519-539.

One of the fundamental articles defining what niche conservatism is, and what the consequences of niche conservatism are for species diversity patterns.

Willig, M. R., Kaufman, D. M., & Stevens, R. D. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual review of ecology, evolution, and systematics* 34:273-309.

A thorough review of the different mechanisms at play during the emergence of diversity patterns.

### **Why might we expect speciation rates to vary with latitude: molecular evolution and species interactions**

Several hypotheses to explain the latitudinal diversity gradient propose that speciation is faster in the tropics ("cradle hypothesis"). There are two main reasons why this might be so. First, higher temperature/energy in the tropics could lead to faster speciation according to the metabolic theory of biodiversity (Brown 2004). This idea proposes that mutation rates are faster at high temperature due to faster enzymatic and chemical reactions, with faster rates of molecular evolution leading to faster divergence between populations and faster speciation rates. While some studies have indeed reported that molecular evolution is faster in the tropics (Wright et al. 2006) this result has been questioned by a recent comprehensive analysis that found rates of molecular evolution to be similar across latitudes in both ectotherms and endotherms (Orton et al. 2018). Second, stronger species interactions in the tropics could explain why there are more species at low latitudes. This hypothesis proposes a positive feedback loop, where stronger species interactions lead to faster speciation in the tropics. Then, the higher number of species leads to stronger species interactions by increasing the number of potential interactions (Roslin et al. 2017). This is therefore a "diversity begets diversity" hypothesis. In 2009, Schemske reviewed the literature, and concluded that species interactions, including parasitism, mutualism and competition, are indeed typically stronger in the tropics compared to temperate regions.

However, this conclusion has since been questioned (Moles and Ollerton 2016), and the link between an increase in the strength of interaction and diversification has not been clearly quantified. Interactions between species may accelerate the rate of morphological evolution through adaptations, but rates of phenotypic evolution in traits that are thought to be involved in species interactions have either been shown to be faster in temperate regions (Lawson and Weir 2014, Roesti et al. 2020), or not different between latitude (Freeman et al. 2021).

Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Annual review of ecology, evolution, and systematics*, 40:245-269.

An important review compiling evidence for how the strength of biotic interactions varies across the latitudinal gradient. This review has been a central argument for supporting the hypothesis that there should be higher speciation rate in the tropics due to stronger intensity of biotic interactions.

Roesti, M., D. N. Anstett, B. G. Freeman, J.A Lee-Yaw, D. Schluter, L. Chavarie, J. Rolland and R. Holzman. 2020. Pelagic fish predation is stronger at temperate latitudes than near the equator. *Nature communications* 11:1-7.

This paper uses 55 years of fisheries data to estimate predation rates for pelagic fishes. The study shows that the predation rate has been higher in the temperate regions than the tropics, and that predation rate is therefore unrelated to species richness.

Roslin, T., B. Hardwick, V. Novotny, W. K. Petry, N. R. Andrew, A. Asmus., and E. M. Slade. 2017. Higher predation risk for insect prey at low latitudes and elevations. *Science* 356:742-744.

A global effort to test whether biotic interactions are stronger in the tropics. The authors coordinated a global network of collaborators to deploy model caterpillars made of green plasticine and record rates of predation on these models. The authors find higher attack rates at low latitudes and low elevations, consistent with higher predation pressure in the tropics.

Lawson, A. M., and Weir, J. T. 2014. Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes. *Ecology Letters* 17:1427-1436.

A study showing that the rate of climatic niche evolution is higher in temperate than in tropical regions. The study uses phenotypic evolution models (such as the Brownian Motion) on phylogenetic data for 111 species pairs of birds. They also find an association between niche evolution and evolution of other traits (song and body mass).

Moles, A. T., and Ollerton, J. 2016. Is the notion that species interactions are stronger and more specialized in the tropics a zombie idea? *Biotropica*, 48.

This article discusses the evidence that species interactions are stronger in the tropics, and proposes that there is relatively weak evidence from data in recent studies.

Freeman, B. G., Schluter D. and J. A. Tobias. 2021. The latitudinal gradient in rates of evolution for bird beaks, a species interaction trait. *Ecology Letters*. (accepted, in press)

This study shows that bird beaks evolve faster in the temperate zone than the tropics (for beak shape) or at similar rates across latitudes (for beak size) in a global analysis of ~ 1,200 sister species of birds. The authors compile evidence from the literature to show that evolutionary rates are typically faster in the temperate zone than the tropics.

Wright, S., J. Keeling, and L. Gillman. 2006. The road from Santa Rosalia: a faster tempo of evolution in tropical climates. *Proceedings of the National Academy of Sciences*, 103:7718-7722.

A test showing that the rate of molecular evolution is faster in tropical than in temperate regions. This idea relates to the fact that the rate of molecular evolution should be related to the rate of speciation. The authors nonetheless show that the increase of the rate of molecular evolution is not due to higher rate of speciation.

### **Empirical evidence: Is speciation rate higher in the tropics or in temperate regions?**

While we have some reasons to expect that speciation rates might vary as a function of latitude, ultimately this is an empirical question that can be addressed with both fossil and phylogenetic data. Related to the “cradle” hypothesis, studies based either on paleontological evidence or birth-death models fitted on phylogenetic trees have found faster speciation rates in the tropics for brachiopods (Jablonski 2006), mammals (Rolland et al. 2014) and birds (Pulido-Santacruz and Weir 2016). However, analyses of recent branch lengths of phylogenetic trees have reported faster speciation rate in the temperate zone than the tropics for birds and mammals (Weir & Schluter 2007), plants (Igea & Tanentzap 2020) and fish (Rabosky et al. 2018). Similarly, new analyses of bird phylogenomic data conclude that speciation is not higher in the tropics where species richness is highest (Harvey et al. 2020). These analyses suggest that current hotspots of richness are not presently hotspots of speciation (Schluter and Pennell 2018), though more research is required to understand if these current richness hotspots were speciation hotspots in the past (Morlon 2020). Overall, recent speciation rates seem to either be faster in the temperate zone or similar between the tropics and temperate regions. We can therefore conclude that the contribution of speciation rate to the latitudinal diversity gradient is likely weak.

Brown, J. H., J. F. Gillooly, A. P. Allen. V. M., Savage and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771-1789.

This highly cited article presents the metabolic theory of ecology. It proposes that speciation is faster in the tropics because increased solar energy speeds up enzymatic reactions and metabolic rates.

Harvey, M. G., G. A. Bravo, S. Claramunt, A. M. Cuervo, G. E. Derryberry, J. Battilana, G. F. Seeholzer, J. S. McKay, B. C. O'Meara, B. C. Faircloth, S. V. Edwards, J. Pérez-Emán, R. G. Moyle, F. H. Sheldon, A. Aleixo, B. Tilston Smith, R. T. Chesser, L. F. Silveira, J. Cracraft, R. T. Brumfield, E. P. Derryberry. 2020. The evolution of a tropical biodiversity hotspot. *Science*, 370:1343-1348.

A large-scale phylogenomic study based on 1,940 individuals of 1,287 species of suboscine passerine birds (98.2% of extant suboscine passerines). Interestingly, this study shows that speciation rate is not higher in the tropics.

Igea, J., and A. J. Tanentzap 2020. Angiosperm speciation cools down in the tropics. *Ecology letters*, 23:692-700.

A recent study showing that speciation rate tends to be slower in the tropics for angiosperms. The authors used phylogenetic information for 60,990 species and the software BAMM (Bayesian Analysis of Macroevolutionary Mixtures); note that this methodology does not attempt to estimate extinction.

Morlon, H. 2020. Diversity hotspots: Coldspots of speciation? *Science* 370:1268-1269.

This commentary summarizes the contradictory results obtained in the various diversification studies in the last decade: most recent studies (based on diversification rate methods - DR) find that speciation rate is higher in the temperate region than in the tropics, while most studies before this (based on SSE) tended to show the opposite. These contradictory results may be related to the fact that DR statistics may be detecting the signal of recent speciation, while SSE may be detecting longer term diversification dynamics.

Pulido-Santacruz, P., & Weir, J. T. 2016. Extinction as a driver of avian latitudinal diversity gradients. *Evolution* 70:860-872.

This study uses state-dependent speciation and extinction models (SSE, in particular a geographic state dependent speciation and extinction model: GeOSSE) to show that speciation rate is higher in the tropics and extinction rate is higher in the temperate regions using the phylogeny of world birds.

Rabosky, D. L., J. Chang, P.O. Title, P. F. Cowman, L. Sallan, M. Friedman, K. Kaschner, C. Garilao, T. J. Near, M. Coll and M. E. Alfaro 2018. An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* 559:392-395.

This article constructed a global phylogeny of teleost fishes (31,526 spp.) and used DR statistics and BAMM models to show that recent speciation rate is higher in temperate regions.

Rolland, J., F. L. Condamine, F. Jiguet, and H. Morlon. 2014. Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS biology* 12:e1001775.

A study showing with state-dependent speciation and extinction models that speciation is faster in the tropics and extinction is higher in the temperate regions using a mega phylogeny of

mammals. The author also ran the analyses at the order level, showing that most orders show similar results, with the exception of Carnivora and Lagomorpha.

Schluter, D. and Pennell 2018. Speciation gradients and the distribution of biodiversity. *Nature* 546:48–55.

This article reviews different patterns regarding the relationship between speciation rate and species richness, as well as species richness and area. One of the main messages of the article is that recent speciation rate may often be higher in places where species richness is low.

Weir, J. T., and D. Schluter. 2007. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* 315:1574-1576.

A classic article showing with the analyses of sister species that speciation and extinction may be faster in the temperate regions for birds and mammals. This article shows that the net diversification rate (the net difference between speciation and extinction rate) is not different between tropical and temperate regions.

### **Do extinction rates vary with latitude?**

There are many recent tests of latitudinal differences in speciation rate but relatively few that have investigated extinction rates. However, several hypotheses propose that extinction rates vary with latitude and could explain the latitudinal diversity gradient. The most famous extinction hypothesis starts with the observation that recent glaciation in temperate regions likely increased extinction rates at high latitudes. For example, a large extent of northern North America and Europe was covered by ice during the last ice age (~ 20,000 years ago). These glaciation events driven by Milankovitch cycles have occurred many times over the Pleistocene, with each glaciation causing population extinctions at high latitudes (Dynesius and Jansson 2000). There are also reasons to expect that extinction rates should be reduced in the tropics, where stable climate has been hypothesized to “protect” species from extinction over the long term (the “museum” hypothesis). However, few studies have been able to detect stronger extinction rates in temperate regions than in tropical regions (Rolland et al. 2014 for mammals, Pulido Santacruz 2016 for birds, and Meseguer and Condamine 2020 for turtles, crocodilia and lepidosauria). One major difficulty in this effort is that extinction is difficult to reconstruct with phylogenies alone. The analysis of large scale fossil databases may help to test such hypotheses in the future (e.g., studies on species durations in the fossil record, Silvestro 2020). A key question given anthropogenic climate change is whether extremely hot periods lead to greater extinction in tropical regions: while a handful of studies support this relationship (see Sun et al. 2012 and Song et al. 2020), it is unclear if this is a general pattern.

Dynesius, M., and R. Jansson 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences*, 97:9115-9120.

A study shedding light on how climatic fluctuations over long time scales have shaped diversity and species characteristics at high latitudes. For example, the authors argue that temperate species, which have most likely experienced repeated rounds of glaciations, should have evolved higher dispersal capacities in order to escape periodic harsh climatic conditions.

Meseguer, A. S. and F. L. Condamine 2020. Ancient tropical extinctions at high latitudes contributed to the latitudinal diversity gradient. *Evolution* 74:1966-1987.

A study showing that Testudines, Crocodylia, and Lepidosauria experienced extinctions at high latitudes when the tropical environment contracted towards the equator during climate cooling. The article also illustrates nicely the hypothesis of a tropical contraction with both phylogenetic and fossil models of diversification.

Pulido-Santacruz, P., and J. T. Weir 2016. Extinction as a driver of avian latitudinal diversity gradients. *Evolution* 70:860-872.

According to this SSE analysis (using GeoSSE type models) of a global phylogeny of birds, extinction should be the driving force of the latitudinal diversity gradient. Speciation and dispersal rates were not significantly associated with latitude.

Rolland, J., F. L. Condamine, F. Jiguet and H. Morlon 2014. Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS biology* 12:e1001775.

A large-scale SSE analysis of a mammals mega-phylogeny showing that the peak of diversity in the tropics is associated with higher speciation and lower extinction rates in the tropics. The results of this study are consistent with the “out of the tropics” hypothesis.

Silvestro, D., S. Castiglione, A. Mondanaro, C. Serio, M. Melchionna, P. Piras, M. Di Febbraro, F. Carotenuto, L. Rook, and P. Raia 2020. A 450 million years long latitudinal gradient in age-dependent extinction. *Ecology letters*,23:439-446.

This article uses recent age-dependent-extinction models to analyze the fossil record of 21 clades of marine invertebrates. These models test whether the probability of extinction is independent of species age. A key result of the model is that, in the tropics, species tend to die either very fast after their appearance or tend to survive during long periods with a relatively low risk of extinction. In the temperate region, species tend to go extinct with the same probability (whatever their age). This result supports the argument that species extinction can be caused by external factors such as climate in temperate species.

Song, H., S. Huang, E. Jia, X. Dai, P. B. Wignall, and A. M. Dunhill 2020. Flat latitudinal diversity gradient caused by the Permian–Triassic mass extinction. *Proceedings of the National Academy of Sciences of the USA* 117:17578-17583.

An analysis of 52,318 occurrences of the marine fossil record showing that tropical extinctions led to a flatter latitudinal diversity gradient after the Permian-Triassic transition (between 252-247 million years ago).

Sun, Y., M. M. Joachimski, P. B. Wignall, C. Yan, Y. Chen, H. Jiang, L. Wang, and X. Lai 2012. Lethally hot temperatures during the Early Triassic greenhouse. *Science* 338.6105:366-370.

This analysis of the fossil record of multiple clades of fish, reptiles and plants and other marine clades shows a peak of extinction in the tropics during the early Triassic (250 million years ago).

### **Geographic range evolution and the development of the latitudinal diversity gradient**

In the sections above, we considered how rates of speciation and extinction might vary between tropical and temperate regions. The third critical ingredient to thinking about the latitudinal diversity gradient we see today is the dispersal of species between latitudinal zones. After all, once formed, species have the opportunity to expand their geographic ranges. Here, we can distinguish two main hypotheses about latitudinal differences in dispersal of species. First, species generated in the tropics might often be able to colonize the temperate zone: this model is called the “out of the tropics” hypothesis (Jablonski 2006). Second, the opposite may occur: species that originate in the tropics may have difficulty in successfully colonizing the temperate zone: this model is called the “tropical niche conservatism” hypothesis (Wiens and Donoghue 2014). Under both hypotheses, the origin of diversity in deep time is assumed to primarily be tropical, given that nearly the entire Earth was “tropical” during the beginning of the Cenozoic when temperatures were higher (~50 Myrs ago). Both hypotheses also predict that lineages progressively accumulate in tropical regions (Cooper et al. 2011, Olalla et al. 2011). These hypotheses can be tested by mapping past dispersal events using both the fossil record and biogeographical reconstruction based on phylogenies (Rolland et al. 2018). Importantly, as described above, there were times in Earth’s history when high latitudes were “tropical” in climate and had high species richness. One possibility is that as this once-widespread “tropical” biome contracted towards the equator as Earth’s climate cooled, species living at higher latitudes within this “tropical” biome colonized lower latitudes while disappearing from higher latitudes (e.g. Pyron and Wiens 2013 for amphibians, Pyron 2014 for squamates, Duchene and Cardillo 2015 for birds or Rolland et al. 2018 for terrestrial vertebrates). This process increased diversity closer to the equator while decreasing diversity towards the poles, generating the latitudinal patterns of diversity that we see today. This process could also be viewed as “local” extinction at high latitudes, while species persist in the tropics. However, more research is needed to know how the latitudinal limits of the tropical biome evolved through time, and if tropical biome contraction towards the equator has truly been the driving force of the dispersal toward the tropics in the Cenozoic.

Cooper, N., R. P. Freckleton and W. Jetz. 2011. Phylogenetic conservatism of environmental niches in mammals. *Proceeding of the Royal Society B* 278:2384–2391.

A phylogenetic analysis of the phylogenetic conservatism across mammals. The authors estimated the strength of the phylogenetic conservatism based on the sigma parameter of a



brownian motion model. Tropical species were found to have more slowly evolving niches than temperate species.

Duchêne, D. A., and M. Cardillo. 2015. Phylogenetic patterns in the geographic distributions of birds support the tropical conservatism hypothesis. *Global Ecology and Biogeography* 24:1261-1268.

A phylogenetic analysis reconstructing the latitudinal distribution of over 9,000 bird species. The study reconstructs shifts of distribution that are consistent with the tropical niche conservatism (more frequent shifts from temperate to the tropical regions than from tropical to temperate regions).

Jablonski, D., K. Roy and J. W. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314:102-106.

A classic study using bivalves to test the “out of the tropics” hypothesis for which higher net diversification in the tropical regions and species are then exported towards the temperate regions.

Mannion, P. D., P. Upchurch, R. B. Benson, and A. Goswami. 2014. The latitudinal biodiversity gradient through deep time. *Trends in ecology & evolution* 29:42-50.

An important review of the paleontological evidence for variations in the shape of the latitudinal diversity gradient through time.

McKenna, D. D. and B. D. Farrell. 2006. Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Proceedings of the National Academy of Sciences of the USA* 103:10947– 10951.

A case study showing with a new phylogeny of Neotropical leaf beetles that the tropical region is both a “cradle” and a “museum” of species.

Olalla-Tárraga, M. A., L. McInnes, L. M. Bini, J. A. F. Diniz-Filho, S. A. Fritz, B. A. Hawkins, J. Hortal, C. D. L. Orme, C. Rahbek, M. Á. Rodríguez, and A. Purvis. 2011. Climatic niche conservatism and the evolutionary dynamics in species range boundaries: global congruence across mammals and amphibians. *Journal of Biogeography* 38:2237–2247.

A study on climatic niche conservatism and how slow niche evolution may impact shifts in geographic distributions.

Pyron, R. A., and J. J. Wiens. 2013. Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. *Proceedings of the Royal Society B: Biological Sciences*, 280:20131622.

One of the first large scale studies of vertebrates using a SSE model (here BiSSE) to reconstruct the past diversification dynamics in the context of the latitudinal diversity gradient. The study finds higher speciation and lower extinction rates in the tropics and stronger dispersal from the temperate regions to the tropics.

Pyron, R. A. 2014. Temperate extinction in squamate reptiles and the roots of latitudinal diversity gradients. *Global Ecology and Biogeography*, 23:1126-1134.

A similar study to Pyron and Wiens 2013 but using a global phylogeny of squamates. The authors use the GeoSSE model to estimate higher speciation rate and lower extinction rate in the tropics, and also the lower dispersal of species from the tropics to the temperate regions than the other way (from the temperate zone to the tropics).

Rolland, J., D. Silvestro, D. Schluter, A. Guisan, O. Broennimann, and N. Salamin, 2018. The impact of endothermy on the climatic niche evolution and the distribution of vertebrate diversity. *Nature Ecology & Evolution* 2:459-464.

This study reconstructs the past distribution for 11,465 species of mammals, birds, amphibians and squamates based on present day points of occurrence, phylogenetic and fossil information. The article shows that a large fraction of tropical lineages originated in temperate regions. Another result is that endotherms tend to evolve their climatic niche faster than ectotherms, this faster evolution may have permitted larger latitudinal ranges in these species.

Wiens, J. J., and M. J. Donoghue 2004. Historical biogeography, ecology and species richness. *Trends in ecology & evolution* 19:639-644.

The authors propose that historical biogeography may have played a major role in the construction of the latitudinal diversity gradient. This idea was also proposed previously by Latham and Ricklefs 1993 *Oikos* using tree data.

Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I. Damschen, T. J. Davies, J.-A. Grytnes, S. P. Harrison, B. A. Hawkins, R. D. Holt, C. M. McCain, P. R. Stephens 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13:1310–1324.

The fundamental article describing the concept of niche conservatism. The authors describe a large variety of topics that can be studied related to niche evolution, such as species invasion, response to climate change, community assembly and species richness patterns.

### **The reasons for tropical niche conservatism: adaptations to temperate regions may be difficult**

The tropical niche conservatism hypothesis stipulates that lineages with a tropical origin rarely colonize temperate regions (Wiens 2007, Wiens and Donoghue 2004). According to this hypothesis, species should follow their climatic preferences through deep time, moving towards the equator when climate is cooling down, and moving towards the poles when climate is warming up. Indeed, this is the primary explanation why some lineages living mostly in the tropics today, like crocodiles or palm trees, have been found in the fossil record of polar regions in the early Cenozoic but not afterward. The question then is: why didn't such species persist at high latitudes during times when Earth cooled? The tropical niche conservatism hypothesis proposes that adaptation to cold climates, in particular to freezing

temperatures, is often very difficult. This is not to say that adaptation to colder climates is impossible: in angiosperms, Zanne et al. 2014 noted three major key adaptation for the colonization of the lineages into temperate regions: a change in growth habits (from woody to herbaceous), leaf phenology (from evergreen to deciduous), and smaller hydraulic conduits to avoid embolism related to frost. In conifers, species have a morphology adapted to heavy snow falls (such as triangle geometry and small leaf areas), and many species have evolved to produce glucose to protect cells from freezing (e.g. woodfrog, Larson et al. 2014) or antifreeze proteins that bind ice crystals (e.g. in bacteria, fungi, insects, vertebrates or plants, e.g. Griffith and Yaish 2004). In order to adapt to stronger seasonality, temperate species have evolved larger climatic niches (Rolland & Salamin 2016), given that they have to adapt to seasonal variations of resources. There have also evolved more specific strategies to avoid winter conditions: the obvious one is seasonal migration (e.g. birds, mammals) latitudinally or altitudinally, molt in order to improve thermic insulation during cool periods and fat storage. We can also list other adaptations, such as thermal reduction of metabolic activity — hibernation or torpor (e.g. marmots, bats) — or the fact that species should minimize the ratio surface/volume of their body. This latter rule has been called the Allen's rule (Allen 1877). Dynesius and Jansson 2000 have also proposed that species should have a larger geographic range in temperate regions in order to shift to lower latitude to avoid the extirpation of population during glaciations. The pattern that temperate species have a larger geographic range than tropical species is called the Rapoport's rule (Stevens 1989).

Allen, J. A., 1877. The influence of physical conditions in the genesis of species. *Radical Review* 1:108–140.

The article that historically launched the hypothesis that climatic conditions should have a systematic impact on the traits of species with latitude.

Griffith, M., and M. W. Yaish 2004. Antifreeze proteins in overwintering plants: a tale of two activities. *Trends in plant science* 9:399-405.

A study on the antifreeze proteins that have evolved in many independent clades of plants.

Larson, D. J., L. Middle, H. Vu, W. Zhang, A. S. Serianni, J. Duman, and B. M. Barnes 2014. Wood frog adaptations to overwintering in Alaska: new limits to freezing tolerance. *Journal of Experimental Biology* 217, 2193-2200.

A case study on an exceptional adaptation to frost tolerance in Alaskan amphibians. The study describes how body temperature drops during the winter and how cells accumulate glucose and glycoproteins to protect them.

Rolland J. and N. Salamin 2016. Niche width impacts vertebrate diversification. *Global Ecology and Biogeography* 25.10:1252-1263.

A large-scale analysis using global phylogenies of birds, mammals and amphibians, showing that climatic specialists tend to have faster rate of speciation and lower rate of extinction. This is inconsistent from analyses of specialist species threatened according to the IUCN status. One

potential explanation is that most specialist lineages live in tropical habitats and experience less extinction on longer time scales.

Stevens, G. C. 1989. The latitudinal gradients in geographical range: how so many species co-exist in the tropics. *The American Naturalist* 133:240–256.

This article presents data and potential explanations for the Rapoport's rule: the pattern that temperate species have larger range size than tropical species. It also proposes that both latitudinal diversity gradient and the Rapoport's rule have the same underlying cause: stronger climatic variations in temperate regions.

Wiens, J.J. 2007. Global patterns of diversification and species richness in amphibians. *The American Naturalist*, 170:S86–S106.

The author analyzes the diversification hypothesis with frogs and salamanders and shows that speciation rate is higher in tropical regions for both clades (using the method of moments estimator).

Zanne, A. E., D. C. Tank, W. K. Cornwell, J. M. Eastman, S. A. Smith, R. G. FitzJohn, D. J. McGlenn, B. C. O'Meara, A. T. Moles, P. B. Reich, D. L. Royer, D. E. Soltis, P. F. Stevens, M. Westoby, I. J. Wright, L. Aarssen, R. I. Bertin, A. Calaminus, R. Govaerts, F. Hemmings, M. R. Leishman, J. Oleksyn, P. S. Soltis, N. G. Swenson, L. Warman and J. M. Beaulieu 2014. Three keys to the radiation of angiosperms into freezing environments. *Nature* 506:89-92.

A large effort to produce an angiosperm phylogeny of 32,223 species and reconstruct the evolution of major traits related to frost adaptation. This study sheds light on the role of growth habit (woody or herbaceous), leaf phenology (evergreen vs deciduous) and hydraulic conduits (xylem vessels and tracheids). The study also discusses whether each frost adaptation was acquired before or after the shift in distribution into temperate regions.

### **Other hypotheses: the carrying capacity of the tropics**

Here, we have focused on evolutionary (speciation and extinction) and historical explanations for the latitudinal diversity gradient. However, it is important to note that many reviews of the latitudinal diversity gradients, especially early on, emphasized ecological factors and invoked the idea of "carrying capacity" to suggest that regions differ in how many species they can hold (i.e. more species can coexist in the tropics than the temperate zone). These ideas ultimately build from the observation that tropical regions, with many species, have high productivity. For example, it has been hypothesized that there are more niches in the tropics and that more productivity would allow for higher carrying capacity in tropical ecosystems (Currie 2004). We do not focus on these ideas for two reasons. First, evidence for a direct link between greater productivity and greater species richness is weak. For example, the "more individuals" hypothesis proposes that more productive regions can harbor more individuals, which will

tend to come from more species via sampling effects, but evidence that the species-rich tropics harbor more individuals than the species-poor temperate zone is mixed (Srivastava & Lawton 1998). In addition, the relationship between productivity and diversity does not seem to extend to marine environments, where the number of species is higher in the tropics while productivity is higher in temperate regions (Sigman and Hain 2012). Second, these ecological hypotheses about the latitudinal diversity gradient can equally be framed using evolutionary and historical explanations. For example, the fact that species have narrower niches and stronger species interactions at low latitudes (Janzen 1967) can also be considered as factors that cause higher speciation and/or lower extinction in the tropics.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *The American Naturalist* 101: 233-249.

A classic article proposing that reduced temperature seasonality in the tropics leads to reduced dispersal, physiological specialization and narrower niches in tropical species.

Sigman, D. M., and M. P. Hain (2012). The biological productivity of the ocean. *Nature Education Knowledge*, 3:1-16.

A review of the important drivers of productivity in the oceans.

Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J. F. Guégan, B. A. Hawkins, D. M. Kaufman, J. T. Kerr, T. Oberdorff, E. O'Brien, J. R. G. Turner. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology letters*, 7:1121-1134.

A study testing important hypotheses for the latitudinal diversity gradient related to energy and diversity.

Srivastava, D. S., and J. H. Lawton 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. *The American Naturalist*, 152:510-529.

This study uses treehole communities to estimate the population density in tropical regions and test the relationship between the productivity of sites and how many individuals live in each site.

### **Using simulations to study the latitudinal diversity gradient**

Recent advances in computing power, in conjunction with the increasing availability of paleoclimate datasets, have allowed scientists to build detailed models that simulate diversity patterns through time. Such simulations can include (or remove) different variables to estimate the importance of particular processes to generating diversity gradients in silico. For example, Rangel et al. 2018 simulated species diversity patterns in South America based on climatic fluctuations in the last hundreds of thousands of years using four biological variables -- the rate of niche evolution, the dispersal distance, the time for speciation and the intensity of competition -- and reported results that roughly matched observations.

Saupe et al. 2019 used a similar approach to propose that a latitudinal diversity gradient could be generated only with speciation, extinction and dispersal and only considering climate changes from the Eemian (last 130,000 years). A recent simulation study by Hagen et al. 2021 has shown that the current latitudinal gradient have been formed in the last millions years mostly due to climate cooling. Such simulation models follow in the tradition of null models like the mid-domain model that proposes tropical species richness is high because there is the greatest opportunity for randomly assigned ranges to overlap near the equator (Arita & Vazquez-Dominguez 2008). Simulation studies might help narrow down what combinations of biological processes can create observed diversity patterns, but general conclusions might be difficult to draw as multiple combinations of processes may create the same spatial diversity patterns.

Arita, H. T., and E. Vazquez-Dominguez. 2008. The tropics: cradle, museum or casino? A dynamic null model for latitudinal gradients of species diversity. *Ecology Letters* 11:653–663.

A simulation study summarizing all the different types of hypotheses permitting the construction of the latitudinal diversity gradient

Colwell R. K. and D. C. Lees. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* 15:70-76.

A comprehensive review describing the geometric effect called the mid-domain model. These studies have demonstrated that major diversity gradients such as the latitudinal diversity gradient may have been created, at least to some extent, by the geometric constraints forcing greater overlap of species ranges close to the equator. The rationale behind the mid-domain hypothesis is that a random draw of species in a bounded latitudinal segment will always lead to a peak of richness in the middle of this segment, because there should be less overlap close to the boundaries (polar regions).

Hagen O., A. Skeels, R. E. Onstein, W. Jetz and L. Pellissier 2021. Earth history events shaped the evolution of uneven biodiversity across tropical moist forests. *Proceedings of the National Academy of Sciences*, 118 : e2026347118.

A very recent study of the latitudinal diversity gradient with simulations and also exploring the differences between the three main tropical regions: Neotropics, Afrotropics and Indomalaya, what is called the pantropical diversity disparity. The authors simulated the evolution of lineages accounting for speciation, extinction, paleoenvironments and paleotectonics. This article suggests an important role of niche evolution and recent climate on current diversity pattern of plants and animals.

Rangel, T. F., N. R. Edwards, P. B. Holden, J. A. F. Diniz-Filho, W. D. Gosling, M. T. P. Coelho, F.A.S. Cassemiro, C. Rahbek and R. K. Colwell. 2018. Modeling the ecology and evolution of biodiversity: Biogeographical cradles, museums, and graves. *Science*, 361:6399.

A study simulating species shifts in distribution in South America over the last 800,000 years. This simulation mimics the pattern of species richness in South America.

Saupe, E. E., C. E. Myers, A. T. Peterson, J. Soberón, J. Singarayer, P. Valdes, and H. Qiao. 2019. Spatio-temporal climate change contributes to latitudinal diversity gradients. *Nature ecology & evolution*, 3:1419-1429.

A study showing that present day diversity can be reproduced by simulating species distribution. The study shows that a peak in the tropics can only be reconstructed if climate is accounted for.

### **Ongoing speciation and latitudinal gradient in intraspecific richness**

It has been suggested that not only species diversity but also intraspecific genetic diversity should be higher in tropical regions. This is what has been found in the review of Lawrence & Fraser 2020, in the study of Miraldo 2016 for mammals and amphibians, and in Manel et al. 2020 for fish). It is not entirely clear why this is the case, and it could be related to the stability of tropical climate that leads to higher persistence of populations. It may also be related to higher rate of molecular evolution (mutation and substitution) in the tropics, which is proposed by the metabolic theory of biodiversity (Dowle et al. 2013). But, as noted above, rates of molecular evolution appear to be similar across latitudes (Orton 2019). More studies are needed to confirm these patterns at the intraspecific scale and understand their causes. Understanding how population density varies with latitude should help to understand how populations are created and how they persist through time, which in turn might help to resolve the mystery of why there are more species in the tropics.

Lawrence, E. R., and D. J. Fraser. 2020. Latitudinal biodiversity gradients at three levels: linking species richness, population richness and genetic diversity. *Global Ecology and Biogeography* 29:770-788.

This article reviews the different expectations for a relationship between genetic diversity and latitude. They also test hypotheses with population richness, range size for 900 species of vertebrates. The article shows that there might be a mismatch between species richness, number of populations per species and genetic diversity and this may be due to historical and contemporary factors.

Miraldo, A., Li, S., Borregaard, M. K., Flórez-Rodríguez, A., Gopalakrishnan, S., Rizvanovic, M., Z. Wang, C. Rahbek, K. A. Marske, D. Nogués-Bravo. 2016. An Anthropocene map of genetic diversity. *Science* 353:1532-1535.

Study displaying a map of intraspecific genetic diversity for 4,500 species of mammals and amphibians. The study shows that mitochondrial genetic diversity peaks in the tropics but also that gaps in the knowledge in those regions also impede our ability to fully understand this pattern.

Dowle, E. J., M. Morgan-Richards, and S. A. Trewick. 2013. Molecular evolution and the latitudinal biodiversity gradient. *Heredity* 110:501-510.

A review delineating the links between molecular rate of evolution, latitude and all potential relationships to speciation rate.

Orton, M. G., J. A. May, W. Ly, D. J. Lee, and S. J. Adamowicz. 2019. Is molecular evolution faster in the tropics? *Heredity* 122:513-524.

One of the most comprehensive tests of the relationship between latitude and rates of molecular evolution. The authors use the sequences of mitochondrial DNA (COI) and computes the molecular rate of evolution for 8,037 lineage pairs of Arthropoda, Chordata, Mollusca, Annelida, Echinodermata, and Cnidaria. They find no particular bias towards faster molecular evolution in the tropics.

Manel, S., P. E. Guerin, D. Mouillot, S. Blanchet, L. Velez, C. Albouy, and L. Pellissier. 2020. Global determinants of freshwater and marine fish genetic diversity. *Nature communications* 11:1-9.

This article computes genetic diversity on a spatial grid using Genbank data, using COI data for 3,815 marine and 1,611 freshwater fish species. The authors show higher genetic diversity in the tropics for both marine and freshwater fish.