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RESEARCH ARTICLE

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Time for speciation and niche conservatism explain the latitudinal diversity gradient in clupeiform fishes

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Abstract

Aim: The latitudinal diversity gradient of increasing species richness from poles to equator is one of the most striking and pervasive spatial patterns of biodiversity. Climate appears to have been key to the formation of the latitudinal diversity gradient, but the processes through which climate shaped species richness remain unclear. We tested predictions of the time for speciation, carrying capacity and diversification rate latitudinal diversity gradient hypotheses in a trans-marine/freshwater clade of fishes.

Location: Global in marine and freshwater environments.

Taxon: Clupeiformes (anchovies, herrings, sardines and relatives).

Methods: We tested predictions of latitudinal diversity gradient hypotheses using a molecular phylogeny, species distribution data and phylogenetic comparative approaches. To test the time for speciation hypothesis, we conducted ancestral state reconstructions to infer the ages of temperate, subtropical and tropical lineages and frequency of evolutionary transitions between climates. We tested the carry capacity hypothesis by characterizing changes in net diversification rates through time. To test the diversification rate hypothesis, we qualitatively compared the diversification rates of temperate, subtropical and tropical lineages and conducted statistical tests for associations between latitude and diversification rates.

Results: We identified four transitions to temperate climates and two transitions out of temperate climates. We found no differences in diversification rates among temperate and tropical clupeiforms. Net diversification rates remained positive in crown Clupeiformes since their origin ~150 Ma in both tropical and temperate lineages. Climate niche characters exhibited strong phylogenetic signal. All temperate clupeiform lineages arose <50 Ma, after the Early Eocene Climatic Optimum.

Main conclusions: Our results support the time for speciation hypothesis, which proposes that climate niche conservatism and fluctuations in the extent of temperate climates limited the time for species to accumulate in temperate climates, resulting in the latitudinal diversity gradient. We found no support for the carrying capacity or diversification rate hypotheses.

KEYWORDS
anchovy, BAMM, BiSSE, carrying capacity, early Eocene climatic optimum, herring, HiSSE, net diversification rates, phylogenetic comparative methods, trans-marine/freshwater

1 | INTRODUCTION

The increasing species richness from the poles to the equator, called the latitudinal diversity gradient, is one of the most striking and pervasive spatial patterns of biodiversity. This pattern is global in scale, observed in living and extinct lineages, and exhibited by nearly all major clades of organisms regardless of their ecology (Buckley et al., 2010; Economo et al., 2018; Fuhrman et al., 2008; Hawkins, 2001; Hillebrand, 2004a, 2004b; Jablonski et al., 2017; O'Brien et al., 2000; Rabosky et al., 2018). The latitudinal diversity gradient has existed off and on for over 325 million years, seemingly diminishing during warm periods of earth's history and returning during cooler periods (Crame, 2001; Leighton, 2005; Mannion et al., 2014; Marcot et al., 2016; Powell et al., 2012; Shiono et al., 2018). Thus, climate appears to have been key to the formation of the latitudinal diversity gradient, although the processes through which climate shaped species richness remain unclear (Mittelbach et al., 2007; Morinière et al., 2016; O'Brien et al., 2000; Pontarp et al., 2019). Resolving these interactions will advance biodiversity theory, improving our ability to explain spatial variation in species richness, model impacts of changing environments on biodiversity and sustainably manage natural resources (Brown, 2014; Pontarp et al., 2019).

There are three leading hypotheses about the formation of the latitudinal diversity gradient: (1) time for speciation, (2) carrying capacity and (3) diversification rate hypotheses (Table 1; reviewed by Mittelbach et al., 2007; Brown, 2014; Hurlbert & Stegen, 2014a; Pontarp et al., 2019). Multiple processes may have generated the latitudinal diversity gradient, in which case studies may reveal support for multiple hypotheses. The time for speciation hypothesis proposes that the tropics have high species richness because species have had more time to accumulate at low latitudes (Mittelbach et al., 2007). Most variations of the time for speciation hypothesis propose that species had more time to diversify in tropical climates because they have been in continuous existence longer than temperate climates, which receded during warm periods of Earth's history (Fischer, 1960; Hawkins et al., 2006; Mittelbach et al., 2007; Wiens & Donoghue, 2004; Zachos et al., 2001). The time for speciation hypothesis assumes that colonization of temperate environments by tropical lineages was limited by (1) climate niche conservatism, the tendency of species to retain ancestral climate niche traits (reviewed by Wiens & Graham, 2005), and/or (2) inherent attributes of temperate latitudes (Pontarp & Wiens, 2017; Wiens & Donoghue, 2004). Otherwise, rapid colonization of temperate areas could quickly eliminate the latitudinal gradient in scenarios that do not involve latitudinal differences in carrying capacities or net diversification rates (Wiens & Donoghue, 2004).

The carrying capacity hypothesis proposes that properties of tropical environments allow them to hold more species than temperate regions (Hurlbert & Stegen, 2014a; Janzen, 1967; Mittelbach et al., 2007). For example, high tropical primary productivity resulting from consistent, high inputs of solar radiation and precipitation has been hypothesized to allow for high species richness (Hawkins et al., 2003). This hypothesis predicts that regional species richness is generally at carrying capacity across latitudes, and consequently, regional net diversification rates have been approximately zero over evolutionary time-scales since the formation of the latitudinal diversity gradient (Janzen, 1967; Mittelbach et al., 2007). The carrying capacity hypothesis can be tested by characterizing temporal patterns of diversification using phylogenies comprised primarily or entirely of extant species (Table 1; Rabosky & Glor, 2010; Rowsey et al., 2018; Condamine et al., 2019; Economo et al., 2019). However, these are considered relatively weak tests of the carrying capacity hypothesis and should be complemented with additional studies that use alternative approaches, such as those that consider multiple clades from a geographic region or incorporate fossil data (Benson et al., 2021; Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015). Few studies have found strong support for the carrying capacity hypothesis, instead finding positive diversification rates over macroevolutionary time-scales and limited evidence of diversification rates slowing to approximately zero across latitudes, which is predicted if global species richness is approximately at carrying capacity (Economo et al., 2019; Marin et al., 2018; McCain et al., 2018), but see Hurlbert and Stegen (2014a), Rabosky and Hurlbert (2015) and Etienne et al. (2019). However, there is evidence that carrying capacity plays a role in regulating regional species richness patterns (Benson et al., 2021; Coelho et al., 2019; McCain et al., 2018) and diversification rates in some lineages, which may lead to interclade differences in the strength of the latitudinal diversity gradient (Betancur-R et al., 2012; Bloom & Egan, 2018).

The diversification rate hypothesis invokes a negative correlation between net diversification rate and latitude to explain the latitudinal diversity gradient (Allen et al., 2006; Janzen, 1967). Many mechanisms have been proposed to produce elevated tropical diversification rates. For example, Jocque et al. (2010) suggested that ecological specialization is characteristic of tropical organisms, and specialization limits dispersal across unfavourable environments, leading to high rates of allopatric speciation. Allen et al. (2006) proposed that high tropical temperatures result in high metabolism, which increases mutation rates, resulting in rapid genetic divergence among populations and speciation. Janzen (1967) hypothesized that high tropical net diversification rates might result from low extinction rates in temporally stable tropical climates. There is no consensus regarding the importance of diversification rates to the latitudinal diversity gradient. Studies have found negative correlations between latitude and diversification rates (Pyron, 2014; Pyron

TABLE 1 Predictions (Core predictions) of latitudinal diversity gradient hypotheses (Hypothesis) tested in this study and established statistical analyses and metrics used to test predictions with phylogenies comprised of extant taxa along with citations of selected studies that discuss the testing of these predictions (Established analyses and metrics)

Hypothesis	Core predictions	Established analyses and metrics
Time for speciation	(1) Temperate lineages are more recently derived on average than tropical lineages (sensu Hawkins et al., 2006)	(a) Ancestral state reconstructions using time-calibrated phylogenies to infer the ages of temperate and tropical lineages (Economo et al., 2018; Miller & Román-Palacios, 2021). (b) Estimates of how recently derived species are on average at temperate versus tropical climates (Hurlbert & Stegen, 2014a; Stevens, 2006), such as mean root distance (MRD; Kerr & Currie, 1999; Hawkins et al., 2006)
	(2) Most temperate lineages are younger than the re-emergence of temperate environments following the Early Eocene Climatic Optimum (~52–50 Ma)	(a) Ancestral state reconstructions using time-calibrated phylogenies to infer the age of temperate lineages (Economo et al., 2018; Miller & Román-Palacios, 2021)
	(3) Transitions between temperate and subtropical/tropical environments are infrequent	(a) Ancestral state reconstructions to infer the frequency of evolutionary transitions between temperate, subtropical and tropical climates (Economo et al., 2018; Miller et al., 2018). (b) Estimates of phylogenetic signal (Economo et al., 2019; Wiens & Donoghue, 2004), such as Pagel's λ (Pagel, 1999) and Blomberg's K (Blomberg et al., 2003)
Carrying capacity	(1) Since the formation of latitudinal diversity gradient, regional net diversification rates have been approximately zero over evolutionary time-scales	(a) Characterization of net diversification rates through time using programs such as BAMM (Condamine et al., 2019; Economo et al., 2019; Rowsey et al., 2018)
Diversification rate	(1) A negative correlation between net diversification rate and latitude	(a) Qualitative comparisons of the diversification rates of temperate, subtropical and tropical lineages using visual approaches such as phylorate, scatter and violin plots. (b) Statistical tests for associations between traits and diversification rates (Economo et al., 2018; Miller & Román-Palacios, 2021; Pyron, 2014; Rabosky et al., 2018) such as ES-sim (Harvey & Rabosky, 2018) and BiSSE (Maddison et al., 2007)

Note: The second time for speciation hypothesis core prediction is specific to variations of this hypothesis that focus on climate (see paragraph two of the introduction).

& Wiens, 2013). However, several studies have failed to identify correlations between latitude and diversification rates (Economo et al., 2019; Miller et al., 2018; Rabosky et al., 2015; Tedesco et al., 2017) and there are several recent reports of faster diversification rates in temperate regions than tropical regions (Harvey et al., 2020; Rabosky et al., 2018; Schluter & Pennell, 2017).

The few tests of latitudinal diversity gradient hypotheses using actinopterygians (ray-finned fishes) yielded conflicting results (García-Andrade et al., 2021; Miller et al., 2018; Miller & Román-Palacios, 2021; Rabosky et al., 2018; Siqueira et al., 2016). Actinopterygians inhabit a range of habitat types known to have distinct lineage diversification dynamics, including coral reefs, coastal areas, the open ocean in marine environments and freshwater lakes and rivers (Bloom et al., 2013; Cowman & Bellwood, 2011; Miller et al., 2018; Rabosky, 2020). Species richness may be governed by different processes in these habitat types, causing habitat-specific deviations in the strength of the latitudinal diversity gradient and variation in the relative importance of different processes in its formation (Hillebrand, 2004b; Hulbert, 2004; Hurlbert & Stegen, 2014b). Rabosky et al. (2018) examined a large dataset of marine fishes that spanned Actinopterygii and found no support for the diversification rate hypothesis but did not directly test other latitudinal diversity gradient hypotheses. Siqueira et al. (2016) reported higher net diversification rates in tropical marine reef fishes relative to extratropical regions, in support of the diversification rate hypothesis. García-Andrade et al. (2021) examined the latitudinal diversity gradient in a clade of freshwater fishes (Poeciliidae) and found support for the time for speciation hypothesis. None of these studies explicitly tested the carrying capacity hypothesis or examined clades spanning marine and freshwater environments (trans-marine/freshwater clades). Trans-marine/freshwater clades, especially those with several transitions between marine and freshwater biomes, can exhibit different diversification dynamics than clades restricted to either freshwater or marine environments (Betancur-R et al., 2012; Bloom & Egan, 2018). Therefore, trans-marine/freshwater clades offer compelling study systems for examining the causes of the latitudinal diversity gradient in lineages represented in multiple biomes.

We tested the predictions of latitudinal diversity gradient hypotheses using Clupeiformes (anchovies, herrings, sardines and relatives), a trans-marine/freshwater clade of actinopterygian fishes, as our study system. The age, ecological diversity and widespread distribution of this group, recent work characterizing clupeiform species diversity and availability of well-resolved clupeiform phylogenies make it an intriguing study system for investigating the latitudinal diversity gradient (Bloom & Lovejoy, 2012, 2014; Egan et al., 2017, 2018a,b; Hata et al., 2020a,b; Lavoué et al., 2013, 2018). This clade of approximately 400 species is globally distributed in freshwater and marine environments and exhibits a latitudinal diversity gradient (Lavoué et al., 2013; Whitehead, 1985; Whitehead et al., 1988). We used established phylogenetic comparative approaches to test the predictions of the time for speciation, carrying capacity and diversification rate hypotheses with an extant species dataset (Table 1; reviewed by Mittelbach et al., 2007; Brown, 2014; Hurlbert & Stegen, 2014a; Pontarp et al., 2019). Our study is distinct from previous work on this topic in several ways. It is one of only a few studies to explore the causes of the latitudinal diversity gradient in ray-finned fishes, and the only study focused on a trans-marine/freshwater clade (García-Andrade et al., 2021; Miller et al., 2018; Miller & Román-Palacios, 2021; Rabosky et al., 2018; Siqueira et al., 2016). We tested predictions of all three latitudinal diversity gradient hypotheses within the same methodological framework. Furthermore, previous studies generally focused on large clades, but see García-Andrade et al. (2021), limiting progress towards an understanding of interclade variation in the importance of different processes to the formation of the latitudinal diversity gradient.

2 | METHODS

2.1 | Phylogeny and taxon sampling

For phylogenetic comparative analyses, we used a time-calibrated clupeiform phylogeny estimated with concatenated Bayesian analyses of one mitochondrial gene (*cytb*) and three nuclear genes (*rag1*, *rag2* and *slc*; Egan et al., 2018a). This phylogeny contained 187 clupeiform species, including representatives of all major lineages, robust sampling of clupeiform ecological diversity and representative sampling of all geographical regions occupied by this clade (Table S1; Egan et al., 2018a; Whitehead, 1985; Whitehead et al., 1988). When possible, we accounted for topological phylogenetic uncertainty in analyses using 100 trees from the Bayesian posterior sample used to generate the maximum clade credibility (MCC) tree (Egan, Bloom, et al., 2018a). For other analyses, we used the MCC tree. We conducted statistical analyses in program R v3.4.0, unless stated otherwise (R Core Team, 2017). We trimmed outgroup and duplicated taxa from phylogenies using the *drop. tip* R function in package *ape* (Paradis & Schliep, 2019), which yielded trees containing 183 species. However, one of our approaches to account for missing taxa allowed us to use a phylogeny containing 205 clupeiform species in several analyses (Section 2.5).

2.2 | Species range data

Geographic range data can provide reliable estimates of the climate niches of species (resource–utilization ecological niche sensu MacArthur & Levins, 1967; Schoener, 2009), including those of marine and freshwater fishes (McNyset, 2005;). Although range-based estimates may not be as precise as experimentally derived niche estimates, they are useful proxies for interspecific comparisons and macroevolutionary studies of climate niche evolution (Economo et al., 2019; McNyset, 2005; Rabosky et al., 2018). We collected species range data from the literature (Borsa et al., 2004; Castro-Aguirre et al., 2002; Hata et al., 2020a,b; Kimura et al., 2009; Loeb & Alcantara, 2013), FishNet2 (www.fishnet2.net) occurrence records and compiled Ocean Biogeographic Information System (www.iobis.org; Grassle, 2000) and Global Biodiversity Information Facility (www.gbif.org; GBIF.org, 2017) occurrence records accessed via AquaMaps (Kaschner et al., 2016). We checked for congruence in species range estimates from different sources and eliminated occurrences if we deemed them erroneous. There is uncertainty about the taxonomy of some clupeiform lineages, many species are poorly studied and identification of several taxa is challenging (Egan, Bloom, et al., 2018a; Lavoué et al., 2014). For lineages with these characteristics (e.g. *Stolephorus* and *Sardinella*), we used recent taxonomy and species distribution studies as primary data sources. We used species range data to code three characters to approximate the climate niche of each species (Table S1): a 'maximum latitude' continuous character describing the absolute value of the latitude at the furthest point of species ranges from the equator; a discrete 'climate zone' character describing the climate (tropical, subtropical or temperate) encompassing most of each species distribution; and a 'tropicality index' character describing the proportion of each species range in the tropics. The climate zone character took into account FishBase (www.fishbase.org) climate zone determinations when available, which are based both on the latitudes encompassed by species ranges and sea surface temperatures. We also coded a binary version of the climate zone character (temperate vs. tropical/subtropical). The tropicality index character was calculated by subtracting the fraction of latitudinal range outside the tropics from the fraction of latitudinal range inside the tropics, following Economo et al. (2019). In accordance with previous studies, we defined tropical, subtropical and temperate zones as comprising the latitudes of $<23.5^0$, 23.5^0 to 35^0 and $>35^0$, respectively (Economo et al., 2019; Köppen, 1884; Rabosky et al., 2018). Using multiple climate niche characters with differing resolutions and slight differences in underlying data allowed us to determine the sensitivity of our results to character coding methodology.

2.3 | Patterns of climate niche evolution

We estimated the evolutionary history of the discrete climate zone character (three-state and binary versions) using 100 trees from the posterior distribution of the Egan, Bloom, et al. (2018a) phylogeny and Bayesian stochastic character mapping using the *make.simmap* phytools function (Revell, 2012). We also estimated the evolutionary history of the discrete climate zone character using the Egan, Bloom, et al. (2018a) phylogeny with an alternative placement of the temperate species, *Clupeonella cultriventris* (see Supporting Methods). We estimated the evolutionary history of the continuous maximum latitude and tropicality index characters using the MCC tree and the *contMap* phytools function and visualized the uncertainty of ancestral state estimates at each node using the *errorbar.contMap* phytools function. Correlations between character states and diversification rates can lead *make.simmap* and *contMap* to produce biased estimates of character evolution (Maddison, 2006). However, we found no evidence for associations between character states and diversification rates (section 3.3), and therefore did not conduct additional analysis to account for this potential source of error. We estimated the rate of maximum latitude character evolution in Clupeiformes using the MCC tree and program BAMM v.2.5.0 (Rabosky, 2014) and set priors for analyses using the *setBAMMpriors* function in BAMMtools (Rabosky et al., 2014). To estimate the degree of climate niche conservatism in Clupeiformes, we calculated two measures of phylogenetic signal for climate niche characters, Pagel's λ (Pagel, 1999) and Blomberg's *K* (Blomberg et al., 2003), using the *phylosig* function in phytools. See Supporting Methods for additional information about the methods we used to infer climate niche evolution.

2.4 | Mean root distance of temperate versus tropical lineages

The time for speciation hypothesis predicts that temperate species are, on average, more recently derived than tropical species. Thus, it predicts a positive correlation between measures of how recently derived species are and latitude and a negative correlation between measures of how recently derived species are and species richness (Hawkins et al., 2006; Hurlbert & Stegen, 2014a). We characterized how recently derived clupeiform species are within 5^0 latitudinal bands by calculating mean root distances (MRD). Mean root distance uses a phylogeny to measure the average number of nodes between species (i.e. tips) and the root of a phylogeny for a set of species and is not a measure of diversification rates (Kerr & Currie, 1999). We used linear regression to test for correlations between MRD and latitude and MRD and species richness.

2.5 | Testing for latitudinal differences in lineage diversification rates

We inferred lineage diversification rates using BAMM, accounting for incomplete sampling in analyses, then qualitatively checked for associations between latitude and diversification rates by visualizing the distributions of diversification rates and character states. We statistically tested for latitudinal differences in diversification rates using the Binary State/Hidden State Speciation and Extinction (*BiSSE/HiSSE*) family of analyses (Beaulieu & O'Meara, 2016; Maddison et al., 2007) and *ES-sim* (Harvey & Rabosky, 2018). We used these methods because they have enough statistical power to detect latitudinal differences in diversification rates with the size of the phylogeny (205 tips) used in this study (Davis et al., 2013; Harvey & Rabosky, 2018; Rabosky & Goldberg, 2017; Singhal et al., 2018). This is in contrast to several other popular methods, which require larger phylogenies (Rabosky & Goldberg, 2017; Rabosky & Huang, 2016). We did not conduct separate tests for latitudinal differences in diversification rates for marine and freshwater species due to insufficient samples sizes. We used estimates of net diversification rates to test for correlations between diversification rates and climate niche rather than considering speciation and extinction rates separately. This is because extinction rate parameter estimates based on phylogenies primarily comprised of extant taxa are often unreliable (Rabosky, 2010) and different combinations of speciation and extinction rates can result in the same net diversification rate estimates with equal likelihood (Louca & Pennell, 2020).

2.5.1 | Estimating lineage diversification rates

We estimated net diversification rates using BAMM. We used a two-step approach to account for incomplete taxon sampling in BAMM analyses. First, we added species to the MCC phylogeny using known sister lineage relationships. This resulted in a phylogeny containing 205 species. Then, we accounted for remaining incomplete taxon sampling by calculating the proportion of species sampled (sampling fraction) at the genus level if possible and at higher taxonomic levels when necessary (Table S2). Eschmeyer's Catalog Of Fishes recognizes 417 valid clupeiform species (Fricke et al., 2020), but does not account for several recent taxonomic revisions, species descriptions or putatively invalid species (Supporting Methods). Such uncertainty regarding species diversity can bias biogeographic analyses, particularly if there are major geographic biases in undescribed species diversity or taxonomic practices (Freeman & Pennell, 2021). To account for this uncertainty in clupeiform species diversity, we compiled two species lists by carefully considering recent research: a low estimate of 393 total clupeiform species and a high estimate of 402 clupeiform species (Table S2). Sampling fractions and diversification rates were calculated for both 393 and 402 species diversity estimates. BAMM produced net diversification rate estimates that were very similar for 393 and 402 species datasets. Therefore, we used output from the 402 species BAMM analysis for *BiSSE/HiSSE* analyses. See Supporting Methods for further description of diversification rate estimation methods.

2.5.2 | Visualizing the distributions of diversification rates and character states

BiSSE/HiSSE have high statistical power, but also high type I error rates, while *ES-sim* has low type I error rates, but less statistical power than *BiSSE/HiSSE* (Davis et al., 2013; Harvey & Rabosky, 2018; Maddison & FitzJohn, 2014; Rabosky & Goldberg, 2015; Rabosky & Goldberg, 2017; Rabosky & Huang, 2016). Due to this trade-off between statistical power and type I error, we qualitatively inspected the distributions of underlying trait and diversification rate data (net diversification rate estimates for both 393 and 402 species datasets) for evidence of associations between character states and diversification rates. This allowed us to determine whether the results of *BiSSE*, *HiSSE* and *ES-sim* were potentially type I or type II errors (i.e. did we obtain a significant result, but the diversification rate and character state distributions did not suggest an association between character states and diversification rates, or did we obtain a non-significant result, but the diversification rate and character state distributions did suggest an association between character states and diversification rates). We accomplished this by visualizing the distribution of *BAMM*-estimated diversification rates and character states using phylorate (diversification rates mapped onto branches of phylogeny; Rabosky, 2014), scatter and violin plots.

2.5.3 | BiSSE/HiSSE

We used the *BiSSE/HiSSE* family of analyses, 205 tip MCC tree and the binary version of the climate zone character to test for differences in diversification rates between tropical and extratropical clupeiforms. *BiSSE* is a parametric method for binary characters that formally models diversification rate parameters (Maddison et al., 2007). *HiSSE* is an extension of *BiSSE* that models the presence of unmeasured 'hidden states' associated with traits of interest that might impact diversification rates (Beaulieu & O'Meara, 2016). *BiSSE* and *HiSSE* have sufficient statistical power to detect differences in diversification rates associated with character states using phylogenies of the size used in this study (Davis et al., 2013; Rabosky & Goldberg, 2017). *BiSSE/HiSSE* use sampling fractions to account for missing sampling by character state. We used the *hisse* function in the *hisse* R package and the 402 species estimate of clupeiform diversity to fit a set of four models with varying complexity, along with two null models (Beaulieu & O'Meara, 2016): (1) a *BiSSE* model in which diversification rates differ between states, (2) a null *BiSSE* model in which diversification rates are equal among states, (3) a *HiSSE* model with two hidden states in which diversification rates vary with traits, (4) a *HiSSE* model with a single hidden state associated with temperate climates in which diversification rates vary with character states, (5) a *HiSSE* model with a single hidden state associated with tropical/subtropical climates in which diversification rates vary with character states and (6) a null *HiSSE* model, sometimes referred to as the CID-2 model, with two hidden states in which diversification rates are independent of character states. We used Akaike information criterion (AIC) to identify the best-fitting *BiSSE* or *HiSSE* model, and considered models to be better than others when AIC scores were at least two units lower, following Burnham and Anderson (2002).

2.5.4 | ES-Sim

We used *ES-sim*, the 205 tip MCC tree and climate zone and tropicality index climate niche characters to test for latitudinal differences in diversification rates. *ES-sim* is a semiparametric tip-rate correlation method that tests for correlations between continuous trait values at the tips of phylogenetic trees and a tip-specific diversification rate statistic (Harvey & Rabosky, 2018). *ES-sim* estimates tip diversification rates as the inverse of the equal splits (*ES*) measure, which most closely approximates speciation rates (Belmaker & Jetz, 2015; Harvey & Rabosky, 2018). The statistical significance of trait–speciation rate associations identified by *ES-sim* is assessed using a null distribution of associations generated by simulating Brownian trait evolution across the empirical tree. The *ES-sim* method has sufficient power to detect correlations between continuous traits and speciation rates in phylogenies of the size used in this study, is robust to incomplete taxon sampling as long as lineages and traits are representatively sampled, as was the case with our dataset, and has a low type I error rate (Harvey & Rabosky, 2018). *ES-sim* does not directly account for incomplete taxon sampling in analyses or accommodate discrete trait data (Harvey & Rabosky, 2018; Rabosky & Huang, 2016). We implemented *ES-sim* in program R and included 1000 bootstrap replicates in each analysis.

3 | RESULTS

3.1 | Clupeiform climate niche evolution

Assembling range data for clupeiforms confirmed the previously reported clupeiform latitudinal diversity gradient (Lavoué et al., 2013), with 30, 61 and 311 temperate, subtropical and tropical species, respectively (based on the 402 species dataset). The 183 species phylogeny contained representative sampling from latitudes and major biogeographic regions: 15, 39 and 129 temperate, subtropical and tropical species, respectively (Figure S1). All three climate niche characters exhibited strong phylogenetic signal: maximum latitude $\lambda = 0.87$ and $K = 0.13$, climate zone $\lambda = 0.\ 0.87$ and $K = 0.15$ and tropicality index $\lambda = 0.82$ and $K = 0.15$.

Stochastic character mapping identified an average of 33 transitions between climate zones (transition frequencies rounded to nearest whole number), including five transitions to temperate climates and six transitions out of temperate climates (Figure 1a; Figure S2). Stochastic character mapping of the binary climate zone character estimated an average of seven transitions between climate zones, including four transitions to temperate climates and three transitions out of temperate climates. When using the alternative position of *Clupeonella*, stochastic character mapping of the binary climate zone character identified an additional transition to temperate climates. However, visualization of stochastic character mapping results suggested three transitions to temperate climates and two transitions out of temperate climates using the unmodified Egan, Bloom, et al. (2018a) phylogeny, and four transitions to temperate climates using the alternative position of *Clupeonella*. Continuous character mapping of maximum latitude and tropicality index characters recovered patterns of climate niche evolution similar to stochastic character mapping (Figure 1b). BAMM inferred a continuously increasing rate (ß) of climate niche evolution (maximum latitude character) throughout the history of Clupeiformes with values of ß ranging from approximately 3–6 (Figure S3).

We report transition times to temperate climates as the mean transition timing estimate from the posterior density of stochastically mapped character histories. Transitions to temperate climates occurred in the most recent common ancestor (MRCA) of *Alosa* spp. (~8 Ma); the MRCA of a clade containing *Clupea* spp. + *Sprattus sprattus* (~18 Ma); and the MRCA of a clade containing *Clupeonella* spp., *Hyperlophus* spp. and *Potamalosa richmondia* (~46 Ma). Analyses using the modified phylogeny identified an additional transition to temperate environments in the MRCA of *Clupeonella* (~26 Ma; Figure 2a). Both transitions from temperate to tropical/subtropical climates occurred within *Alosa*. All transitions to temperate climates histories were inferred to have occurred within the past 50 Ma, regardless of the position of *Clupeonella*. However, the phylogeny with the more likely position of *Clupeonella* within Ehiravinae inferred more recent transitions to temperate environments in the MRCA of *Clupeonella* (~26 Ma) and *Hyperlophus* + *Potamalosa* (~36 Ma; Figure 2). All transitions from temperate to subtropical/tropical climates were estimated to have occurred within the past 5 Ma.

3.2 | Mean root distance of temperate versus tropical lineages

We found that low diversity temperate sets of clupeiform species were more recently derived than high diversity tropical sets. MRD was negatively correlated with latitude ($R^2 = 0.89$, $F_{1,15} = 123$, $p < 0.001$) and positively correlated with species richness ($R^2 = 0.97$, $F_{1,15} = 1059$, $p < 0.001$; Figure S4).

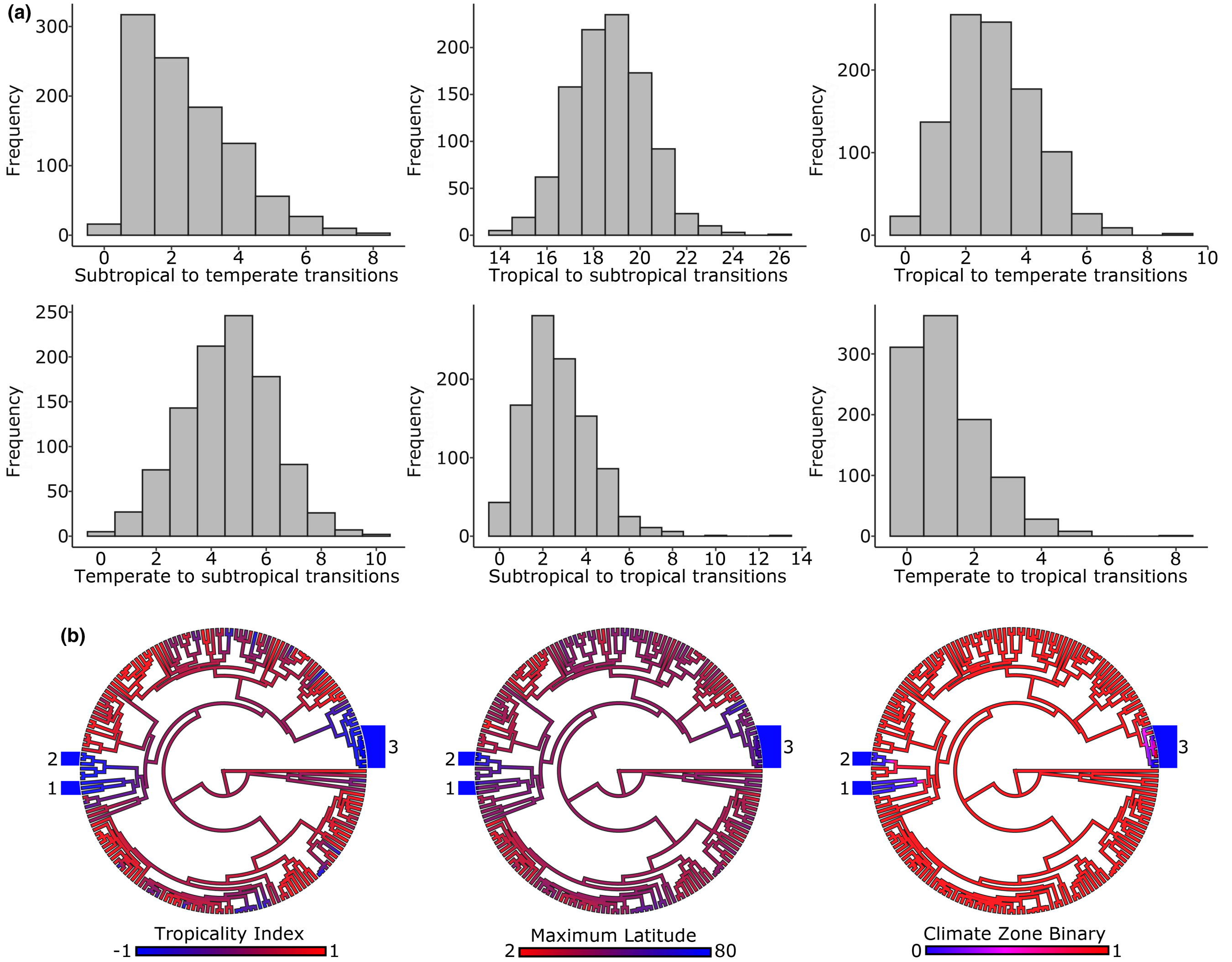

FIGURE 1 (a) Summary of character state transitions in the posterior set of stochastically mapped climate zone character histories generated using 100 trees sampled from the Bayesian posterior of the Egan, Bloom, et al. (2018a) clupeiform phylogeny. Each tree was used in 10 iterations of stochastic character mapping, yielding a total of 1000 mapped character histories. (b) Evolution of tropicality index, maximum latitude and climate zone (binary coding) climate niche characters was inferred using the Egan, Bloom, et al. (2018a) maximum clade credibility tree. Visualizations of continuous characters and the binary character were generated via continuous character mapping and density mapping respectively. Blue rectangles demarcate temperate clades: (1) *Clupeonella cultriventris* + *Hyperlophus vittatus* + *Potamalosa richmondia*, (2) *Clupea* spp. + *Sprattus sprattus* and (3) *Alosa* spp.

3.3 | Testing for correlations between climate niche and lineage diversification rates

BAMM produced net diversification rate estimates that were very similar for 393 and 402 species datasets (Figure 3; Table S3; Figure S5). Bayes factors supported lineage diversification rate models with four rate shifts for both the 393 and 402 species datasets (Bayes factors of 2.90 and 4.96, respectively; Table S3). However, support for the four-rate models relative to the null model was weak, because Bayes factors greater than 20 are typically considered to provide strong evidence that one diversification rate model is better than another (Rabosky, 2014; Rabosky et al., 2017). Bayes factors were calculated

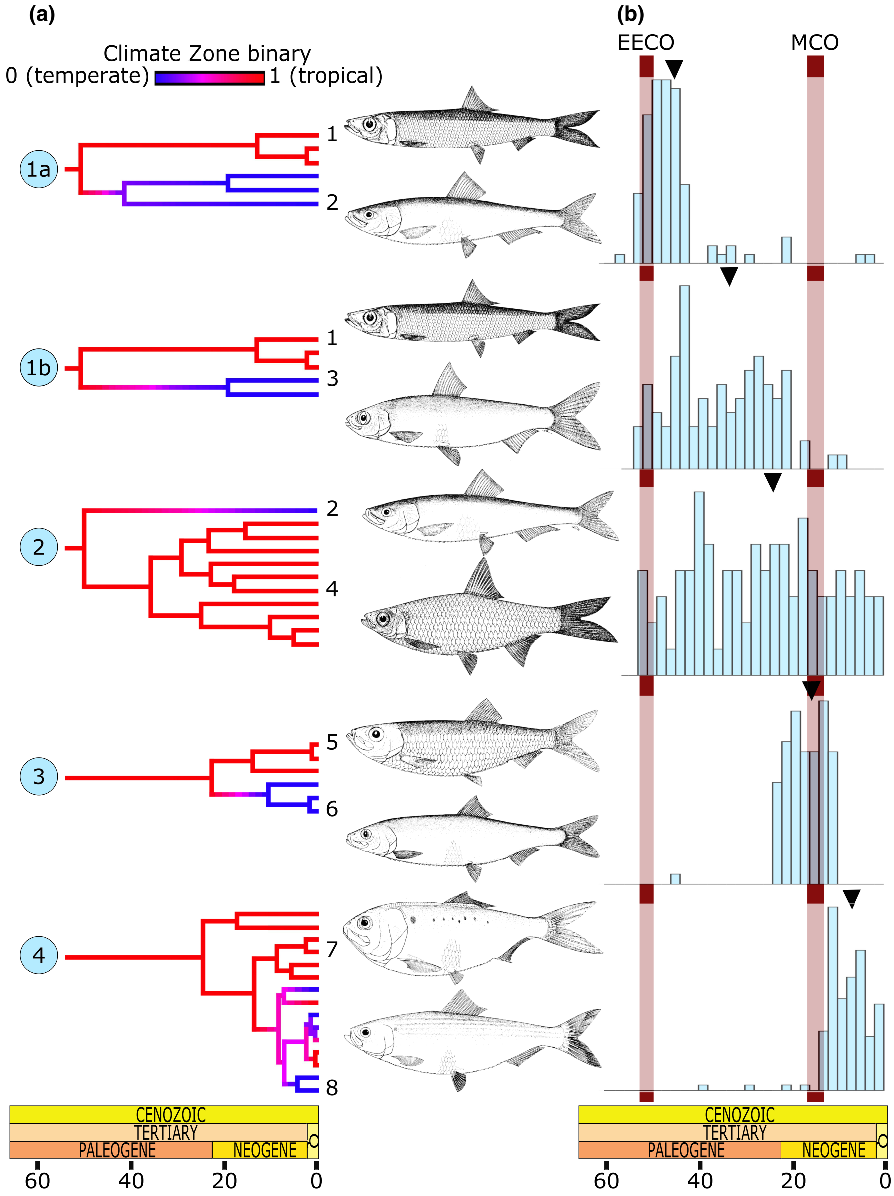

FIGURE 2 (a) Four transitions from tropical to temperate zones based on stochastic character mapping of the binary climate zone character on 100 trees from the posterior distribution of the Egan, Bloom, et al. (2018a) clupeiform phylogeny. Results from stochastic character mapping of the binary climate zone character are presented as continuous density maps. Transition 1a is the first transition when using the unmodified phylogeny (*Clupeonella cultriventris* sister to *Hyperlophus vittatus* + *Potamalosa richmondia*. Transition 1b is the first transition when using the modified phylogeny (*Clupeonella* in Ehiravinae)). Transition 2 is the additional transition to temperate environments in *Clupeonella* that is inferred when using the modified phylogeny (see methods section 2.3). Line drawings along the tips of density maps depict representative temperate clupeiforms and tropical relatives and numbers along tips show the positions of illustrated species: (1) *Dussumieria elopsoides*, (2) *Clupeonella cultriventris*, (3) *Potamalosa richmondia*, (4) *Clupeoides borneensis*, (5) *Sprattus muelleri*, (6) *Clupea pallasii*, (7) *Brevoortia patronus* and (8) *Alosa aestivalis*. (b) Histograms summarizing timing of transitions to temperate environments from the posterior set of 1000 stochastically mapped climate zone character histories using the MCC tree from Egan, Bloom, et al. (2018a). Black arrows show the mean timing of each transition. Maroon shading shows the timing of the early Eocene climatic optimum (EECO) and the Miocene climatic optimum (MCO). Clupeiform line drawings reproduced with permission from Whitehead et al. (1988).

by comparing models with >1 shift to the 1-shift model. This is because the posterior probability of the null, 0-shift model was low, and thus was sampled infrequently in the Bayesian posterior and BAMM was unable to accurately compute a prior or posterior probability for this model (Rabosky, 2014). We found that clupeiform lineage diversification rates remained positive over time, including in major clupeiform lineages and in temperate and tropical clupeiform clades when examined individually (Figure 3; Figures S6 and S7). Qualitative observations of net diversification rates and climate niche evolution were not suggestive of any associations between climate niches and diversification rates (Figure 3; Figures S5 and S8). Statistical analyses found no evidence for associations between diversification rates and climate niches. *ES-sim* did not find any statistically significant correlations between the continuous climate niche characters and diversification rates (maximum latitude character $p = 0.687$ and tropicality index character $p = 0.401$). The most strongly supported models in the *BiSSE*/*HiSSE* suite of analyses were *HiSSE* models, but the AIC values for the full *HiSSE* model and the null climate niche-independent diversification rates model were very similar and less than the two AIC unit threshold indicating stronger support for one model over another (AIC of 1686.1 for the full *HiSSE* model vs. an AIC of 1686.2 for the null *HiSSE* model; Table 2).

4 | DISCUSSION

Our analysis of Clupeiformes, an ecologically diverse, trans-marine/freshwater clade of fishes, provides a detailed exploration of the processes that gave rise to higher species richness in tropical climates than temperate climates. Our results support the time for speciation hypothesis, suggesting that climate niche conservatism and limited time for speciation in temperate environments played central roles in forming the latitudinal diversity gradient.

4.1 | Time for speciation explains the clupeiform latitudinal diversity gradient

Our results are consistent with the major predictions of the time for speciation hypothesis (Table 1). All clupeiform climate niche

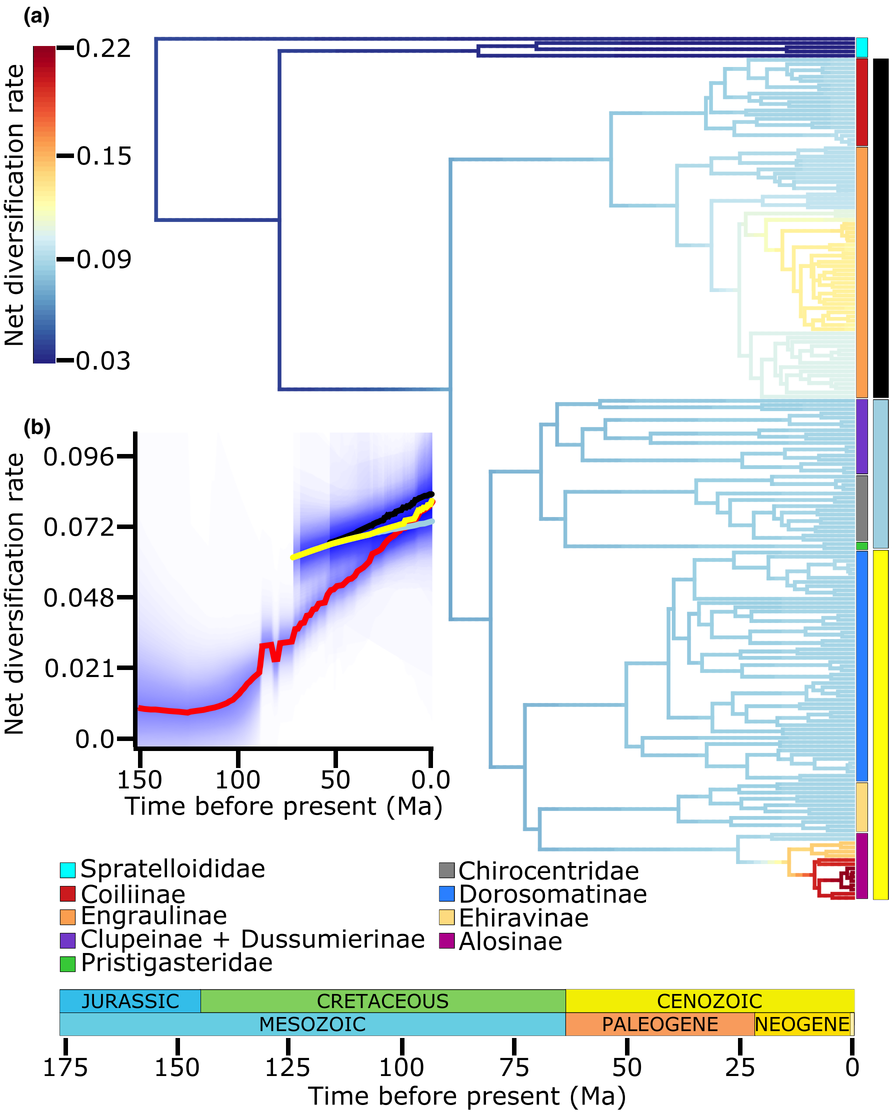

FIGURE 3 Summary of clupeiform net diversification rates estimated using BAMM, the Egan, Bloom, et al. (2018a) MCC phylogeny with additional species added (205 species total) and the 402 species estimate of clupeiform diversity. (a) Maximum clade credibility tree showing mean net diversification rates in clupeiforms. The leftmost (most proximal) set of bars along the phylogeny tips demarcate major clupeiform clades described in the figure legend and the rightmost (most distal) set of bars along the phylogeny tips (yellow, cyan and black) show the clades referenced in Figure 3b. Yellow and cyan clades contain temperate species and all three clades contain tropical and subtropical species. (b) Mean net diversification rates through time estimated in all clupeiforms (red) and three early-diverging clupeiform lineages containing the bulk of clupeiform species diversity (yellow, cyan and black; corresponding to the rightmost bars along the tips of the phylogeny). Figures S6 and S7 show net diversification rates through time plots for additional clupeiform clades.

TABLE 2 Summary of the state-dependent BiSSE/HiSSE analyses used to test for correlations between diversification rates and climate niche characters

	Parameters				Results		
Model	States	Hidden states	Free parameters associated with (τ)	Free parameters associated with (ε)	lnLik	AIC	Delta AIC
BiSSE null	0A, 1A	NA	1,1,0,0	1,1,0,0	−848.3	1704.7	18.6
BiSSE	0A, 1A	NA	1,2,0,0	1,2,0,0	−847.9	1707.9	21.8
HiSSE null (CID-2)	0A, 1A	0B, 1B	1,1,2,2	1,1,2,2	−836.1	1686.2	0.1
HiSSE full	**0A, 1A**	**0B, 1B**	**1,2,3,4**	**1,2,3,4**	**−830.1**	**1686.1**	**0.0**
HiSSe tropical	0A, 1A	0B	1,2,3,0	1,2,3,0	−834.9	1691.8	5.7
HiSSE temperate	0A, 1A	1B	1,2,0,3	1,2,0,3	−832.1	1686.2	0.1

Note: Analyses used the 205 tip MCC tree. Model = state-dependent model used to test for differences in diversification rates and the binary version of the climate zone character. States = character states used in analyses, hidden states = hidden states associated with observed traits in analyses. Free parameters associated with τ = free model parameters associated with net turnover (τ). Free parameters associated with (ε) = free model parameters associated with extinction fraction (ε). LnLik, log likelihood of models. AIC, Akaike information criterion estimates for models. The best supported model is shown in bold text.

characters exhibited strong phylogenetic signal. Transitions between temperate and subtropical/tropical environments were uncommon. All temperate clupeiform lineages were inferred to have originated within the past 50 Ma and, on average, temperate clupeiforms are more recently derived (i.e. sets of clupeiforms from temperate latitudes have higher MRDs) than tropical clupeiforms. Coupled with the lack of evidence we found for the carrying capacity and diversification rate hypotheses and our age estimates for temperate clupeiform lineages, these results suggest that limited time for speciation in temperate environments and niche conservatism were the primary drivers of the clupeiform latitudinal diversity gradient (Wiens & Donoghue, 2004).

Our study contributes to a multidisciplinary body of evidence from a range of taxa, including ray-finned fishes, supporting the time for speciation hypothesis and highlights the key role of large-scale climate events in shaping global species richness patterns (Belmaker & Jetz, 2015; Economo et al., 2018, 2019; García-Andrade et al., 2021; Jablonski et al., 2013; Marin et al., 2018; Miller et al., 2018; Miller & Román-Palacios, 2021; Rabosky et al., 2018; Shiono et al., 2018). Our study is the first to find support for the time for speciation hypothesis in a trans-marine/freshwater clade of fishes, indicating that although clades containing biome transitions may exhibit distinct regional diversification patterns (Betancur-R et al., 2012; Bloom & Egan, 2018; Coelho et al., 2019), shared forces may govern the distribution of species richness at larger spatial scales, both in clades that exhibit biome conservatism and clades that exhibit biome lability (Hillebrand, 2004a). Not all studies involving ray-finned fishes supported the time for speciation hypothesis, indicating that processes that contributed to the latitudinal diversity gradient may vary among clades, particularly among younger clades (Mittelbach et al., 2007). For example, Siqueira et al. (2016) found that the diversification rate hypothesis best explained the latitudinal diversity gradient in some families of marine, reef-associated fishes (Chaetodontidae, Labridae, Pomacentridae and Sparidae). The age of these clades is one potential explanation for these contrasting results. Most of the diversification within these clades occurred during the past 50 Ma (Hughes et al., 2018; Siqueira et al., 2016), and thus were not subjected to some of the major climate events (e.g. the Early Eocene Climatic Optimum) that appear to have shaped the distribution of species richness in Clupeiformes and other older fish lineages (García-Andrade et al., 2021; Miller et al., 2018; Miller & Román-Palacios, 2021; Rabosky et al., 2018).

The origins of temperate clupeiform lineages correspond to cool global temperatures during the late Eocene and Oligocene (~36–26 Ma) and following the Miocene Climatic Optimum (<14.5 Ma), suggesting that these two cool climate periods during Earth's history promoted the diversification of extant temperate clupeiform lineages (O'Brien et al., 2020; Zachos et al., 2001). Furthermore, we inferred that the majority of in situ temperate diversification and all transitions from temperate to subtropical/tropical climates occurred after the Miocene Climatic Optimum. The onset of these cooling periods has been associated with mass extinctions at temperate latitudes, followed by colonization of temperate latitudes by novel lineages and in situ temperate diversification in a range of taxa, such as marine and freshwater ray-finned fishes, ants and woody plants (Buckley et al., 2010; Chen et al., 2013; Crame, 2018; Economo et al., 2018; Miller et al., 2018; Miller & Román-Palacios, 2021; Near et al., 2012; Shiono et al., 2018). Reduction in the strength of the latitudinal diversity gradient during warm periods of Earth's history, distributional shifts tracking climates in a range of taxa and a pervasive pattern of climate niche conservatism also point to the importance of climate as a regulator of global diversity patterns (Crame, 2001; Leighton, 2005; Weins & Graham, 2005; Powell et al., 2012; Jablonski et al., 2013; Brown, 2014; Mannion et al., 2014; Marcot et al., 2016; Shiono et al., 2018).

4.2 | No support for alternative latitudinal diversity gradient models

The diversification rate hypothesis predicts a negative correlation between net diversification rates and latitude. We identified variability in speciation and net diversification rates in Clupeiformes, but found no associations between latitude (i.e. climate niche) and lineage diversification rates. These findings concur with several recent studies on a variety of taxa concluding that geographical variation in diversification rates was not the primary cause of the latitudinal diversity gradient (Economo et al., 2018, 2019; García-Andrade et al., 2021; Harvey et al., 2020; Marin et al., 2018; Miller et al., 2018; Miller & Román-Palacios, 2021; Rabosky et al., 2015; Rabosky et al., 2018; Schluter & Pennell, 2017; Tedesco et al., 2017). Reports of clades with higher diversification rates in tropical relative to temperate areas are not uncommon, but these clades are generally nested within larger clades that do not appear to exhibit the same pattern of elevated tropical diversification rates (Pyron, 2014; Pyron & Wiens, 2013; Siqueira et al., 2016). For example, Pyron and Wiens (2013) and Pyron (2014) report negative correlations between net diversification rate and latitude in the tetrapod clades Amphibia and Squamata. However, Marin et al. (2018) found evidence for only a slightly negative correlation between net diversification rates and latitude when the entire tetrapod lineage was examined and concluded that latitudinal variation in diversification rates was not the primary driver of the squamate latitudinal diversity gradient. Additionally, multiple clades exhibit higher diversification rates in temperate regions than in tropical regions or geographic variation in diversification rates unassociated with latitude (Belmaker & Jetz, 2015; García-Andrade et al., 2021; Harvey et al., 2020; Miller et al., 2018; Rabosky et al., 2018; Schluter & Pennell, 2017). This suggests that diversification rates may play a secondary role in modulating spatial patterns of species richness in some clades, strengthening the latitudinal diversity gradient in some cases and weakening it in others (Pyron, 2014; Schluter & Pennell, 2017).

The carrying capacity hypothesis predicts that over evolutionary time-scales net diversification rates remain approximately zero (Hurlbert & Stegen, 2014a; Mittelbach et al., 2007). However, we found that diversification rates remained positive since the origin of crown clupeiforms approximately 150 Ma and may have even increased slightly during the past ~75 million years. We also found that net diversification rates within major tropical clupeiform lineages and all four temperate lineages remained positive throughout their history. Although we found no support for the carrying capacity hypothesis, it is important to consider that studies using datasets comprised entirely of extant species, such as ours, are relatively weak tests of this hypothesis (Harmon & Harrison, 2015; Hurlbert & Stegen, 2014a; Rabosky & Hurlbert, 2015). Therefore, our study should be complemented with additional tests of the carrying capacity hypothesis, including those that use fossil data. We did not examine diversification dynamics within smaller clades at regional scales, but there is evidence that ecological limits have slowed regional net diversification rates in some lineages, including within clupeiforms (Betancur-R et al., 2012; Bloom & Egan, 2018; Coelho et al., 2019). For example, Bloom and Egan (2018) identified Neotropical clupeiform lineages exhibiting slowdowns in net diversification rates, possibly resulting from interspecific competition. Our study concurs with several recent studies also identifying positive net diversification rates over evolutionary time-scales in large clades of organisms and across latitudes using both extant species and fossil datasets (Belmaker & Jetz, 2015; Diaz et al., 2019; Economo et al., 2019; Pyron, 2014). However, there is still no consensus regarding the role of carrying capacities in the formation of the latitudinal diversity gradient and the range of temporal and spatial scales at which carrying capacities can regulate species richness (Diaz et al., 2019; Rabosky & Hurlbert, 2015).

4.3 | Diversification rate heterogeneity in Clupeiformes

Unlike several recent studies, we did not identify a positive correlation between latitude and diversification rates (Harvey et al., 2020; Rabosky et al., 2018; Schluter & Pennell, 2017). There are likely undescribed clupeiform species, but cryptic clupeiform diversity appears to primarily be restricted to in the tropics (Whitehead, 1985; Whitehead et al., 1988; Lavoué et al., 2008; Bloom & Lovejoy, 2012; Egan, Simons, & Bloom unpublished data). Therefore, it is unlikely that we failed to identify a positive correlation between latitude and diversification rates because we underestimated temperate species richness. We documented a modest amount of variation in clupeiform net diversification rates, which may have contributed to regional-scale heterogeneity in species richness. The fastest diversification rates in clupeiforms occurred in the temperate and subtropical Alosinae (shads and menhadens), which occur along coasts and in drainages of the Atlantic Ocean in the northern hemisphere. Alosinae also exhibits high rates of ecological niche and life-history evolution, including evolutionary transitions between freshwater and marine habitats and origins of migratory behaviour (Bloom & Egan, 2018; Bloom & Lovejoy, 2014; Egan, Bloom, et al., 2018a). These preliminary, qualitative observations suggest that repeated evolutionary habitat transitions, migratory behaviour or a combination of these factors may have promoted speciation in this clade. Additionally, we found that a lineage of largely tropical, marine anchovies primarily distributed along the northern Atlantic coasts of South America and in the Gulf of Mexico and Caribbean Sea also exhibited fast diversification rates. In contrast to Alosinae, this group did not appear to exhibit rapid rates of ecological niche and life-history evolution, and thus, different mechanisms may have been responsible for accelerated net diversification rates in this clade (Bloom & Egan, 2018; Bloom & Lovejoy, 2012; Whitehead et al., 1988). Freshwater habitat use has been positively correlated with speciation rates in fishes, possibly a result of an increased likelihood of provincialism and isolation in freshwater, relative to marine environments (Bloom et al., 2013; Tedesco et al., 2017). Testing for correlations between diversification rates and marine versus freshwater habitat occupancy was outside the scope of this study. However, the numbers of marine and freshwater clupeiform species (~67%, 26% and 7% of clupeiform species are marine, freshwater and diadromous, respectively; Whitehead, 1985; Whitehead et al., 1988; Egan et al., unpublished data) and our finding that diversification rates vary little within Clupeiformes, apart from the two accelerations discussed above, did not suggest that colonization of freshwater habitats led to faster diversification rates in clupeiforms.

5 | CONCLUSIONS

Using Clupeiformes, a trans-marine/freshwater clade of fishes, and phylogenetic comparative approaches, we found support for the time for speciation hypothesis. This hypothesis proposes that climate niche conservatism and fluctuations in the extent of temperate climates limited the time for species to accumulate in temperate climates, resulting in the latitudinal diversity gradient. We found no support for the carrying capacity or diversification rate latitudinal diversity gradient hypotheses. This study is one of only a few to explore the causes of the latitudinal diversity gradient in ray-finned fishes and the only study focused on a trans-marine/freshwater clade (García-Andrade et al., 2021; Miller et al., 2018; Miller & Román-Palacios, 2021; Rabosky et al., 2018; Siqueira et al., 2016). Most, but not all studies involving fishes have found support for the time for speciation hypothesis (Siqueira et al., 2016). Additional research on other clades of trans-marine/freshwater fishes and lineages with different ecological niches, followed by meta-analyses, is needed to further characterize inter-clade variation in the strength of the latitudinal diversity gradient and relative importance of different processes in its formation.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available in the supporting materials.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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