



SYNTHESIS

The Origins of the Latitudinal Diversity Gradient: Revisiting the Tropical Conservatism Hypothesis

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ABSTRACT

Aim: Understanding the origins of species richness patterns (especially high tropical richness) is a long-standing challenge at the intersection of biogeography, ecology, and evolutionary biology. One hypothesis that can potentially explain the latitudinal richness gradient is the tropical conservatism hypothesis (TCH). The TCH proposes that there are presently more species in tropical regions because many clades originated in the tropics and have only colonised the temperate zones more recently, leaving less time for speciation to build up temperate richness, and with niche conservatism limiting temperate colonisation by tropical clades. Here, we review the empirical evidence for the TCH. We first define this hypothesis, outline its major predictions, and describe its relationship to similar hypotheses. We then perform a systematic review to quantitatively evaluate the support for (and against) its major predictions. Finally, we describe several areas for future research.

Location: Global.

Time Period: Present to ~750 million years ago.

Major Taxa Studied: All (especially plants and animals).

Methods: We perform a systematic review of the evidence for the TCH over the last ~20 years.

Results: Most predictions of the TCH were supported in a significant majority of the studies that examined them. Further, a significant majority of relevant studies rejected the role of higher tropical diversification rates in driving the latitudinal diversity gradient (contrary to the diversification-rate and out-of-the-tropics hypotheses). Surprisingly, the importance of diversification rates did not depend on the ages of the clades studied.

Main Conclusions: Our results generally support the TCH, but also highlight several important issues moving forward. Most studies tested very few predictions of the TCH, and the pivotal role of colonisation time was often untested. Many studies analysed phylogenetic diversity measures, but their relevance for explaining richness patterns remains disturbingly unclear. Finally, we discuss several unresolved questions about the TCH and the origins of richness patterns.

1 | Introduction

The higher species richness of the tropics relative to temperate zones is one of the most obvious and longest-known patterns in

biogeography and ecology (Hawkins 2001). Yet, the evolutionary and ecological causes underlying this pattern remain unresolved. Dozens of hypotheses have been proposed (Pianka 1966), but with little agreement as to which is most likely. There have

been many review papers on this topic. These often argue for (or against) a particular hypothesis as the primary explanation (e.g., Mittelbach et al. 2007; Brown 2014; Fine 2015; Pontarp et al. 2019; Brodie and Mannion 2023; Saupe 2023), but without systematically reviewing and quantitatively evaluating the published evidence for and against that hypothesis.

One relatively well-cited hypothesis to explain high tropical species richness is the tropical conservatism hypothesis (TCH hereafter). This name was suggested ~20 years ago (Wiens and Donoghue 2004), but the elements of the hypothesis were proposed by several prominent evolutionary ecologists in the 1990s (Brown and Lomolino 1998; Farrell et al. 1992; Futuyma 1998; Latham and Ricklefs 1993; Ricklefs and Schluter 1993). The main idea behind the TCH is that many clades originate in tropical climates, and species in these clades then have difficulty successfully colonising temperate regions because of their cold climates (i.e., their tropical climatic niche is conserved). The more recent colonisation of the temperate zone then leaves less time for richness to accumulate there. As was noted in many of the original papers, this combination of limited dispersal and recent colonisation could also help explain many other richness patterns, such as a reverse latitudinal diversity gradient in some clades (i.e., higher temperate richness) and the lower richness of deserts.

Over the past 20 years, many studies have tested the TCH empirically, with some studies claiming to support it (e.g., Kerkhoff et al. 2014; Economo et al. 2018), and others claiming to refute it (e.g., Algar et al. 2009). Yet, no papers have attempted to systematically evaluate the support for this hypothesis across published studies. To advance our understanding of the latitudinal diversity gradient, it is crucial to stand back and assess what past studies reveal in the aggregate. Given the many separate studies that have now been published on the TCH, a quantitative analysis can advance the field more than another conceptual review that picks and chooses particular examples favouring one hypothesis over another. A quantitative approach can identify general patterns and show which predictions have the greatest and the least support. It can also identify crucial gaps to be filled.

To our knowledge, no previous papers have critically reviewed the TCH across studies. The TCH was evaluated (along with other hypotheses) in a valuable study by Jansson et al. (2013). However, they provided new analyses, not a systematic review. Further, there were problems in how the hypotheses were defined by Jansson et al. (2013), such that their results show the opposite of their conclusions (see Section 6 below). A new quantitative analysis is clearly needed at this point, along with a review of how these hypotheses are defined.

Here, we review the empirical evidence for the TCH. We first describe this hypothesis, its relationship to similar hypotheses, and its predictions. We then perform a systematic review to quantitatively evaluate the support for (and against) its different predictions. Finally, we describe areas for future research.

2 | What Is the Tropical Conservatism Hypothesis?

The TCH is an explanation for the latitudinal diversity gradient that has three main components (Figure 1). The first is that

many groups with high tropical richness today originated in tropical climates and successfully spread to the temperate zone more recently or not at all. This recent temperate colonisation left less time for richness to build up there (i.e., limited time-for-speciation; Stephens and Wiens 2003) relative to the tropics. Second, the origin of many clades in the tropics may be explained by tropical climates being far more extensive across the Earth's surface until relatively recently (the past ~30–40 million years; Morley 2000; Beerling and Woodward 2001; Ziegler et al. 2003). Third, the failure of many clades and species to successfully expand their geographic ranges into the temperate zone may be explained by their inability to tolerate and adapt to cold temperatures. Thus, niche conservatism (i.e., the retention of the ancestral tropical niche) helps explain the origin and maintenance of the latitudinal diversity gradient over time.

There are also extensions of the TCH to other richness patterns. The combination of niche conservatism and recent colonisation time can help explain many climatic and ecological richness gradients, such as high temperate richness and richness along gradients of precipitation and elevation. Similarly, differences in colonisation time among regions or habitats can drive richness patterns regardless of climate. We define niche conservatism here as the retention of niche-related ecological traits over time (following Wiens et al. 2010), including climatic distributions.

3 | How Is the TCH Different From Similar Hypotheses?

Dozens of hypotheses have been proposed to explain the latitudinal diversity gradient. The TCH is different from many other hypotheses in focusing on the three processes that directly impact species richness: dispersal, speciation, and extinction (Ricklefs 1987). These are the only three processes that can directly change the number of species in a region or habitat. Here, we compare the TCH to three other hypotheses that also directly consider speciation, extinction, and/or dispersal: the diversification rate, evolutionary time, and out-of-the-tropics hypotheses.

The diversification-rate hypothesis (Fischer 1960) posits that ecological differences between the tropics and temperate zone lead to higher diversification rates in tropical clades. The diversification rate is the speciation rate minus the extinction rate, or the rate of net species accumulation over time. This hypothesis does not assume that diversification rates are constant over time, either within or among clades.

The TCH is largely agnostic about diversification rates. However, a reasonable argument can be made that the reason why the larger area of the tropics in the past led to more clades originating there is that a larger area leads to higher diversification rates (Fine and Ree 2006). We address this further below (Section 7.4).

The evolutionary-time hypothesis (ETH; Fischer 1960) suggests that there are more species in the tropics because the tropics are older. Therefore, clades will tend to originate in the tropics and have more time to accumulate richness there. All else being equal, an extant clade that successfully colonised the temperate zone more recently will have fewer species than a tropical

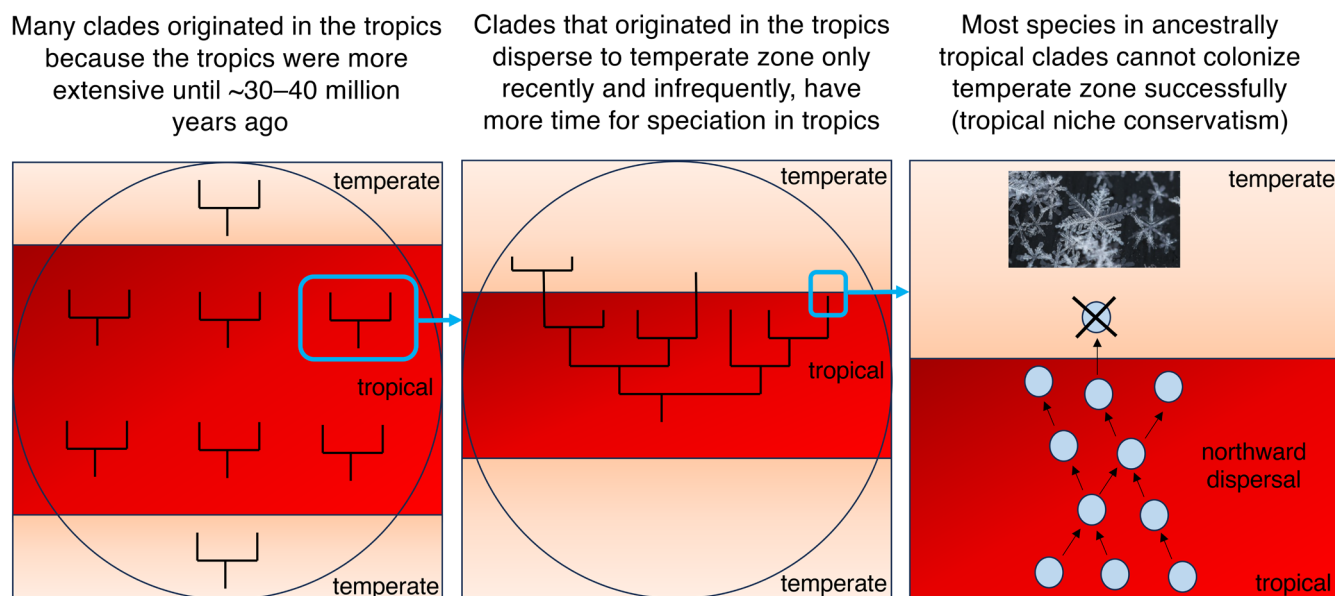


FIGURE 1 | The three main parts of the tropical conservatism hypothesis (TCH) in chronological order. Left: Under the TCH, many clades originate in the tropics because the tropics were more extensive in area until relatively recently (past ~30–40 million years), such that it would be more likely for clades to originate there than in the temperate zone. Note that some groups still originate in the temperate zone, despite their smaller area. One tropical clade is highlighted in blue: The modern diversity and distribution of this clade is shown in the middle panel. Middle: Under the TCH, the primary reason why there are more species in the tropics is because clades with higher tropical species richness today originated in the tropics, and successfully colonised the temperate zone only recently (and infrequently). Therefore, there is more time for species richness to accumulate in the tropics through in situ speciation, and more limited time for richness to accumulate in the temperate zone, leading to higher tropical richness. A small clade with eight species is shown (five tropical, three temperate), and the world is divided into temperate and tropical areas. One species is highlighted in blue: the detailed distribution of this species is the subject of the right panel. Right: A key aspect of the TCH is that clades of tropical origin have difficulty successfully colonising the temperate zone (presumably because of their inability to adapt to cold winter temperatures). This helps explain why temperate regions are colonised infrequently by tropical clades, and helps explain the origin and maintenance of the gradient over time. Here, we illustrate individuals of a tropical clade (blue circles) dispersing northward over time, but individuals that cross into the temperate zone die without successfully reproducing.

clade that was present and speciating in the tropics longer. The evolutionary-time hypothesis is part of the TCH (not a competing hypothesis). The evolutionary-time hypothesis and TCH do not assume that species richness increases exponentially over time, nor that richness is unbounded into the future. Instead, they simply assume that richness patterns are related to colonisation times among regions, for the group and timeframe under study.

The out-of-the-tropics (OTT) hypothesis (Jablonski et al. 2006) posits that clades have higher origination (=diversification) rates in the tropics, and that ancestrally tropical clades expand their ranges to also encompass the temperate zone. Thus, the diversification rate hypothesis is part of the OTT. The OTT and TCH overlap in predicting colonisation of the temperate zone from the tropics, but the OTT does not incorporate the role of colonisation time in driving richness patterns, does not address the role of climate and niche conservatism in limiting tropical-to-temperate dispersal, and does not postulate why more clades originate in the tropics (beyond higher tropical diversification rates).

There can also be synergies among these hypotheses, especially from studies that incorporate the fossil record. For example, a group may have limited extant richness in a region because it successfully colonised the region only recently (i.e., limited evolutionary time) whereas older colonisation events there were

unsuccessful and went extinct (i.e., low diversification rates; e.g., Miller and Wiens 2017). Similarly, the extinction of some tropical species and clades at higher latitudes, as the temperate zone expanded ~30–40 Myr ago, may have contributed to the present-day latitudinal diversity gradient (Meseguer and Condamine 2020). However, these high-latitude tropical extinctions would lower overall richness in tropical climates, not temperate climates. These extinction patterns inferred from fossils do not make diversification rates and colonisation times from extant taxa meaningless for explaining present-day richness patterns. Indeed, only colonisations of a region that survived to the present day contribute to modern richness in that region, even if many earlier colonisations went extinct. Furthermore, not all clades have dispersed to all regions, and so the absence of a clade in a region does not necessarily indicate that they went extinct there.

In a thought-provoking opinion piece, Saupe (2023) argued against hypotheses based on colonisation times, claiming instead that all hypotheses must be based on rates. They provided no supporting evidence for this opinion, and failed to cite analyses showing that colonisation times are generally more important than dispersal rates or diversification rates for explaining regional richness patterns. For example, a meta-analysis of 15 studies found that colonisation time explained ~73% of the variation in richness among regions (on average), with diversification rates and dispersal rates together explaining only ~17% (Li and

Wiens 2019). Saupe (2023) stated that arguments based on colonisation time (like the TCH) “implicitly assume that high latitude regions were devoid of life over much of Earth history.” Instead, explanations based on time explicitly assume that particular clades successfully colonised particular regions later than others, not that some regions were entirely “devoid of life”. Indeed, the TCH assumes that high-latitude regions were once tropical, not lifeless (Figure 1). All spatial richness patterns depend directly on speciation, extinction, and dispersal (e.g., Ricklefs 1987), but the timing of these processes are also demonstrably important, not just their rates.

Finally, we acknowledge that hypotheses like the TCH and OTT are more complex than the evolutionary time and diversification rate hypotheses. Indeed, the evolutionary time hypothesis is part of the TCH, and the diversification rate hypothesis is part of the OTT. But these simpler hypotheses may be inadequate to explain the latitudinal diversity gradient. For example, the evolutionary time hypothesis does not address why a clade originated where it did, and the diversification rate hypothesis does not address why diversification rates vary. Neither hypothesis explains why dispersal does not simply obliterate the gradient over time. Compound hypotheses (like the TCH) attempt to address these limitations of simpler hypotheses.

4 | Climate and Ecological Limits Are Not Competing Hypotheses With the TCH

Many papers have treated climate and related variables (e.g., energy, productivity) as a competing hypothesis to explain richness patterns (e.g., the “species-energy relationship” hypothesis; Tolmos et al. 2022), relative to hypotheses that incorporate speciation, extinction, and dispersal (like the TCH). But the processes of speciation, extinction, and dispersal must underlie any climate-diversity relationship and any spatial richness pattern in general (Ricklefs 1987).

Similarly, ecological limits (i.e., carrying capacity, diversity-dependent diversification) are sometimes treated as a competing hypothesis relative to the TCH, evolutionary time, and diversification-rate hypotheses (e.g., Mittelbach et al. 2007; Rabosky 2009; Vamوسي and Vamوسي 2010; Etienne et al. 2019; Machac 2020). Other authors have questioned the empirical and theoretical support for the idea that ecological limits determine regional richness patterns (e.g., Harmon and Harrison 2015). Ecological limits involve constraints on the number of species in a region due to competition for limited resources. Simulations show that ecological limits directly impact richness by modifying colonisation times or diversification rates (Pontarp and Wiens 2017). Ecological limits cannot modify richness without acting on the rates or timing of speciation, extinction, and dispersal (e.g., Pontarp and Wiens 2017; Etienne et al. 2019). Therefore, ecological limits are not a competing hypothesis relative to the TCH, evolutionary time, or diversification-rate hypotheses: ecological limits involve a different level of explanation (i.e., a factor that potentially influences colonisation times and diversification rates). Given this, it would be nonsensical to say (for example) that the ecological-limits hypothesis is supported over the diversification-rates hypothesis if ecological limits impact richness through their effects on diversification rates.

5 | How to Test the Tropical Conservatism Hypothesis

Testing the TCH is easier said than done. The TCH is relatively complex, more so than the diversification rate and evolutionary-time hypotheses. Nevertheless, one can derive predictions from its different parts, which we explain below. We then address the empirical support for each of these predictions through a systematic review of the literature in Section 6. We provide a flow chart for testing the main predictions in Figure 2.

5.1 | Clades With High Tropical Species Richness Originated in the Tropics

A clade with many tropical species and fewer temperate species could originate in either climatic zone. Model-based methods (Bayesian, likelihood) for reconstructing ancestral regions can be used to estimate where a clade arose (e.g., Ree et al. 2005; Ree and Smith 2008; Landis et al. 2013), and simulations show that these estimates can be accurate (Ree and Smith 2008; Landis et al. 2013). Finding a tropical origin for a clade with higher tropical richness supports this prediction of the TCH. Conversely, finding temperate origins of a clade with high tropical richness would immediately reject the TCH, evolutionary time, and OTT hypotheses. But even better evidence for the TCH would come from estimating when each of multiple biogeographic regions was colonised by the clade and finding a strong, positive relationship between colonisation time and richness among these regions: this could support the TCH (and evolutionary-time hypothesis), if the tropical regions have higher richness and earlier colonisation times. There is no requirement that the TCH be analysed by treating the world as two climatic zones (tropical, temperate). Instead, the world can be divided into multiple large-scale regions (using areas of endemism or other approaches), with some regions that are tropical and some that are temperate, or with intermediate climates.

5.2 | Clades With High Tropical Species Richness Should Have Higher Phylogenetic Diversity in the Tropics

If a clade originated in the tropics, it may show higher metrics of phylogenetic diversity in tropical regions. Specifically, its deepest branches should be in the tropics, with more recent divergence among temperate species. Many studies have tested this idea and related the results to the TCH (Table 1). However, the relationship between the time that a clade has been present in a region and the various phylogenetic diversity metrics remains poorly understood. For example, Oliveira et al. (2016) used simulations to show that many phylogenetic diversity metrics were impacted by time, species richness, and diversification rates, and not time alone. Thus, significant differences in these metrics among regions might not reflect colonisation times. In these simulations, mean phylogenetic distance (Webb 2000) and phylogenetic-species variability (Helmus et al. 2007) appeared to have the potential to reflect time and not just richness. However, in these simulations, the true “time” was the ages of clades and not colonisation times of regions, leaving their relevance unclear.

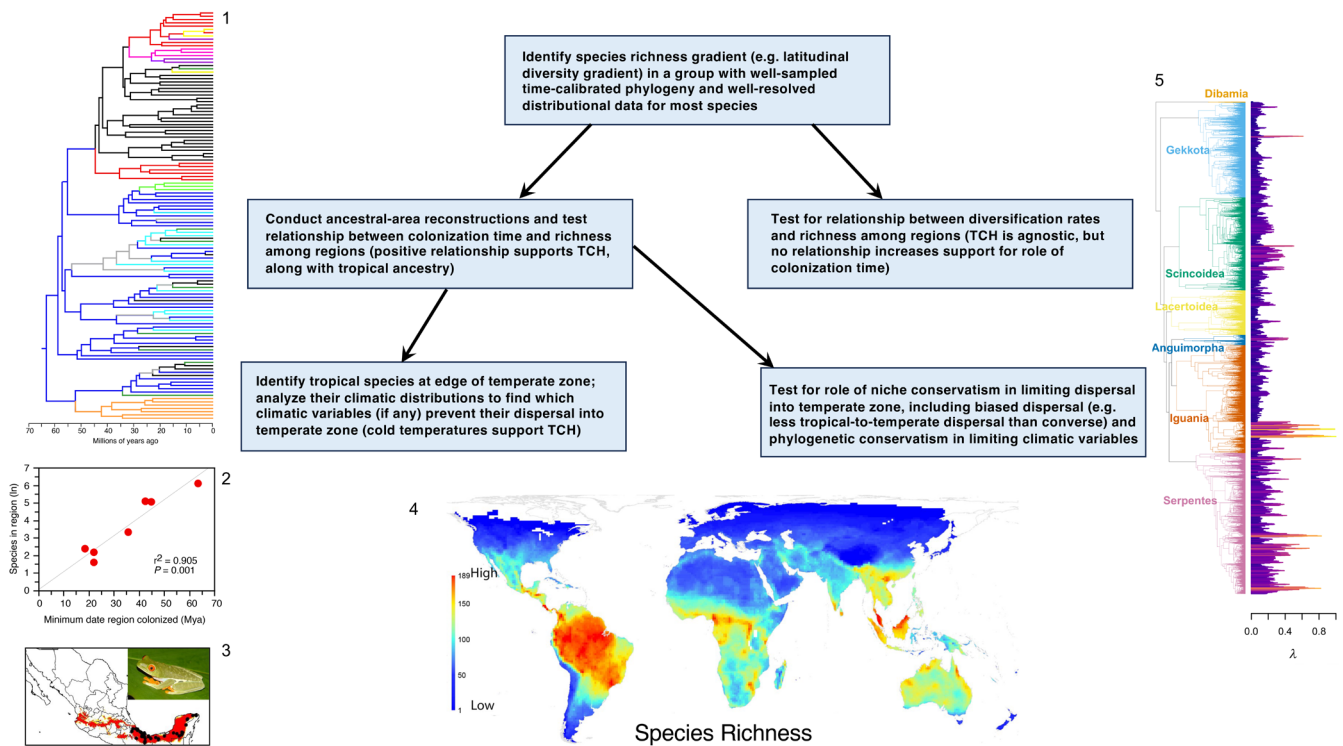


FIGURE 2 | A general outline for testing the main components of the tropical conservatism hypothesis (TCH). Our review found that relatively few studies test more than one or two predictions of the TCH, and almost no recent studies contain all of these components. Note that several creative approaches have been used to test other components of the TCH, such as the effect of the larger area of tropical regions in the past (e.g., Fine and Ree 2006; Romdal et al. 2013). 1 = A time-calibrated phylogeny of treefrogs (Hylidae) illustrating maximum likelihood reconstruction of ancestral areas. Dark blue is tropical South America and red is temperate North America. 2 = The relationship between the oldest colonisation of each region (inferred from 1) and the current richness there today. 3 = Results of niche modelling analysis showing that temperature seasonality potentially explains the northern range limits of the tropical red-eyed treefrog (*Agalychnis callidryas*) in eastern Mexico (1–3 from Wiens et al. 2006). Black circles are localities and red areas are climatically suitable based on this variable. 4 = Global species richness of squamate reptiles in 96 × 96 km grid cells (image modified from Stephens et al. 2025). 5 = Time-calibrated phylogeny of squamate reptiles including estimated speciation rates (image modified from Moreira et al. 2024).

Algar et al. (2009) did simulate diversification and colonisation along an environmental gradient, but they did not test if phylogenetic diversity measures reflected colonisation times. Other studies have used simulations to address the performance of phylogenetic diversity measures (e.g., Mazel et al. 2016; Tucker et al. 2017), but not their ability to capture differences in colonisation times among regions. In summary, additional studies are urgently needed to address whether measures of phylogenetic diversity accurately reflect how long regions have been colonised: for example, by simulating colonisation and diversification of species within and among regions over time, tracking when each region was first successfully colonised, and then testing whether phylogenetic diversity measures based on extant species accurately reflect that oldest colonisation time.

5.3 | Diversification Rates Need Not Be Higher in Tropical Clades

For a given group of organisms, the presence of both higher species richness and higher diversification rates in the tropics relative to temperate regions can support the diversification-rate hypothesis. Yet, supporting the diversification rate hypothesis

does not necessarily rule out the TCH, because a strong effect of colonisation time could also be present (i.e., these hypotheses are not mutually exclusive).

Under the TCH, more clades are thought to arise in the tropics because the tropics had greater area in the past (when Earth's climate was warmer), up until ~30–40 million years ago (Morley 2000; Beerling and Woodward 2001; Ziegler et al. 2003). This greater area may have led to higher richness through higher diversification rates in tropical clades (Fine and Ree 2006). However, under this hypothesis, this difference in diversification rates should apply to clades > 30 Myr old. Furthermore, other causes of higher tropical diversification rates besides area should be ruled out, to strongly infer a role for greater area (and not some other impact of tropical regions on diversification).

Estimating diversification rates is not trivial, and a study's conclusions could depend on the methods used. Reviewing the efficacy of these methods for studying the origins of richness patterns would require a dedicated paper (see instead Wiens 2024). Nevertheless, recent analyses suggest that species-level rates may be misleading about large-scale patterns that arose over deeper timescales (Stephens et al. 2025).

TABLE 1 | Summary of studies that tested the tropical conservatism hypothesis.

Group and predictions	Summary for each prediction		
	Supports	Rejects	Ambiguous
Animals			
Ancestral areas	15 (75%)	3 (15%)	2 (10%)
Mean age of clades	127.8 (<i>n</i> = 13)	126.7 (<i>n</i> = 3)	54.5 (<i>n</i> = 2)
Phylogenetic diversity	8 (62%)	3 (23%)	2 (15%)
Mean age of clades	153.3 (<i>n</i> = 3)	140.0 (<i>n</i> = 1)	
Diversification rates	10 (37%)	15 (56%)	2 (7%)
Mean age of clades	152.5 (<i>n</i> = 10)	145.5 (<i>n</i> = 15)	272.5 (<i>n</i> = 2)
Niche conservatism	11 (92%)	1 (8%)	0
Mean age of clades	202.8 (<i>n</i> = 8)	50 (<i>n</i> = 1)	
Plants			
Ancestral areas	4 (40%)	2 (20%)	4 (40%)
Mean age of clades	98.2 (<i>n</i> = 4)	262.5 (<i>n</i> = 2)	181.2 (<i>n</i> = 4)
Phylogenetic diversity	15 (70%)	0	7 (30%)
Mean age of clades	206.9 (<i>n</i> = 15)		281.9 (<i>n</i> = 7)
Diversification rates	3 (23%)	9 (69%)	1 (8%)
Mean age of clades	300.0 (<i>n</i> = 2)	99.8 (<i>n</i> = 8)	200 (<i>n</i> = 1)
Niche conservatism	10 (83%)	0	2 (17%)
Mean age of clades	173.4 (<i>n</i> = 10)		205.0 (<i>n</i> = 2)

Note: Only groups that showed a latitudinal diversity gradient were included here. Other richness patterns are addressed elsewhere in Table 2 and Table S2. For each major group, we summarise which predictions of the TCH were tested and which were supported. We also show the mean age of the clades that were the focus of each study (crown-group age; in millions of years before the present), and the number of clades with this information in each category. For ancestral areas, the TCH predicts that the ancestral area will have the highest richness. For phylogenetic diversity, the TCH predicts higher phylogenetic diversity in the more species-rich region. For diversification rates, the prediction is less obvious, and so we merely indicate whether the region with the highest richness had higher diversification rates (supports), lower (rejects), or was ambiguous. Note that some studies tested more than one prediction. Full data are given in Dataset S1.

5.4 | Time-Integrated Area

A more direct way to test the effect of past area on current species richness is the time-integrated area approach pioneered by Fine and Ree (2006). They estimated the area of 11 biomes (e.g., Neotropics, North American eastern temperate) and found that tree species richness was more strongly related to the past area of these biomes than their current areas, especially in the Eocene.

5.5 | Evidence for Climatic Niche Conservatism

Under the TCH, climatic niche conservatism is thought to limit the dispersal of species and clades from tropical regions into temperate regions. Niche conservatism refers to the maintenance of ancestral traits (like tropical climatic distributions) over time within a species or clade. Various lines of evidence have been used to support climatic niche conservatism, and we give three examples here.

One line of evidence is a strong phylogenetic signal in climatic-niche variables (e.g., lambda: Pagel 1999; K-statistic: Blomberg et al. 2003), such that closely related species tend to occur in

similar climates. These analyses are most relevant if applied to the specific climatic variables that limit tropical-to-temperate dispersal (e.g., freezing temperatures), as inferred based on species-distribution modelling or related approaches.

Another line of evidence is limited dispersal from the tropics to the temperate zone, in comparison to dispersal within climatic zones or from the temperate zone to the tropics (although the TCH does not make predictions about temperate-to-tropical dispersal). Rates of change among climatic zones can be estimated from ancestral reconstructions on time-calibrated phylogenies (e.g., Pyron and Wiens 2013).

A third line of evidence involves the shape of latitudinal diversity gradients. Romdal et al. (2013) predicted that latitudinal richness gradients would be steeper in groups that originated during warmer periods of Earth's history and shallower in groups that originated during cooler periods. Thus, groups originating in warm periods are more likely to be tropical and to have difficulty colonising temperate regions (leading to a steep latitudinal gradient) whereas groups from cool periods would more easily colonise temperate regions (leading to a flatter latitudinal gradient).

6 | Is the Tropical Conservatism Hypothesis Generally Supported by Empirical Studies?

We reviewed empirical studies that potentially addressed the TCH. We searched Google Scholar for “tropical conservatism hypothesis” separately for each year from 2006 to 2022 (from 20 August, 2023 to 3 September, 2023). Because the TCH was published in 2004, we did not expect papers that focused on testing it to be published that same year or the year after. We sorted papers by relevance within each year (using Google Scholar), and examined the 40 most relevant papers for each year (additional details in Table S1). We generally found few relevant studies by the fourth page of results (i.e., last 10). We found >200 relevant studies (Dataset S1). Nevertheless, these papers should be considered only a sample of studies from each year. We give full details on the search methods, using the PRISMA Eco-Evo checklist (O’Dea et al. 2021), in Appendix S1.

We did not review every paper on the latitudinal diversity gradient from the past 20 years (there are too many). Instead, we focused on those potentially testing the TCH. Our review might be considered biased towards studies that supported the TCH because we used “tropical conservatism hypothesis” as a keyword. Yet, we found many studies that concluded that their analyses rejected it, or that barely mentioned it (e.g., Jablonski et al. 2006). The sampled studies generally focused on the causes of diversity patterns, not the TCH specifically. For example, among the 221 studies in Dataset S1, only 9 (4%) mentioned “tropical conservatism” or “tropical niche conservatism” in their titles. Further, among 99 sampled studies here that addressed the latitudinal diversity gradient in plants and animals (Table 1), many more analysed diversification rates ($n=41$; which are crucial to competing hypotheses) than ancestral areas ($n=26$; which are crucial to the TCH).

We focused primarily on the latitudinal diversity gradient, but we also included studies that focused on other patterns that are potentially explained by the same factors underlying the TCH (e.g., inverse latitudinal diversity gradients, elevational richness, and climate-richness relationships). We excluded review papers and simulation studies. We categorised studies based on what richness pattern they addressed, and whether they estimated ancestral areas, phylogenetic diversity metrics, diversification rates, and niche conservatism, and whether each of these results supported the predictions of the TCH (see above). We relied on the conclusions of the original studies as to whether a prediction was supported or not, rather than critiquing the methodology of every study (or selectively including studies based on our methodological preferences). Nevertheless, we acknowledge that estimating ancestral areas, diversification rates, and niche conservatism is not trivial, nor is estimating species richness and phylogenies.

We describe results for animals and plants separately, focusing on the latitudinal diversity gradient first (Figure 3; summary in Table 1; data for all studies in Dataset S1). Most studies focused on a single clade each (e.g., birds), and we also considered species numbers in each study (Dataset S1; Table S2). In animals, 21 studies reconstructed ancestral areas, and 75% ($n=16$) found that the ancestral area (i.e., tropical) was the most species-rich, whereas 15% ($n=3$) found that it was not, and 10%

($n=2$) reported ambiguous results. Similarly, 12 studies examined phylogenetic diversity patterns, and the TCH predictions were supported in 8 (62%), rejected in 3 (23%), and ambiguous in 2 (15%). A total of 27 animal studies examined diversification rates. These rates were higher in the tropics in 10 studies (37%), lower in 15 (56%), and ambiguous in 2 (7%). Among analyses of niche conservatism, 5 studies analysed transition rates, and 60% found more temperate-to-tropical dispersal than tropical-to-temperate, whereas 40% found the converse. All 5 studies that analysed phylogenetic signal in climatic distributions supported it (100%). These patterns from study numbers were consistent with those from species numbers (animals and plants; Table S2).

Results were similar in studies of the latitudinal diversity gradient in plants (Figure 3; Table 1). Ten studies analysed ancestral areas, and 4 found the ancestral area to be the most species-rich (40%), whereas 2 did not (20%), and 4 were ambiguous (40%). A total of 22 studies analysed phylogenetic diversity patterns, and all 15 with unambiguous results supported the TCH (68%), whereas 7 were ambiguous (32%). Among 13 plant studies that analysed diversification rates, 3 found higher rates in the tropics (23%), whereas 9 did not (69%), and 1 was ambiguous (8%). Among the 12 studies that tested for niche conservatism, 10 supported it (83%) and 2 gave mixed results (17%).

We also combined the data for plants and animals and tested whether the proportions of studies supporting versus rejecting each component were significantly different using chi-squared tests (in R version 4.3.1; R Core Team 2023; code in Dataset S2). We found significant support for each prediction favouring the TCH, and for rejecting the diversification-rate hypothesis. Specifically, we found significant support for tropical regions being the inferred ancestral area (19 supporting vs. 5 rejecting; chi-squared = 14.08; $p=0.0002$), having higher phylogenetic diversity (23 vs. 3; chi-squared = 27.77; $p<0.0001$), and lower diversification rates (13 higher vs. 24 lower; chi-squared = 5.40; $p=0.0201$), and with significant support for niche conservatism (21 vs. 1; chi-squared = 32.82; $p<0.0001$). Studies with ambiguous results for a given question were excluded from these tests.

We also tested whether the support for these TCH predictions might depend on clade ages. Schluter (2016) found that support for the diversification-rate hypothesis increases with clade age (see also Pontarp and Wiens 2017). We did not find significant corroboration for this idea (R code in Dataset S2, data in Datasets S3–S5). In animals, the mean ages of studies that supported (as opposed to rejected) the diversification-rate hypothesis were almost equal (152.5 vs. 145.5 Myr; Welch’s two-sample, unpaired t -test; $p=0.8719$; $t=0.1640$; $df=15.40$; $n=25$; Table 1). In plants, the mean ages were far more different and in the expected direction (supporting mean = 300.0; rejecting mean = 99.8), but this difference was caused by one very old clade in the supporting category and one very young one in the rejecting category, and the difference was not significant ($p=0.4989$; $t=0.9981$; $df=1.01$; $n=10$). Combining the data from plants and animals also yielded a non-significant result (supporting mean = 177.1; rejecting mean = 129.6; $p=0.3100$; $t=1.0531$; $df=14.14$; $n=35$).

Results from other richness patterns were generally similar (Table 2; Table S3). These results generally showed the most

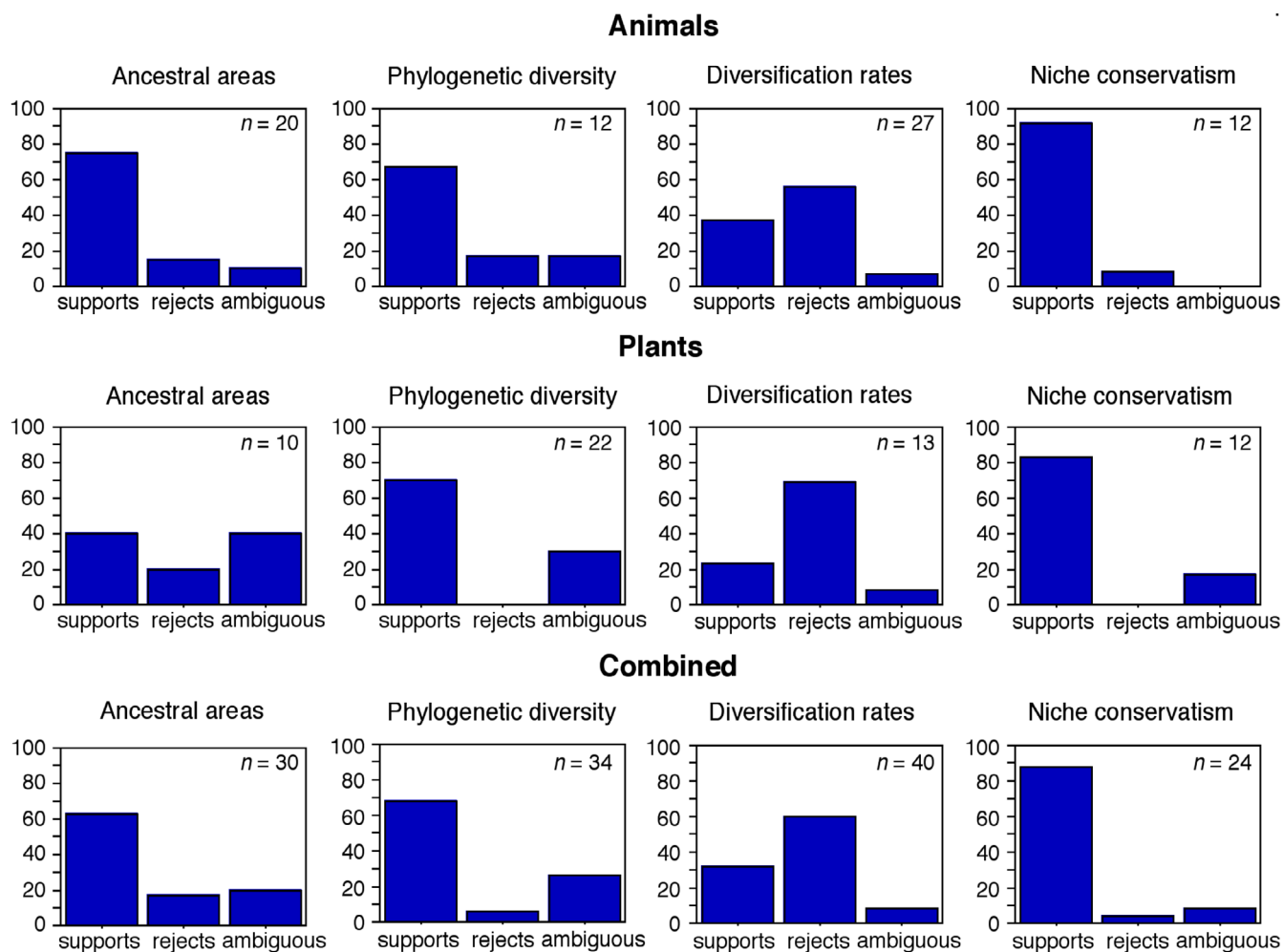


FIGURE 3 | Summary of empirical support for the tropical conservatism hypothesis (TCH) based on published studies of the latitudinal diversity gradient. Each graph shows the percentage of studies supporting or rejecting a given prediction of the TCH based on our systematic review, with the sample size (total number of included studies). We list studies showing higher diversification rates in the tropics as “supporting”, although the TCH is largely agnostic about diversification rates. Summary data for plants and animals are given in Table 1 (the combined data combine the plant and animal data).

species-rich area as being ancestral and having the highest phylogenetic diversity (but not for phylogenetic diversity for elevation and climate), with strong support for niche conservatism and generally weak or mixed support for the role of diversification rates.

In summary, these empirical studies significantly supported the predictions of the TCH. These included terrestrial species (including plants, insects, and vertebrates, with similar support from animals and plants; Figure 3), marine groups (fish; Miller et al. 2018), and freshwater species (more fish; Miller and Román-Palacios 2021).

We found few relevant studies of other major taxa, besides animals and plants (Dataset S1). A study of fungi (Treseder et al. 2014) suggested that older phyla tend to occur near the equator in warmer, wetter climates, as predicted by the TCH. Another study (Looney et al. 2016) found an inverse latitudinal diversity gradient in a fungus genus (*Russula*), with an older origin and higher diversification rates in the temperate zone. Two studies of the latitudinal diversity gradient in marine protists found higher diversification rates in the tropics (Allen and Gillooly 2006; Vieira et al. 2021), with one also finding tropical

origins. A study of an elevational gradient in protists supported niche conservatism based on phylogenetic clustering (Fernández et al. 2022).

Our conclusions differ substantially from Jansson et al. (2013), who reviewed 111 phylogenetic studies of vertebrates, insects, and plants. They concluded that their results supported the out-of-the-tropics (OTT) hypothesis but not the TCH or diversification-rate hypothesis. They found that most sampled clades originated in the tropics, as predicted by the TCH and OTT. However, they found no significant difference in diversification rates between tropical and temperate sister lineages. Thus, their results did not actually support the OTT hypothesis. Their basis for rejecting the TCH was the many transitions from the tropics to the temperate zone (fewer tropical-to-temperate transitions than temperate-to-tropical is more consistent with the TCH). However, many tropical-to-temperate transitions might be expected in their data because: (a) they only included clades that occurred in both temperate and tropical regions (i.e., roughly half of plant families have remained exclusively tropical, a pattern supporting the TCH; Ricklefs and Renner 1994), and (b) most sampled clades originated in

TABLE 2 | Summary of studies that examined other species richness patterns.

Richness pattern	Supports	Rejects	Ambiguous
Inverse latitudinal diversity gradient			
Ancestral areas	6 (100%)	0	0
Phylogenetic diversity	1 (100%)	0	0
Diversification rates	2 (33%)	4 (67%)	0
Niche conservatism	5 (83%)	0	1 (17%)
Elevational richness gradient			
Ancestral areas	3 (100%)	0	0
Phylogenetic diversity	3 (27%)	4 (36%)	4 (36%)
Diversification rates	1 (33%)	2 (67%)	0
Niche conservatism	1 (100%)	0	0
Climate-diversity relationship			
Ancestral areas	2 (67%)	0	1 (33%)
Phylogenetic diversity	0	1 (100%)	0
Diversification rates	1 (100%)	0	0
Niche conservatism	3 (100%)	0	0
Biome/habitat richness			
Ancestral areas	7 (88%)	0	1 (12%)
Phylogenetic diversity	3 (75%)	0	1 (25%)
Diversification rates	0	4 (100%)	0
Niche conservatism	4 (67%)	0	2 (33%)
Regional richness			
Ancestral areas	3 (100%)	0	0
Phylogenetic diversity	3 (75%)	0	1 (25%)
Diversification rates	0	2 (100%)	0
Niche conservatism	1 (100%)	0	0
Latitudinal richness			
Ancestral areas	0	0	0

(Continues)

TABLE 2 | (Continued)

Richness pattern	Supports	Rejects	Ambiguous
Phylogenetic diversity	3 (43%)	1 (14%)	3 (43%)
Diversification rates	0	0	0
Niche conservatism	0	0	0

Note: Groups that showed the latitudinal diversity gradient (higher tropical richness) are included in Table 1 instead. For each major group, we summarise which predictions were tested and which were supported. For ancestral areas, the TCH predicts that the ancestral area will have the highest richness. For phylogenetic diversity, the TCH predicts higher richness in the more species-rich region. For diversification rates, the prediction is less obvious, and so we merely indicate whether the region with the highest richness had higher diversification rates (supports), lower (rejects), or was ambiguous. Note that some studies tested more than one prediction. The data are also summarised (by plant vs. animals) in Table S2. Full data are given in Dataset S1. Inverse latitudinal diversity gradient refers to higher temperate than tropical richness. Climate-diversity relationship refers to richness that is related to one or more climatic variables. Biome/habitat richness refers to the pattern in which a given biome/habitat has higher richness than others (e.g., rainforest vs. savanna). Regional richness and latitudinal richness refer to spatial richness patterns that are not clearly classifiable as the typical latitudinal or inverse latitudinal diversity gradients.

the tropics. In summary, the results of Jansson et al. (2013) are largely congruent with ours, specifically regarding clades originating in the tropics and not having higher tropical diversification rates.

Importantly, their review was based on searching for phylogenetic studies of animals and plants, and not for studies of the TCH. Therefore, this potential source of bias in our results does not apply to theirs, even though their results are largely congruent with ours. Furthermore, the meta-analysis by Li and Wiens (2019) also yielded congruent results (i.e., regional richness patterns generally explained by colonisation times and not diversification rates nor dispersal rates), and was not based on searching for studies of the TCH. There was no overlap in the papers included in their meta-analysis and in ours. Therefore, our results do not appear to be explained by a biased selection of studies favouring the TCH.

7 | Future Research

7.1 | More Studies Need to Simultaneously Test More Predictions of the TCH

We found that most studies tested only one or two predictions of the TCH (Table 1). For example, among animal studies, 51 examined the latitudinal diversity gradient (Dataset S1), but only 20 analysed ancestral-area reconstructions, 13 phylogenetic diversity, 27 diversification rates, and 12 niche conservatism. Similarly, among plant studies, 50 examined the latitudinal diversity gradient (Dataset S1), but only 10 analysed ancestral-areas, 22 phylogenetic diversity, 13 diversification rates, and 12 niche conservatism. To test the TCH, more studies should address all or most of its predictions (Figure 2), especially the role of colonisation time.

7.2 | The Relevance of Phylogenetic Diversity Metrics (and Other Proxies) Remains Highly Uncertain

The relevance of phylogenetic diversity metrics to the TCH remains understudied. Additional simulation studies are needed to determine whether these metrics can accurately reflect colonisation times and diversification rates. Otherwise, we see little point in using these metrics to analyse richness patterns, especially given that other methods can estimate colonisation times and diversification rates far more directly.

Other proxies for colonisation time may also be problematic. For example, a study of Chinese angiosperms examined mean ages of genera across grid cells (Lu et al. 2018). However, this index may be irrelevant to how long plants have been present and speciating in each grid cell. Similarly, many studies have compared mean ages of families in different regions, but it is unclear what this metric means for colonisation times. Galván et al. (2025) recently concluded that time did not explain high tropical richness in tetrapods, but they only analysed climatic stability and only in the last 5 Myr. By contrast, Stephens et al. (2025) found that global richness patterns were explained by diversification and dispersal at ancient timescales (> 80 Myr ago), and that only considering recent timescales could be positively misleading.

7.3 | The Role of Diversification Rates

We found mixed results about whether diversification rates underlie the latitudinal diversity gradient. A significant majority of studies suggested that they do not (Figure 3). We also addressed whether the variability in results among studies might be explained by clade ages (Schluter 2016; Pontarp and Wiens 2017). We did not significantly support this idea, even though our sample size almost doubled that of Schluter (2016). Overall, these results further weaken the support for the diversification-rate hypothesis (and the related OTT hypothesis).

7.4 | Why Would More Clades Originate in the Tropics?

There is now evidence that many clades that are more diverse in the tropics arose in the tropics, and that these ancient tropical origins are important for explaining their high tropical richness. But why did more clades arise in the tropics in the first place? According to the TCH, more clades arose in the tropics because the tropics were more widespread until the last ~30–40 million years ago. Although important studies have supported this idea (e.g., Fine and Ree 2006; Romdal et al. 2013), we think it remains the weakest link. New types of data and analyses to address this question would be valuable.

Similarly, the relationship between this aspect of the TCH and diversification rates needs more study. Hypothetically, the larger area of the tropics in the past led to greater species richness and more tropical clades because larger areas can increase the potential for speciation and decrease extinction. There is support for the idea that clades with larger range areas have higher diversification rates, including studies in both plants and animals (e.g.,

Hernández-Hernández and Wiens 2020; Li and Wiens 2022). However, we did not find that tropical diversification rates were generally higher (Figure 3).

7.5 | What Prevents Tropical Species and Clades From Invading The Temperate Zone?

The main point of the 2004 paper was not to argue that the TCH was true (Wiens and Donoghue 2004). Instead, it emphasised the need to uncover the ecological basis for large-scale biogeographic patterns (and the role of large-scale biogeography in explaining richness patterns). It suggested that one key to understanding the latitudinal diversity gradient might be to reveal why so many tropical clades failed to successfully colonise the temperate zone (i.e., the ecology behind the biogeography).

Based on our review, relatively few studies addressed this. For example, an analysis of the latitudinal diversity gradient in New World treefrogs (Hylidae) found that it was explained by ancient tropical origins, recent temperate colonisation, and the failure of tropical clades to enter temperate North America (Figure 2; Wiens et al. 2006). Temperature seasonality (specifically cold winters) appeared to set the northern range limits of the tropical clades (Figure 2). Recent analyses found parallel evolution of physiological tolerances to cold in the two clades that colonised temperate North America (Moen et al. 2022). In plants, freezing temperatures were a key factor setting range limits in several studies (e.g., Wang et al. 2011; Qian and Chen 2016; Segovia et al. 2020; Qian et al. 2022), and in creating a large-scale boundary between tropical and temperate floras (Althaus et al. 2025). Additional studies along these lines are needed.

There are many other related questions. For example, is it really freezing temperatures that prevent tropical clades from invading temperate regions, or are other climatic (e.g., aridity), abiotic, or biotic factors involved? Why do species in tropical clades not simply adapt to cooler conditions at the edge of the tropics? Is adaptation in temperate-adjacent populations limited by gene flow with more tropical populations? Are there trade-offs that make it difficult for a single species to span tropical and temperate climates? We found relatively few relevant studies (e.g., Barros et al. 2018; Koehler et al. 2012). There have been reviews of the general factors underlying niche conservatism and niche change (e.g., Wiens et al. 2010; Crisp and Cook 2012; Donoghue and Edwards 2014), but more empirical studies are needed specifically at the tropical–temperate interface.

Another related question is: do large-scale climatic factors set similar boundaries between tropical and temperate regions in plants and animals? Separate analyses of biogeographic regions in animals (land vertebrates; Holt et al. 2013) and plants (Carta et al. 2022) suggest that in the Northern Hemisphere these two groups converge on broadly similar boundaries in southern Asia, northern Africa, and southern Mexico. Intriguingly, in the Southern Hemisphere, patterns are very different. In plants, there are separate temperate regions in southern South America, Africa, and Australia. These separate temperate regions are absent in animals, suggesting that they are dispersing more readily between tropical and temperate areas in the Southern Hemisphere.

8 | Conclusions

The higher species richness of tropical regions relative to temperate regions is one of the oldest patterns in ecology, but its causes remain unresolved. The tropical conservatism hypothesis (TCH) integrates evolution, ecology, and biogeography to explain this pattern. We performed a systematic review of ~100 empirical studies of the latitudinal diversity gradient that tested one or more predictions of the TCH. We found that most studies that tested these predictions supported them. Specifically, a significant majority of studies found that groups originated in the tropical regions where they were most species-rich, with higher phylogenetic diversity metrics in tropical regions, and with evidence for niche conservatism. Conversely, a significant majority of studies rejected the diversification-rate hypothesis (and by extension, the out-of-the-tropics hypothesis). Furthermore, we did not find that diversification rates were more important in significantly older clades. We also point out several unresolved areas for future studies, such as the relevance of phylogenetic diversity measures, why more groups originated in the tropics, and the causes underlying the failure of many tropical clades to successfully colonise temperate regions. More broadly, we suggest that progress in this field will come from further quantitative syntheses of the existing literature (rather than opinions), from new empirical analyses that directly incorporate colonisation time (among other factors), and studies that address the processes underlying the range limits of clades.

Author Contributions

John J. Wiens and Michael J. Donoghue conceived the study, conducted the research, and wrote the paper.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code used are available as Datasets S1–S5, which are freely available on figshare at: <https://doi.org/10.6084/m9.figshare.25505086>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.