

Opinion

The latitudinal taxonomy gradient

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Emerging large-scale datasets coupled with statistical advances have provided new insights into the processes that generate the latitudinal diversity gradient (LDG). But many of these studies run into an old, if often underappreciated, problem: The interpretation of the data critically depends on the consistent application of criteria to define what constitutes a species. This is particularly pernicious for the LDG because good species have been easier to recognize in temperate than in tropical regions. We provide evidence that this latitudinal taxonomy gradient exists, discuss how this potentially impacts inferences about latitudinal variation in ecoevolutionary processes such as population differentiation and speciation, and provide a roadmap for how to mitigate taxonomic biases in the study of biodiversity patterns.

Studying the latitudinal diversity gradient: a progress report

One of the most prominent features of Earth's biodiversity is the spectacular abundance of species in the tropics and the relative paucity of species in more temperate areas. The **latitudinal diversity gradient (LDG)**; see [Glossary](#) has been observed across many (but not all) groups of organisms [1,2] and during many geological time periods [3,4]. While a multitude of hypotheses to explain the LDG have accumulated in the literature [5–7], it has been depressingly difficult to exclude previous ideas.

But the tide appears to be turning, and we seem to be making new progress on the problem of the LDG. For example, contrary to the expectations of many conceptual models, species pairs in the temperate regions appear to have diverged more recently, on average, than those in the tropics, suggesting that **speciation rates** in the temperate regions of the world are currently, or at least in the past several million years, higher than those in the tropics. This is a robust finding that has been replicated in mammals [8], birds [8–10], angiosperms [11], and teleost fishes [12] and is further supported by evidence that trait evolution is faster in the temperate zone in birds [13]. An emerging consensus seems within view that the long-term stability of tropical biomes (at least compared with temperate regions that have experienced many glaciation cycles) appears to be a more important factor in generating the LDG than latitudinal differences in speciation rates [7,14]. Likewise, new analyses using other types of data are shedding further light on the possible mechanisms for these patterns [15].

While we are enthusiastic about the opportunities enabled by expanded datasets and new methods to handle them, we would like to draw researchers' attention to a potential Achilles heel of many of these studies – they often critically depend on the assumption that scientists' ability and proclivity to recognize good species (as defined by, e.g., the **biological species concept**) are the same across latitudes. Here we argue that while most good biological species are recognized as such in the temperate zone, many good biological species in the tropics are not currently recognized as distinct species, generating a taxonomic debt at low latitudes. (We note that whatever the species concept, we are implicitly assuming that there are lineages that are good species and those that are not, though reality may often be messier [16].) We are not the first to suggest this [17–21] and suspect that many researchers are aware that there are

Highlights

Phylogenetic data has revealed, among other things, that recent speciation rates appear to be faster in the temperate regions than in the more biodiverse tropics, but that tropical species harbor more population substructure and within-species genetic diversity. These findings have upended conventional explanations for the existence of the latitudinal diversity gradient.

These inferences are, however, critically dependent on species' being defined in a consistent way across latitudes. Evidence from case studies suggests that this assumption is not met. Instead, many good tropical species are not (yet) recognized, creating a taxonomic debt in the tropics.

Understanding the ecological and evolutionary processes that generate the latitudinal diversity gradient will require engaging seriously with taxonomic practice and developing strategies to mitigate the biases that it may create.

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geographic biases in how species definitions are applied. Our argument here is threefold: First, there is a **latitudinal taxonomy gradient (LTG)**, where good species are less likely to be recognized as such if they live in the tropics; second, this has pernicious consequences for the inferences we have been making; and third, far from an insolvable caveat we must add to the discussion sections of our papers to placate the pedants, there are practical things we can do to mitigate the effects of the LTG.

The LTG is real: evidence from birds

As suggested earlier, we believe that many researchers likely have some sense that the LTG is a real issue. There are two main problems that prevent good biological species from being recognized, and both are expected to be more severe in the tropics. First, the **cryptic species** problem (Box 1) arises when good species are ‘hiding in plain sight’ because of their phenotypic similarity. Second, the **allopatry** problem (Box 2) results from the difficulty of deciding whether to rank divergent, geographically isolated populations as distinct species. Another potential contributor to the LTG is that species in the temperate zone may be oversplit, with some recognized species that are not actually good species.

However, the LTG primarily exists as folk knowledge, and there has been, at least in our reading, no comprehensive analysis of the problem; such an analysis is beyond the scope of the present opinion article and would be a very challenging undertaking. To make the challenge more concrete, we review patterns of bird taxonomy and, for a higher-resolution view, examine taxonomic practice in one genus of birds, the tapaculos (*Scytalopus*). Birds are a good starting point for thinking about the LTG because they are a focal taxon for many global analyses, their species concept is relatively well agreed upon (the biological species concept [22]), and their reasonably stable taxonomy has received exceptional scrutiny [23]. We do not think that birds are unique in their taxonomic patterns; in fact, we expect that the LTG is even steeper in less-studied groups of organisms that potentially harbor far more cryptic species.

Box 1. The cryptic species problem

Taxonomy was historically based on the examination of phenotypes in museum collections. However, in the past two decades, we have learned that species that look similar but are in fact divergent genetically (and in hard-to-measure aspects such as chemical or behavioral traits) are common in many taxonomic groups [69]. A prime example is the Neotropical skipper butterfly *Astrartes fulgerator*. Detailed studies of this species in northwestern Costa Rica had demonstrated that this was a generalist species whose caterpillars used a broad range of host plants. However, molecular methods revealed that this species actually consisted of a complex of many distinct species that were mostly sympatric with each other, most of which differed in their caterpillar host plants and were hence host specialists [64]. Such cryptic species are thought to disproportionately occur in the tropics. For example, there are an estimated ~3000 undescribed species of freshwater Neotropical fishes (on top of the 6000 described species in this region [48]), and the taxonomic debt in the tropics is likely to be even more massive for species-rich but understudied groups such as insects. Importantly, it is difficult even to quantify the shape and steepness of the LDG in such groups, let alone test processes for how the LDG was generated.

In this opinion article, we focus particularly on birds, in large part because their relatively stable taxonomy means that they are often used to examine the LDG. Situations in which multiple cryptic species of birds live in the same forest, as in the butterfly described above, are rare. Instead, cryptic species in tropical birds tend to occur along environmental gradients. For example, some newly described *Scytalopus* tapaculo species live at different elevations on the same mountain slope [28], a pattern that is replicated across regions in tropical birds [70]. In the Neotropics, another large potential source of cryptic bird species is differentiation across major rivers in the Amazon Basin; recent fieldwork has demonstrated cases in which birds in adjacent river basins are phenotypically similar but nevertheless exhibit strong reproductive isolation where they come into contact with one another (in headwaters regions), indicating they are in fact cryptic species [71]. While the study of headwaters regions to investigate cryptic species in the lowland Neotropics is in its infancy, similar cases of differentiation across space in the temperate zone (e.g., forest birds in western versus eastern North America) were typically subjected to detailed taxonomic treatments many decades ago.

Glossary

Allopatry: species or populations that are geographically isolated and therefore do not have the opportunity to interbreed.

Biological species concept: under this concept, species are defined by the presence of reproductive isolation.

Cryptic species: multiple good species by some other criterion, such as the biological species concept, are phenotypically indistinguishable.

Latitudinal diversity gradient (LDG): the pattern of higher species richness in tropical regions than in temperate regions.

Latitudinal taxonomy gradient (LTG): the claim, put forth here, that criteria for delimiting species may be inconsistently applied across the globe, leading to an undercounting of true species richness in the tropics.

Speciation rates: the rate (i.e., per unit time) at which new species form.

Box 2. The allopatry problem

In island systems – and in island-like systems such as mountains – species may consist of a string of geographically isolated (allopatric) populations. Deciding whether differentiated allopatric populations constitute distinct species is inherently difficult and poses a particular challenge for the biological species concept, which guides avian taxonomy, and emphasizes interbreeding: If populations interbreed freely, they are the same species, but if they fail to interbreed, or if such interbreeding is limited to narrow hybrid zones, they are distinct species [22,72]. This is difficult to measure for allopatric populations, which, by definition, do not currently encounter each other in real life. Instead, researchers attempt to infer whether allopatric populations would be likely to interbreed if they did come into contact with one another, asking whether the observed genetic and phenotypic divergence of allopatric populations is on par with levels of divergence of undisputed (sympatric) species within the same group [73–75]. Indeed, the majority of newly described species of tropical birds (e.g., in Figures 1 and 2 in main text) are the result of taxonomic rearrangement, where allopatric populations are reclassified as distinct species.

We illustrate how new data help to address the allopatry problem by zooming in on one species of *Scytalopus* tapaculo. In 1990, *Scytalopus magellanicus* was classified as a high Andean species found from Colombia to Chile. Decades of research led to the insight that this single ‘species’ was a complex of around one dozen vocally and genetically distinct allopatric populations [28]. These differences are dramatic; levels of genetic divergence within this single ‘species’ are similar to levels of genetic divergence within temperate genera, with multiple cases in which populations are estimated to have last shared a common ancestor more than 5 million years ago (i.e., roughly the same time that the hominin lineage split from chimpanzees), and song, an important premating reproductive barrier, matches the genetics – songs are similar within geographic groups with similar genetics but differ markedly between geographically adjacent, genetically differentiated groups. Here we emphasize the importance of using estimates of reproductive barriers to address the allopatry problem rather than relying solely on genetic divergence, as evidenced by cases in which populations that diverged in allopatry have fused back together upon secondary sympatry [76].

A prediction that follows from the LTG is that increasing taxonomic effort over time will disproportionately lead to the accumulation of newly described species in the tropics. This prediction is borne out when we examine recent records of newly described species of landbirds in the Americas: the number of new tropical birds recognized as distinct species increases at a rate over ten times faster than the number of newly recognized temperate bird species (Figure 1). The divergence between tropical and temperate species accumulation curves shows no signs of slowing down and may even be increasing. For example, an additional 41 species of Central and South American species were formally recognized in 2020 alone, compared with zero in North America. For birds, this surplus of newly recognized tropical species is primarily the result

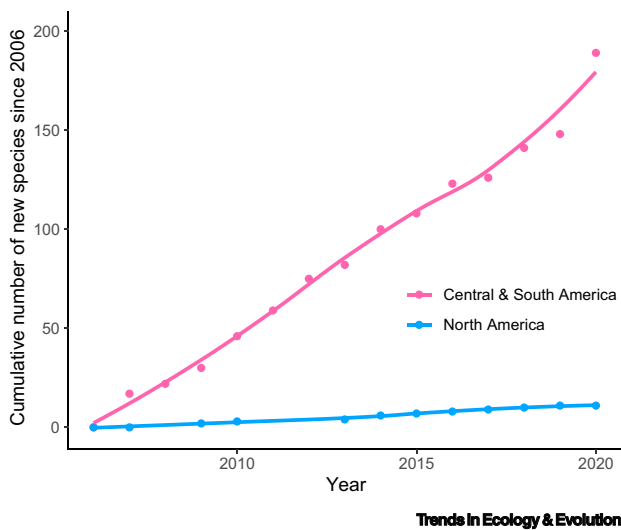


Figure 1. Most newly recognized species of landbirds in the Americas live in Central or South America. There are 189 more recognized species in Central and South America in 2020 than in 2006, but only 11 more recognized species in North America over the same time frame; most of these newly recognized North American species live in Mexico. Decisions on changes to species-level taxonomies in these regions are made by the North American Checklist Committee and the South American Checklist Committee. We extracted data on additions and subtractions of recognized species (‘splits’ and ‘lumps’) from the online archives of these committees and plotted net changes in species richness from 2006. (The first year with archived data from the North American Checklist Committee was 2007.) Trends in each region are visualized with locally weighted smoothing lines.

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of a steady drip of studies addressing the allopatry problem for particular groups (Box 2) rather than the discovery of cryptic species (Box 1).

Scytalopus tapaculos provide an illustrative case study in geographic biases in taxonomic effort and practice (Figure 2). These birds live primarily in Andean forests, where they spend their days scurrying around inside dense vegetation, noticeable only when they sing a series of rhythmic sputtering notes that can last a minute or more. They are 50 shades of gray in color and mostly indistinguishable – to the point that a modern field guide uses a single illustration for four different species [24]! Traditionally, avian taxonomists defined species limits in birds on the basis of detailed study of drawers of museum specimens. A row of *Scytalopus* specimens from across the Andes might look essentially identical, and, correspondingly, few species were recognized: in 1990, there were 11 recognized species of *Scytalopus* [25]. The past several decades, however, have seen a flourishing of fieldwork in the topographically complex Andes, generating important data on living *Scytalopus* that have revolutionized taxonomy in this group. In particular, fieldworkers have documented substantial geographic variation in song, which is an important pre-mating reproductive barrier in birds [22,26] and is genetically controlled in the larger group of birds, suboscines, to which *Scytalopus* belongs. Combined with the advent of modern sequencing, these intensive field studies have led to the realization that dozens of allopatric populations (plus a few cryptic species) deserve to be recognized as species in their own right

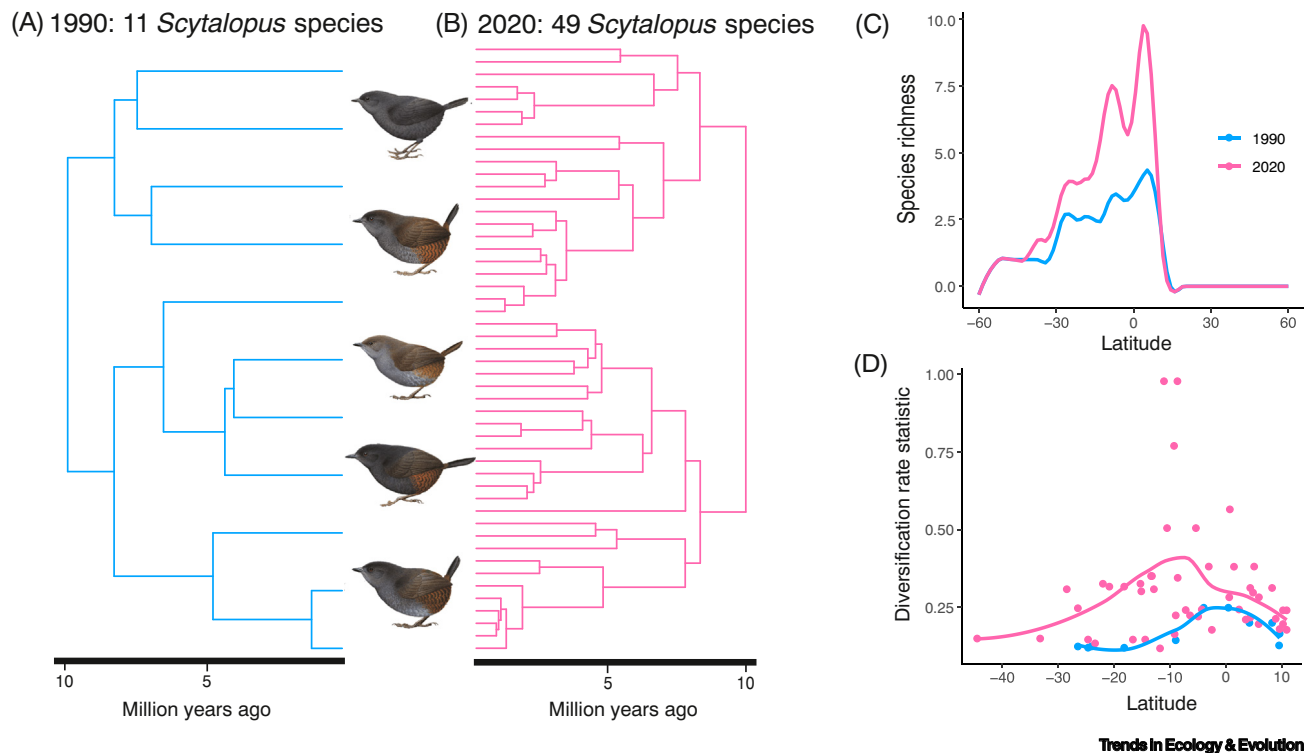


Figure 2. Greater taxonomic effort in the tropics steepens the latitudinal diversity gradient and may influence ecoevolutionary inferences: a case example in the bird genus *Scytalopus*. In 1990, 11 species of these mouse-like birds were recognized; decades of intense fieldwork led to the development of genetic and behavioral (voice) datasets that support the recognition of 49 species (A and B; 2020 phylogeny from [29], subsetted in A to species recognized in 1990 [25]). This quadrupling of species richness within *Scytalopus* has shifted the latitudinal diversity gradient for this group such that the tropical peak is twice as high as it was in 1990 (C; illustrated with smoothed lines), and it also somewhat altered latitudinal patterns in estimates of recent speciation rate, as measured by the diversification rate statistic [77] (D). We argue that patterns are likely to be similar for many tropical lineages, while taxonomy has been relatively stable for temperate zone groups. Illustrations reproduced, with permission, from *Birds of the World* (Cornell Lab of Ornithology; <https://birdsoftheworld.org/bow/home>).

[27–29]. In the past three decades, the species richness for this group has more than quadrupled: a total of 49 species of *Scytalopus* are now recognized, with many more populations likely to be recognized as distinct species in the next decade [30].

While we focus on the LDG in this article, we note that taxonomic practice likely impacts additional ecological and evolutionary inferences. For example, it has been hypothesized that stronger sexual selection might lead to faster speciation rates in birds [31]. However, testing this could become an exercise in circular reasoning if taxonomists emphasize male plumage differences when defining species limits, leading to more recognized species in sexually dimorphic groups, and then evolutionary biologists use sexual dimorphism as a proxy for the intensity of sexual selection [32,33].

Scytalopus species are an extreme example of a tropical group whose true diversity was hidden from taxonomists until recently, but the general pattern is replicated in other South American bird groups [34–37], with similar results from Asian and African tropical birds [38–42]. The concordance between proxies for reproductive isolation and deep genetic divergences indicates that recognizing new species of *Scytalopus* and other tropical birds represents taxonomic progress [43], not taxonomic inflation [44] (Box 2). While we do not have the expertise to evaluate these claims, similar patterns have been reported in other groups of organisms, including plants [45,46], mammals [47], and freshwater fishes [48].

Of course, the plural of anecdote is not data; one aim of this opinion article is to inspire other researchers to really dig into these questions more quantitatively. But the evidence we have presented is strongly suggestive of an LTG. We therefore advocate for taking a proactive approach to the ramifications of this suggestive pattern for testing ecological and evolutionary hypotheses about the LDG, even if our current picture of taxonomic practice is far from complete.

Why does the LTG matter?

These latitudinal differences in recognizing species have consequences for research in ecology and evolution. Most obviously, if good tropical species are not recognized, that means the LDG is likely steeper than currently recognized. But our greater concern is that the LTG may influence the results of studies of the evolutionary and ecological processes that generate these gradients. Here we consider five specific areas of inquiry from across ecology and evolutionary biology where the latitudinal gradient in taxonomy may affect inferences.

(i) Latitudinal patterns in speciation rates

One of the most exciting findings of the past decade is that recent per-lineage speciation rates are faster at high latitudes in a variety of taxa [8,9,11,12]. As discussed in the introduction, this emerging generality has upended some long-standing explanations for the LDG [14]. However, this is also the result expected, given a latitudinal bias in taxonomy, where recent speciation events are recognized as such more often in the temperate zone than in the tropics. It is also notable that nearly all the evidence for these patterns comes from differences in terminal branch length; while this has the advantage that these results are not a result of the conflation of speciation and extinction further back in the tree [49], rates estimated from terminal branch lengths are the most sensitive to taxonomic revisions.

(ii) Latitudinal patterns in within-species genetic diversity (i.e., phylogeographic diversity)

There is evidence that tropical species contain more genetic diversity than temperate species [50–53]. These findings suggest that tropical species have more structured populations; since the formation and persistence of isolated populations has been proposed to be a rate-limiting step in speciation (but see [54]), the question then becomes why tropical subpopulations do

not persist or become distinct species as quickly as temperate ones [55]. However, these results are also consistent with what we expect, given the LTG [17], and are potentially sensitive to future taxonomic changes that reclassify single tropical species with high within-species genetic diversity as multiple distinct species, each with lower to moderate levels of within-species genetic diversity. If consistent application of species criteria leads to the recognition of more allopatric species in the tropics, it also highlights the importance of studying the evolutionary processes that explain the transition from allopatry to sympatry to understand how diversity builds up within regional biotas [56].

(iii) Latitudinal patterns in vulnerability to climate change

Accumulating evidences suggests tropical species are often more physiologically specialized than temperate species, potentially rendering them more vulnerable to climate change [57–59]. This pattern may be even stronger than currently realized. For example, tropical insects with relatively broad thermal tolerances have been found on closer inspection to actually consist of multiple species with smaller distributions and narrow thermal tolerances, suggesting they may be more sensitive to warming temperatures than previously thought [58].

(iv) Latitudinal patterns in extinction risk

Tropical regions harbor many microendemic species [60–62]. Species with restricted ranges tend to have small population sizes and to be more vulnerable to extinction, and, indeed, there is evidence for plants that extinction risk is higher in the tropics [63]. Again, the LTG may mask this apparent pattern. For example, the wonderfully named Bearded Helmetcrest (*Oxypogon guerinii*), a hummingbird found in high elevations of Colombia and Venezuela that was previously ranked by the International Union for Conservation of Nature (IUCN) as ‘Least Concern,’ is now considered to comprise four allopatric species, each with a small range. While two species remain of ‘Least Concern,’ one is now ranked as ‘Critically Endangered’ and another as ‘Vulnerable.’ Taxonomic changes should be driven by analyses of phenotypic and genetic divergence, not conservation needs, but it seems likely that addressing the LTG will have repercussions for assessments of extinction risk.

(v) Latitudinal patterns in coexistence mechanisms

Many explanations for how so many species can coexist in the tropics invoke tight coevolutionary processes [6], such as the Janzen-Connell hypothesis. But cryptic species can influence our inferences of how important this actually is. For example, consider the butterfly living in northwestern Costa Rica [64] described in Box 1. When it was classified as a single species using many host plants, host plant specialization would have been viewed to be unimportant to speciation and coexistence in this group. But the discovery that this single generalist ‘species’ actually contains multiple host-specialist species turns the table and suggests coevolutionary processes to be highly important to diversification in this group.

Solutions for the LTG: a working toolkit

The ultimate solution to the LTG is to consistently apply criteria for what constitutes a species across latitudes. This will require funding and training taxonomists working to describe Earth’s biodiversity, particularly taxonomists based in biodiverse tropical nations. A corollary of supporting taxonomic research is to use the research outputs. Here, taxonomic decision-makers play an important role in ensuring that taxonomy is nimble and responsive to new information; avoiding change to maintain stability of nomenclature in the face of new information not only slows down description of Earth’s biodiversity but also actively impinges upon our ability to study the ecoevolutionary processes that have generated it. Last, while it is tempting to solve taxonomic conundrums via ‘shortcuts,’ such as using simple thresholds of genetic

divergence to define species as is done in microbial phylogenetics [65], adopting such an approach would make it impossible to study the role of speciation, defined by the evolution of reproductive isolation, in shaping the LDG.

However, we cannot sit on our hands and bemoan taxonomic inequities; researchers can often address the potential bias exerted by the LTG head-on. We describe four possible solutions to 'taxonomy-proof' studies below and suggest that one or more of these options may be available for most specific research questions.

(i) Study populations, not species

Many big questions about evolutionary processes – such as understanding the tempo and drivers of genetic and phenotypic evolution (but not the evolution of reproductive isolation) – can be tested by studying populations regardless of taxonomic rank [8,66,67].

(ii) Restrict studies to latitudinal bands with relatively uniform taxonomic practice

For example, North America from ~20° to 70°N or Australia from ~10° to 40°S [8].

(iii) Use sympatric species

The LTG, at least for vertebrates, primarily arises because of the allopatry problem (Box 1). Latitudinal differences in the recognition of sympatric species are likely to be minimal for vertebrates. Some questions, such as about latitudinal variation in the processes that govern community assembly and diversity buildup, can be made immune to the LTG by studying sympatric species [55].

(iv) Use a 'future taxonomy' to stress-test results

Some taxonomic groups have competing taxonomies. For example, a recent taxonomy attempts to apply consistent species criteria across all birds [23]. This can be viewed as an effort to flatten the LTG and an approximation of what taxonomies might look like in the future [23,68]. Researchers can test whether results of analyses on status quo taxonomies hold when using alternative taxonomies that attempt to diminish the LTG [9].

Concluding remarks

While the causes of the LDG remain contentious, a new influx of (phylo)genetic and location data have provided tantalizing clues and have suggested that some long-standing hypotheses can be ruled out. However, our ability to resolve this problem will depend on thinking critically about the LTG; we need not only to better quantify the extent of taxonomic biases but also to understand how such biases may influence our inferences about evolutionary and ecological processes (see Outstanding questions). By highlighting this potential problem for studies of the drivers of the LDG, we aim to inspire consideration, not despair. We argue that studies investigating the LDG can account for taxonomic biases or design approaches, such as those that leverage population-level information, that are relatively immune to such issues. A full accounting of and explanation for the major patterns of Earth's biodiversity will require integrating perspectives and information not only from ecology and evolutionary biology, but also from the more human dimensions of biodiversity research.

Declaration of interests

The authors have no interests to declare.

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Outstanding questions

How widespread and how steep is the latitudinal taxonomy gradient? Using case studies, we have demonstrated that taxonomic practice differs between temperate and tropical regions and argue that this is likely pervasive. However, to our knowledge, no study has quantified this across multiple taxonomic groups; such information, which is challenging to obtain, is critical for understanding the severity of the problem.

How robust are inferences to taxonomic practice? We discuss some approaches that could be used to mitigate the potential confounding effects of taxonomic biases, but these have not been widely used. It is critically important to evaluate, for example, whether the recent findings of higher speciation rates in temperate regions relative to the tropics and greater within-species genetic diversity in the tropics are robust to the latitudinal taxonomy gradient.

How can biodiversity scientists 'future-proof' analyses to taxonomic changes? Particularly for taxa that live in the tropics, we speculate that over the coming decades, the number of recognized species will continue to increase. While the broad trends appear clear, it is, of course, impossible to know the future taxonomy of any specific clade; we will therefore need strategies for forecasting possible taxonomic changes and for mitigating against a variety of possible outcomes.

Is the latitudinal taxonomic gradient primarily a result of the failure to identify cryptic species or putative species living in allopatry? We have argued that the evidence from birds suggests it is primarily the latter, but it remains unclear whether this applies to other taxonomic groups.

How can we facilitate crosstalk between taxonomists and other biodiversity scientists? Ecologists and evolutionary biologists often fail to consider how taxonomy is established in practice, and this can cloud their interpretations. Taxonomists who make decisions with other considerations in mind (e.g., stability of nomenclature) may fail to think through the implications of their decisions for ecoevolutionary studies.

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We argue that better communication between these two often distinct groups would be mutually beneficial and that facilitating this will likely require novel initiatives and incentives.

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