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Ecological constraints coupled with deep-time habitat dynamics predict the latitudinal diversity gradient in reef fishes

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We develop a spatially explicit model of diversification based on palaeohabitat to explore the predictions of four major hypotheses potentially explaining the latitudinal diversity gradient (LDG), namely, the 'time-area', 'tropical niche conservatism', 'ecological limits' and 'evolutionary speed' hypotheses. We compare simulation outputs to observed diversity gradients in the global reef fish fauna. Our simulations show that these hypotheses are non-mutually exclusive and that their relative influence depends on the time scale considered. Simulations suggest that reef habitat dynamics produced the LDG during deep geological time, while ecological constraints shaped the modern LDG, with a strong influence of the reduction in the latitudinal extent of tropical reefs during the Neogene. Overall, this study illustrates how mechanistic models in ecology and evolution can provide a temporal and spatial understanding of the role of speciation, extinction and dispersal in generating biodiversity patterns.

1. Introduction

The global increase in species diversity towards the equator, referred to as the latitudinal diversity gradient (LDG), is one of the most striking biodiversity patterns on Earth. The LDG has been described for most taxonomic groups at different spatial scales and for different periods of time [1,2]. A myriad of ecological and historical hypotheses have been proposed to explain why species diversity is higher in the tropics [3–5]. Among the main hypotheses, the 'time-area' (TA), the 'tropical niche conservatism' (TNC), the 'ecological limits' (EL) and the 'evolutionary speed' (ES) hypotheses are still under scrutiny (box 1). Although these four hypotheses are widely accepted and non-mutually exclusive [16], there is still no consensus about the macroevolutionary processes underlying the LDG, and a lack of mechanistic understanding remains.

At the macroevolutionary scale, processes that drive regional species diversity (i.e. speciation, extinction and dispersal) are difficult to parse with current methods. Recent empirical studies employed correlative approaches based on curve-fitting methods, providing information about the factors potentially explaining the global spatial variation in species richness [17,18]. However, these studies failed to provide a mechanistic understanding of the roles of speciation, extinction and dispersal in shaping large-scale patterns of species diversity [19]. In parallel, macro-evolutionary models based on dated phylogenies or fossils have been used to compare speciation, extinction and dispersal rates between tropical and temperate

Box 1. Major macroevolutionary hypotheses and associated mechanisms.

Time-area hypothesis

The TA hypothesis posits that the LDG is primarily driven by habitat dynamics [6]: tropical regions that covered larger areas over geological periods should support larger populations on average [7] than temperate regions. The maintenance of large populations over time should in turn increase the chances of speciation and decrease the chances of extinction [6,7].

To evaluate the predictions of the TA hypothesis, we used a habitat-driven spatial model of diversification that simulates the evolution of species ranges in a gridded, changing landscape (SPLIT model, [8,9]). The distance over which species can disperse in the changing landscape is controlled by a dispersal parameter (d). New species arise in individual cells of a species' range with a given probability (probability of speciation, p_s). Finally, if a species is not able to colonize any habitat cell, then it will be considered extinct. The model is thus able to simulate the effect of habitat changes on species diversity and diversification without explicitly considering the effect of area, which is an outcome of the simulated mechanism.

In this study, we seek to evaluate the influence of alternative macroevolutionary hypotheses that also depends on habitat changes over time. Consequently, the influence of habitat dynamics on reef fish diversity must be considered for the evaluation of these hypotheses. We opted for a nested design where each hypothesis was evaluated in conjunction with the effect of habitat changes over time, as postulated by the TA hypothesis (see below).
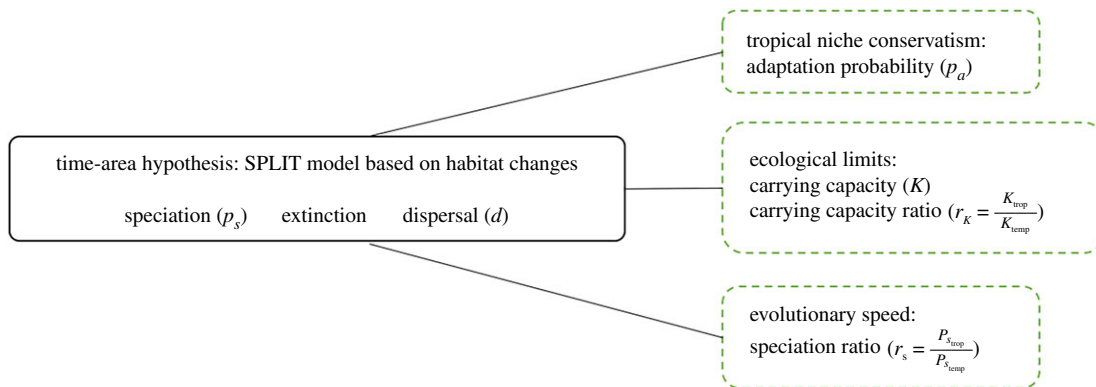

Tropical niche conservatism

The TNC hypothesis posits that stable tropical climates promote specialization [10,11], which limits the dispersal of tropical species towards non-optimal temperate regions. We simulated the effect of TNC on the degree of specialization of tropical species by limiting their dispersal towards temperate cells (see below).
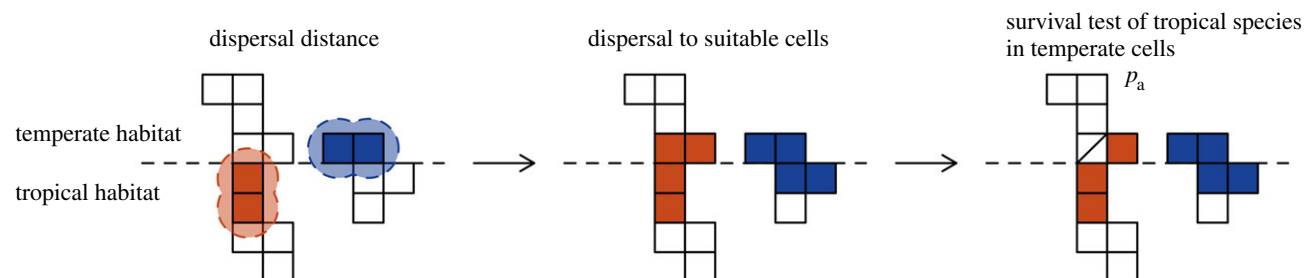
Whenever a species from a tropical habitat (orange species) colonizes a cell of temperate habitat, it survives with a probability p_a. A p_a of 0 means that species from a tropical habitat cannot colonize a temperate habitat (strict niche conservatism), while a p_a of 1 means that species from a tropical habitat colonize a temperate habitat without any constraints (niche volatility). Thus, this mechanism acts by only reducing the probability of directional dispersal out of the tropics. In the example above, the orange species survives in only one of the two cells colonized during the dispersal phase, while the blue species (from a temperate habitat) colonizes without constraints.

Ecological limits

The EL hypothesis posits that the amount of energy received by ecosystems limits the number of species that can co-occur in a region (carrying capacity, [11,12]). Thus, high latitudes should be able to sustain fewer species than low latitudes. We modulated the carrying capacity (K) of each cell of the grid depending on the latitude of the cell (see below).
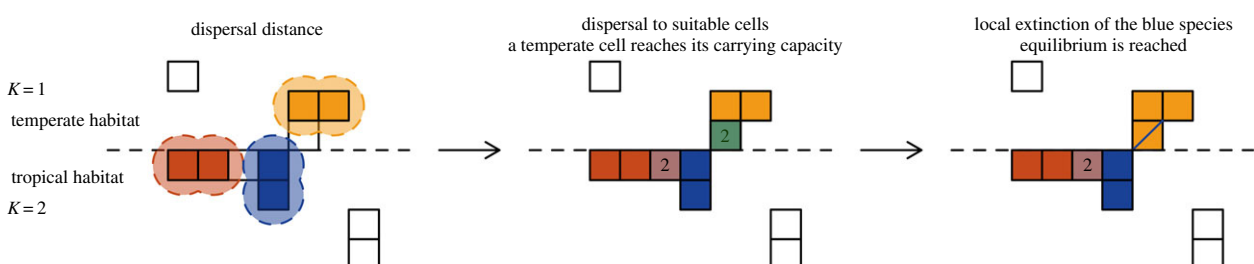
We introduced the carrying capacity ratio, r_K, which quantifies the difference in carrying capacity between tropical and temperate habitats. At each time step, the colonization of saturated cells (species richness $> K$) is balanced by local extinction. To select species that first go extinct locally, we consider a trade-off between dispersal and competition, and we hypothesize that species with the highest d are the best dispersers and the worst competitors. In the example above, one temperate cell is saturated, causing local extinction of the best disperser. This mechanism has no influence if cells' Ks are not reached and influences sympatric speciation, dispersal and extinction if cells' Ks are reached.

Evolutionary speed

The ES hypothesis posits that mutation and speciation rates depend on metabolic rates that are correlated with temperature [13,14]. Thus, speciation rates of tropical lineages should be higher than speciation rates of temperate lineages [15]. We introduced a difference in speciation rates between temperate and tropical regions (see below).
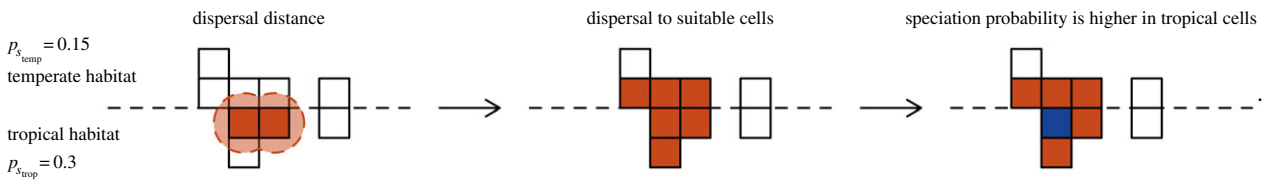
The speciation ratio r_s quantifies the difference in speciation probability between tropical habitat cells (high temperatures, $p_{s_{trop}} = p_s$) and temperate habitat cells (low temperatures, $p_{s_{temp}} = p_s r_s$). An r_s of 0 means that the speciation rate of temperate regions is null, and an r_s of 1 means that there are no differences in ES between temperate and tropical regions. In the illustration above, the speciation probability of the orange species is 0.15 in temperate cells and 0.3 in tropical cells.

regions [20,21]. For example, the Geographic State Speciation and Extinction model (GeoSSE, [22]) has been used to test for differences in speciation, extinction and dispersal rates between tropical and temperate lineages of many vertebrate groups [20,23]. However, such studies do not evaluate the link between observed differences in evolutionary rates and diversity patterns, nor do they allow for a mechanistic explanation of those differences (e.g. density dependence, metabolism and geography). To do so, we must better understand how biotic and abiotic factors together have influenced the formation and maintenance of biodiversity gradients [24,25].

Recently developed spatially explicit diversification models allow the consideration of macroevolutionary processes in explanations of biodiversity patterns [9,26]. These models have previously been used to (i) provide theoretical predictions about the effect of spatial processes [27], (ii) assess the influence of past environmental changes on biodiversity gradients [9,28,29], and (iii) test alternative macroevolutionary and ecological hypotheses [4,30]. The advantage of mechanistic models of diversification over correlative models (i.e. those looking for a link between an explanatory variable and a diversity pattern) is that multiple predictions of alternative hypotheses can be compared simultaneously to observed patterns of biodiversity [28]. In addition, mechanistic models allow one to assess the influence of a particular factor (e.g. climate) in isolation by controlling for other factors, which is particularly relevant when testing multiple hypotheses in ecology and biogeography.

Leprieur and co-workers [9] proposed a mechanistic model of diversification, namely, the spatial diversification of lineages through time (SPLIT) model, which consists of simulating the evolutionary dynamics of species ranges by linking speciation, extinction and dispersal processes to habitat changes caused by plate tectonics. Using this model, Leprieur and co-workers [9] showed that tropical reef habitat dynamics played a major role in shaping the longitudinal gradient of tropical reef fish diversity. In the context of the LDG, the original SPLIT model allows exploring the predictions of only the TA hypothesis, as this model does not consider mechanisms proposed by

the TNC, EL and ES hypotheses (box 1). In this study, we therefore propose a new formulation of the SPLIT model that allows comparing the predictions of the TA, TNC, EL and ES hypotheses (box 1) to latitudinal patterns of reef fish diversity, considering changes in both habitat configuration and climatic conditions through geological time. We focus on spiny-rayed fishes (i.e. Acanthomorpha), which are a dominant group of vertebrates with thousands of species found in shallow reefs worldwide. We based the simulations on the reconstruction of potential coastal habitat in temperate and tropical regions over the last 130 Myr.

2. Methods

(a) Spatial diversification model

Our study builds on the SPLIT model proposed by Leprieur and co-workers [9]. The SPLIT model is neutral in the sense that species are considered ecologically equivalent and not to interact with each other. This model provides simulated species ranges through time as well as phylogenetic trees from which one can estimate species diversity metrics (α and β) and evolutionary rates (speciation and extinction) (see the electronic supplementary material and [28] for full methodological details). It is therefore particularly adapted to evaluating the predictions of the TA hypothesis, which does not consider the influence of ecological constraints between temperate and tropical climates (box 1). To evaluate the predictions of the TNC, EL and ES hypotheses, we extended the SPLIT model to simulate mechanisms leading to differences in speciation and dispersal rates between tropical and temperate regions (box 1).

The diversification and biodiversity of reef fishes are closely linked to reef habitat [31,32]. Thus, we simulated the evolution of the distribution of reefs based on the reconstruction of potential reef habitat over geological time [9]. We employed an absolute plate motion model based on marine magnetic anomalies and fracture zone tracks in the crust of today's ocean basins [33]. We generated synthetic palaeobathymetry by combining oceanic palaeobathymetry grids derived from palaeo-oceanic crustal age grids with continental palaeogeographic data [9]. By combining
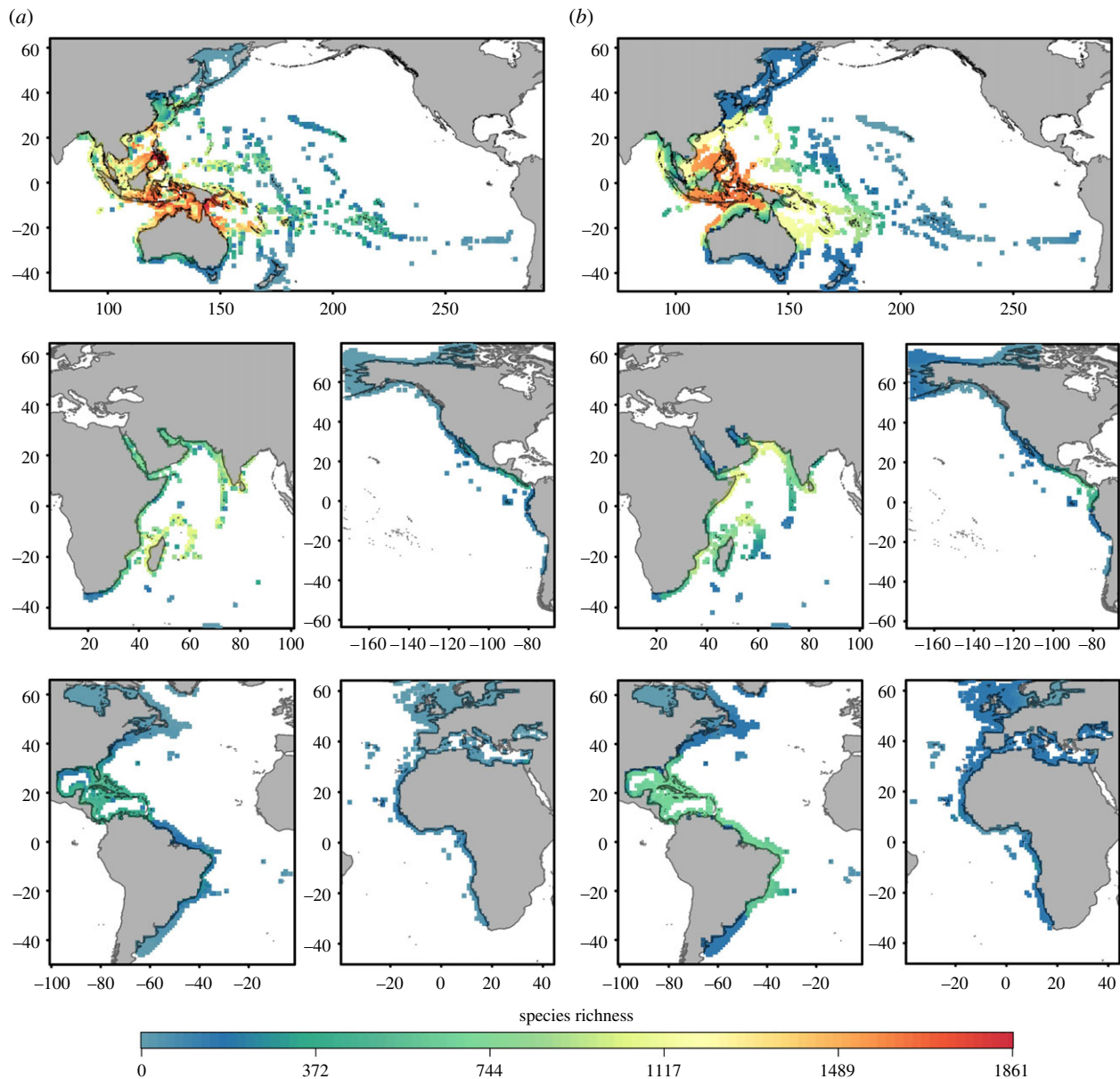
Figure 1. (a) Observed and (b) simulated patterns of reef fish species richness. The simulated species richness was predicted by the EL model with the following parameters: $d = 4$, $p_s = 5 \times 10^{-5}$; and $r_K = 0.1$. This simulation provided a good prediction of global species richness ($R^2 = 0.69$) and was the best simulation according to the Bayesian information criterion procedure. (Online version in colour.)

reconstructed shallow marine habitats with tropical limits obtained from the occurrences of tropical coral fossils, we generated one map per million years of tropical and temperate shallow marine habitats (1° resolution) favourable for reef fish colonization (electronic supplementary material and figure S1). To provide a realistic simulation of the evolution of spiny-rayed fish diversity over time, we started all the simulations at 130 Myr, between 10° N and 30° N and between −10° E and 10° E [34], which are roughly the estimated date and places of occurrence of the first known acanthomorph fossil (†*Rubiesichthys gregalis*), respectively.

Simulations were run under a sympatric speciation mode with fixed values of the dispersal ($d = 4$) and speciation ($p_s = 5 \times 10^{-5}$) parameters. These parameters were determined to provide realistic predictions of species richness and compositional variation (β-diversity) under the sole effect of habitat dynamics (electronic supplementary material). Based on this background set of parameters, we ran independent simulations with the addition of latitude-dependent mechanisms, as postulated by the TNC, EL and ES hypotheses, with parameter values (p_a, r_K, r_s which correspond to the adaptation probability, the carrying capacity and speciation, respectively) ranging from

0.01 to 0.99. Note that simulations run under the TA hypothesis displayed the following parameters: $p_a = 1$, $r_K = 1$ and $r_s = 1$. For each set of parameters, we ran 10 independent simulations. Although a combination of all the mechanisms into one model may provide a better fit between simulated and observed data, our goal was to evaluate the relative importance of each mechanism in shaping the LDG. We also evaluated the predictions of the TA, TNC, EL and ES hypotheses under the allopatric speciation mode (electronic supplementary material, Methods and Discussion).

(b) Diversity gradients

We gathered distribution data for 4670 spiny-rayed reef fish species from the Ocean Biogeographic Information System (OBIS, electronic supplementary material) to assess whether the TA, TNC, EL and ES models provided realistic predictions of species richness and compositional variation (β-diversity) due to species replacement (turnover, [35]). We mapped species richness using a 1°-resolution grid covering all continental shelves globally (figure 1; electronic supplementary material). For all pairwise grid cell combinations, we calculated the

Table 1. Model parameters of the best simulations run under the under the TA, EL, TNC and ES models. (For each best simulation, the goodness-of-fit measures (BIC and R^2) that were used to compare simulated and observed data for species richness and β-diversity caused by species turnover are also shown (see methods and the electronic supplementary material for more details).)

	TA	EL	TNC	ES
model parameters				
d	4	4	4	4
p_s	5×10^{-5}	5×10^{-5}	5×10^{-5}	5×10^{-5}
r_K	—	0.1	—	—
p_A	—	—	1×10^{-4}	—
r_S	—	—	—	0.7
species richness				
R^2	0.46	0.69	0.55	0.50
p-value	$<2 \times 10^{-16}$	$<2 \times 10^{-16}$	$<2 \times 10^{-16}$	$<2 \times 10^{-16}$
BIC	7.53×10^4	7.13×10^4	7.35×10^4	7.44×10^4
species turnover				
R^2	0.38	0.38	0.41	0.39
p-value	0.001	0.001	0.001	0.001
BIC	-1.16×10^7	-1.17×10^7	-1.15×10^7	-1.16×10^7

turnover component of the Jaccard dissimilarity index (β_{jtu}) using the R package *betapart* [36].

For each simulation run under the TA, TNC, EL and ES hypotheses, we compared observed and simulated patterns of species richness and β-diversity using the Bayesian information criterion (BIC). Specifically, we employed a hierarchical selection procedure based on the BIC to provide the set of simulations that best predict species richness and β-diversity simultaneously (electronic supplementary material). For each set of best simulations, we also calculated the coefficient of determination (R^2) from simple linear regression models to measure the fit between observed (response variable) and simulated (explanatory variable) species richness patterns [9,30]. Similarly, we compared simulated and observed matrices of β-diversity using multiple-regression models [37], with 1000 permutations of the observed matrices from which we extracted the R^2.

For each set of best simulations, we finally evaluated the influence of the simulated mechanisms on various metrics describing the evolution of the LDG. We calculated the latitudinal richness through time, which represents the total number of species found at the same latitude, at each time step of each simulation. We used the *segmented* R package [38], which fits segmented linear regressions and iteratively searches for breakpoints, to identify simulated and observed latitudinal richness breakpoints. As past climatic and tectonic changes are expected to have had a strong influence on compositional variation, we also identified latitudinal β-diversity breaks at each time step of each simulation. For each degree of longitude, we calculated the Jaccard dissimilarity index between each 1° cell and its adjacent cell to the north, and we extracted the turnover component, allowing us to identify latitudinal β-diversity breaks.

(c) Diversification through time

From our simulations, we calculated the speciation and extinction rates of tropical and temperate lineages as well as dispersal rates into and out of the tropics (OTT). To do so, we counted the number of speciation/extinction/dispersal events at each 5 Myr time step and divided it by the number of tropical or temperate lineages at that time and by the duration of the time step to render the speciation/extinction/dispersal rate per lineage per Myr.

All analyses have been performed in R [39]. The model presented in this paper is available at https://github.com/theogab/SPLIT.

3. Results

(a) Diversity gradients

(i) Global predictions

In addition to the well-described diversity difference between the Indo-Pacific and Atlantic regions (figure 1a), different southern latitudinal breaks in species richness were found between these two regions (Indo-Pacific: −18° N, 24° N and 43° N; Atlantic: 4° N, 24° N and 41° N; see the electronic supplementary material, table S1). Overall, each model provided simulations that closely matched the empirical data for global species richness (figure 1 and table 1; electronic supplementary material, figure S3) and, to a lesser extent, those for species turnover (table 1). However, the EL model best predicted the global distribution of species richness (figure 1 and table 1), followed by the TNC, ES and TA models (table 1 and figure 3; electronic supplementary material, figure S8). We observed that low values of r_K (EL) and p_a (TNC) greatly improved the predictions of species richness compared to simulations run under the TA model (electronic supplementary material, figures S4 and S6). Each model predicted higher speciation rates in the tropical lineages than in the temperate lineages (figure 2), with a marked decrease at the end of the Neogene. We also predicted a higher extinction rate of tropical lineages, with peaks at the end of the Cretaceous and the end of the Neogene (figure 2). We simulated a complex history of transition rates between tropical and temperate habitats with high poleward dispersal during the late Cretaceous and early Palaeogene and high dispersal towards the tropics during the early Cretaceous, late Palaeogene and Neogene. In the following sections, we describe the outputs of the best simulations under each model and, more specifically, the evolution of the LDG through geological time.
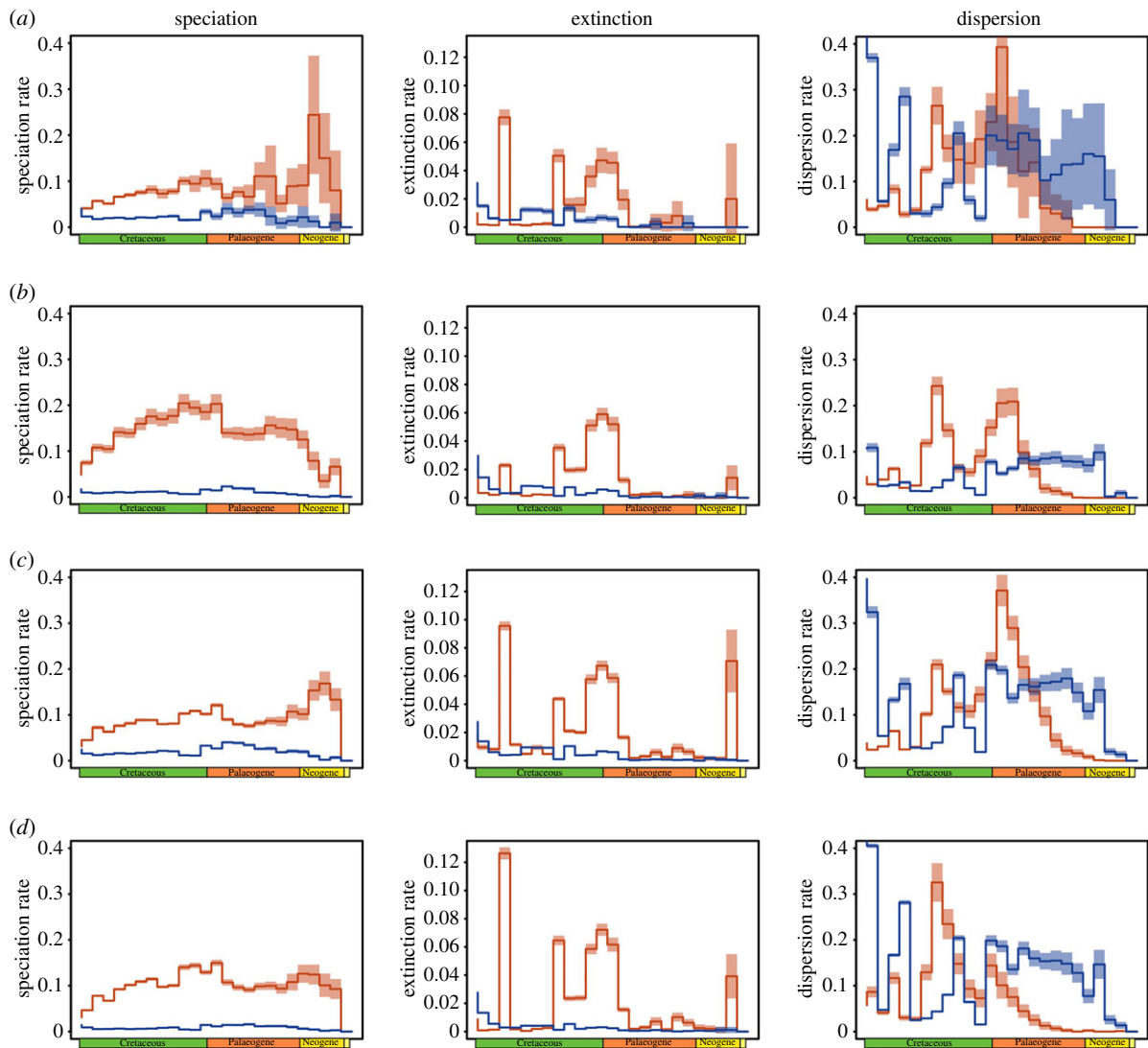
Figure 2. Diversification rates through time from each model under sympatric speciation. We calculated the speciation, extinction and dispersal rates of tropical and temperate lineages in each simulation for time periods of 5 Myr. The rates are calculated as the number of events (inside and outside the tropics) divided by the number of lineages (tropical and temperate lineages, respectively) divided by the length of the time period (here, 5 Myr). The rates are thus expressed as events per species per Myr. Note that widespread lineages are considered both tropical and temperate. For each mechanism, we calculated the rates for the 10 simulations run with the set of parameters that rendered the best simulations. (*a*) The TA model, (*b*) the TNC model, (*c*) the EL model and (*d*) the ES model. In the first two columns, orange represents the tropical lineages and blue the temperate lineages. In the third column, orange represents the dispersal towards the poles and blue the dispersal towards the tropics. (Online version in colour.)

(ii) Time-area

The TA model predicted the formation of the LDG during the middle Eocene (figure 3*a*; electronic supplementary material, figure S3a). Compared to the observed LDG, the TA model over-estimated species richness at subtropical and temperate latitudes (greater than 26° N), with latitudinal breaks in species richness for the Indo-Pacific region at −22° N and 46° N and for the Atlantic region at 18° N (figure 3*a*; electronic supplementary material, figure S3a and table S1). This model did not generate any latitudinal breaks in species turnover in the past (electronic supplementary material, figure S9a).

(iii) Tropical niche conservatism

The TNC model predicted a steeper and narrower modern LDG (figure 3*b*; electronic supplementary material, figure S3b) than the TA model, with breaks in species richness at −18° N and 23° N for the Indo-Pacific region and breaks at −2° N and 30° N for the Atlantic region (electronic

supplementary material, table S1). We also did not observe any latitudinal breaks in species turnover (electronic supplementary material, figure S9b). The TNC model predicted a steep decline in species richness towards the tropics beginning at the end of the Miocene owing to the contraction of the tropics (figure 3*b*; electronic supplementary material, figures S13 and S14). Notably, this model generated high poleward dispersal rates during the late Cretaceous and early Palaeogene, despite the strong dispersal constraint that we imposed.

(iv) Ecological limits

The EL model predicted a strong LDG with breaks in species richness at −19° N and 23° N and −21° N and 29° N for the Indo-Pacific and Atlantic regions, respectively (figure 3*c*; electronic supplementary material, figure S3c). Similar to the TNC model, the EL model revealed a steep decline in species richness towards the poles in relation to the contraction of the tropics during the Pliocene and Quaternary periods.
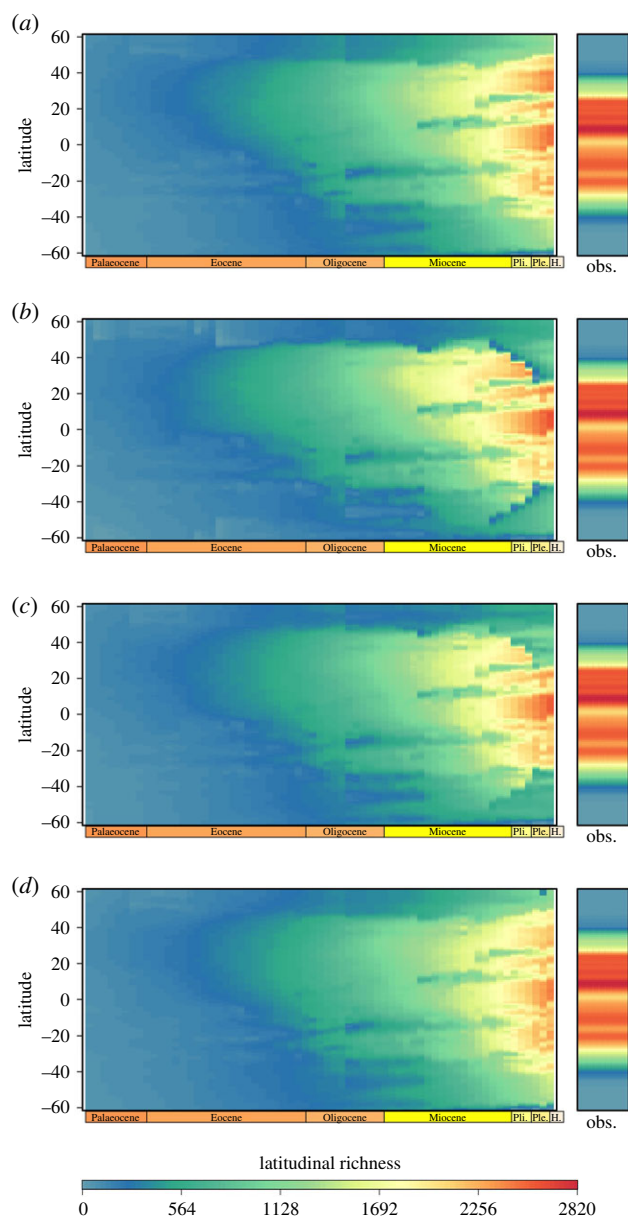
Figure 3. Evolution of the LDG in reef fishes according to simulations run under (*a*) the TA model, (*b*) the TNC model, (*c*) the EL model and (*d*) the ES model. We present the latitudinal variation in reef fish species richness during geological periods from the Palaeocene to the Holocene. For each mechanism, we calculated the species richness of the best simulation across latitudes at each time step. These simulated patterns can be compared to the observed latitudinal variation in species richness located on the right of each plot (obs.). *Pli*, Pliocene; *Ple*, Pleistocene; *H*, Holocene.

Furthermore, the EL model predicted strong latitudinal breaks in species turnover at high latitudes (electronic supplementary material, figure S9c). The EL model generated globally lower speciation rates and higher extinction rates of tropical lineages than the TA and TNC models (figure 3).

(v) Evolutionary speed

Similar to the TA model, the ES model generated a slight LDG with breaks in species richness at −23° N and 46° N for the Indo-Pacific region and breaks at 2.9° N and 40° N for the Atlantic region (figure 3*d*; electronic supplementary material, figure S3d). We did not observe a significant latitudinal break in species turnover (electronic supplementary material, figure S9d). The ES model generated globally

lower speciation rates and higher extinction rates of tropical lineages than the TA and TNC models (figure 3).

4. Discussion

The uneven distribution of biodiversity on Earth ultimately results from the heterogeneous outcome of speciation, extinction and dispersal [40,41]. Various historical and ecological factors have been proposed to explain biodiversity gradients [3–5]. However, we still lack integrated models that can be used to evaluate the effect of these different factors and their interactions [42]. In this study, we use a mechanistic modelling approach to evaluate how historical and ecological factors may influence reef fish diversity in space and time according to alternative hypotheses. Our results reveal that palaeohabitat dynamics determined the LDG in reef fishes during deep geological time but that only ecological constraints related to the contraction of the tropical habitat during the Neogene (−23 to 2.5 Myr) explain the current shape of the LDG.

Habitat dynamics are expected to be major determinants of biodiversity gradients [5,9]. For example, several studies have shown that species richness and composition are closely linked to habitat changes caused by past tectonic events [9,29,43–45]. However, owing to the lack of palaeoenvironmental and palaeontological data, little empirical evidence supports the influence of past habitat dynamics on the LDG [5,18]. In the simulations run under the TA hypothesis, large and stable areas of tropical habitat (electronic supplementary material, figure S13) maintained high diversification rates (electronic supplementary material, figure S15), which gradually increased species richness in the tropics (figure 3*a*). These simulations also revealed a slowdown of tropical lineages' speciation rates during the Neogene (figure 2*a*), with relatively similar speciation rates between tropical and temperate lineages at the end of the Neogene, which could be related to the shrinkage of tropical reef habitats during this period (electronic supplementary material, figures S13 and S14). This result is particularly consistent with a recent phylogenetic-based study [21] that showed relatively little variation in recent speciation rates in marine fishes for the latitudinal range that we considered here (i.e. between −60° and 60° N, see the electronic supplementary material, figure S16 for acanthomorph reef fishes). Overall, these findings provide support for the hypothesis that the LDG is the result of the deep-time history of clades in relation to the dynamics of tropical habitats [46–49], hence explaining the temporal variability in this pattern [50].

Although palaeohabitat dynamics alone can generate an LDG in reef fishes, the TA model failed to predict all the features of the modern LDG, such as the position of latitudinal breakpoints in species richness. Indeed, the TA model was found to over-estimate species richness at subtropical and temperate latitudes, especially in the Northern Hemisphere (figure 2*a*). The addition of mechanisms considering the response of species to climatic conditions, as proposed by the EL and TNC hypotheses, markedly improved the prediction of the latitudinal variation in both species richness and species turnover. This result suggests that the steepness of the LDG and observed latitudinal breaks in species turnover are generated by ecological constraints acting at the limits between tropical and temperate environments. This mechanism is not unexpected, given that contemporary patterns of species richness and species turnover are strongly associated

with climatic conditions [45,51]. The fossil record also shows that past climatic changes left a strong imprint on the LDG [50,52,53], while comparative studies have demonstrated the importance of climatic variations in diversification dynamics [25,54]. In our simulations, palaeohabitat dynamics controlled global differences in species richness and diversification rates between tropical and extratropical areas, while climate-based processes controlled the steepness of the species richness gradient and the position of latitudinal breaks in species turnover. Consequently, these mechanisms are expected to act in concert to shape the LDG at different spatial and temporal scales.

However, differentiating the predictions of alternative climate-based mechanisms (i.e. mechanisms considering a response to climatic conditions) using our model remains challenging. First, the ES model generates predictions similar to those of the TA model, which makes these processes difficult to differentiate in comparative studies. This suggests that the full complexity of the LDG cannot be predicted by simple differences in speciation rates between tropical and temperate lineages. Second, the EL and TNC models yield more realistic predictions of the latitudinal variation in species richness and β-diversity (electronic supplementary material, figure S6). In the literature, one can find evidence supporting both hypotheses. On the one hand, studies focusing on the influence of palaeotemperature variations on extinction rates of tropical lineages suggest that niche conservatism limits species adaptation to a changing environment [54]. On the other hand, the results from studies focusing on density dependence support a difference in carrying capacity between temperate and tropical regions [55]. When evaluated jointly, both mechanisms seem to influence different macroevolutionary processes [25], suggesting that their relative influences could work closely together [56]. In our simulations, we observed small differences in the predictions of these hypotheses. Overall, the EL model rendered better predictions for the variables we chose. Notably, it generated more obvious latitudinal breaks in species turnover. In this case, new species that appeared inside a biome (tropical or temperate) outcompeted those that colonized the biome, limiting exchanges between biomes and increasing species replacement at the boundaries between tropical and temperate habitats. Furthermore, according to the EL model, the saturation of temperate habitats prevented the speciation rates of temperate lineages from increasing at the end of the Neogene, despite the expansion of temperate habitats (electronic supplementary material, figures S13 and S14). In both EL and TNC simulations, the position of the boundary between tropical and temperate environments is key. Thus, our predictions using those models should be interpreted carefully as they are dependent on the reef-forming corals fossil record that we used as a proxy for tropical climate. Hence, the tropical limit is an approximation that might suffer from dating, palaeo-localization inaccuracy or data gap, especially further back in time ([57], electronic supplementary material, Discussion).

This study demonstrates the importance of using multiple biodiversity metrics to evaluate alternative hypotheses in the fields of ecology, evolution and biogeography rather than focusing on a single diversity metric [25]. Our results showed that considering not only species richness but also β-diversity allows better comprehension of the mechanisms shaping the LDG. Our findings also illustrate the importance of the temporal scale used when evaluating how alternative

hypotheses may explain the modern LDG. In all our simulations, the tropics were considered either 'a cradle' or 'a museum' [58], depending on the time scale. Tropical habitats can be considered cradles on a very deep time scale because most lineages originated in the tropics owing to a much warmer climate and extensive tropical and subtropical habitat in the Mesozoic (figures 2 and 3). Tropical habitats can also be considered museums on a shorter time scale because they allowed the survival of tropical lineages during the expansion of temperate habitats starting in the middle of the Neogene.

The OTT ([10]) model posits that the tropics support more species because lineages there have higher speciation rates, lower extinction rates and higher net emigration over immigration than do lineages in extratropical regions. Our simulations based solely on the influence of habitat dynamics tend to support the predictions of the 'OTT' model from the mid-Cretaceous to the mid-Palaeogene but tend to reject it for other time periods, which stresses the temporal characteristic of this model [59]. Furthermore, even with a strong influence of TNC, our simulations under the sympatric mode of speciation revealed a higher net rate of emigration over immigration in tropical lineages than in temperate lineages in those time periods. Given this perspective, the results from macroevolutionary models should be interpreted carefully as an estimate of higher rates of dispersal towards temperate habitats for lineages with tropical origins does not always constitute evidence against TNC [20,23]. In that sense, our results are concordant with the findings of Siqueira *et al.* [23], but allowed a deeper understanding of the potential causes of differences in diversification rates and temporal shifts in dispersal rates in reef fishes.

5. Conclusion and perspectives

In this study, we showed that the additional consideration of climate-based processes in the habitat-driven SPLIT model [9,28] significantly improved predictions of the modern LDG. Using a process-based modelling approach, we revealed how large-scale macroevolutionary dynamics and *in situ* environmental processes can interact in space and time to generate observed patterns of biodiversity. The simple formalism of the model presented in this study allows a broad range of modifications and improvements [28], facilitating the integration of a more complex process. We suggest that incorporating competition and trait evolution under selective pressures in a moving landscape could allow prediction of greater differences in β-diversity and evolutionary rates with alternative mechanisms. This kind of model would consider process-based mechanisms to establish a link between micro- and macroevolutionary scales [60].

References

1. Hillebrand H. 2004 On the generality of the latitudinal diversity gradient. *Am. Nat.* **163**, 192–211. (doi:10.1146/annurev-ecolsys-112414-054102)

2. Kinlock NL *et al.* 2018 Explaining global variation in the latitudinal diversity gradient: meta-analysis confirms known patterns and uncovers new ones. *Glob. Ecol. Biogeogr.* **27**, 125–141. (doi:10.1111/geb.12665)

3. Willig MR, Kaufman DM, Stevens RD. 2003 Latitudinal gradients of biodiversity: patterns, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* **34**, 273–309. (doi:10.1146/annurev.ecolsys.34.012103.144032)

4. Mittelbach GG *et al.* 2007 Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* **10**, 315–331. (doi:10.1111/j.1461-0248.2007.01020.x)

5. Fine PVA. 2015 Ecological and evolutionary drivers of geographic variation in species diversity. *Annu. Rev. Ecol. Evol. Syst.* **46**, 369–392. (doi:10.1146/annurev-ecolsys-112414-054102)

6. Jetz W, Fine PVA. 2012 Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLoS Biol.* **10**, e1001292. (doi:10.1371/journal.pbio.1001292)

7. Rosenzweig ML. 1995 *Species diversity in space and time*, p. 436. Cambridge, UK: Cambridge University Press.

8. Leprieur F, Descombes P, Gaboriau T, Cowman PF, Parravicini V. 2016 Plate tectonics drive tropical reef biodiversity dynamics. *Nat. Commun.* **7**, 11461. (doi:10.1038/ncomms11461)

9. Descombes P, Gaboriau T, Albouy C, Heine C, Leprieur F, Pellissier L. 2017 Linking species diversification to palaeo-environmental changes: a process-based modelling approach. *Glob. Ecol. Biogeogr.* **27**, 233–244. (doi:10.1111/geb.12683)

10. Wiens JJ *et al.* 2010 Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* **13**, 1310–1324. (doi:10.1111/j.1461-0248.2010.01515.x)

11. Hutchinson GE. 1959 Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* **93**, 145–159. (doi:10.1086/282070)

12. MacArthur R. 1965 Patterns of species diversity. *Biol. Rev. Camb. Philos. Soc.* **40**, 510. (doi:10.1111/j.1469-185X.1965.tb00815.x)

13. Rohde K. 1992 Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**, 514. (doi:10.2307/3545569)

14. Allen AP, Gillooly JF, Savage VM, Brown JH. 2006 Kinetic effects of temperature on rates of genetic divergence and speciation. *Proc. Natl Acad. Sci. USA* **103**, 9130–9135. (doi:10.1073/pnas.0603587103)

15. Allen AP, Brown JH, Gillooly JF. 2002 Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* **297**, 1545–1548. (doi:10.1126/science.1072380)

16. Brown JH. 2014 Why are there so many species in the tropics? *J. Biogeogr.* **41**, 8–22. (doi:10.1111/jbi.12228)

17. Sandel B, Dangremond EM. 2012 Climate change and the invasion of California by grasses. *Glob. Chang. Biol.* **18**, 277–289. (doi:10.1111/j.1365-2486.2011.02480.x)

18. Belmaker J, Jetz W. 2015 Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. *Ecol. Lett.* **18**, 563–571. (doi:10.1111/ele.12438)

19. Gavin MC *et al.* 2017 Process-based modelling shows how climate and demography shape language diversity. *Glob. Ecol. Biogeogr.* **26**, 584–591. (doi:10.1111/geb.12563)

20. Rolland J, Condamine FL, Jiguet F, Morlon H. 2014 Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biol.* **12**, e1001775. (doi:10.1371/journal.pbio.1001775)

21. Rabosky DL *et al.* 2018 An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* **559**, 392–395. (doi:10.1038/s41586-018-0273-1)

22. Goldberg EE, Lancaster LT, Ree RH. 2011 Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Syst. Biol.* **60**, 451–465. (doi:10.1093/sysbio/syr046)

23. Siqueira AC, Oliveira-Santos LGR, Cowman PF, Floeter SR, Algar A. 2016 Evolutionary processes underlying latitudinal differences in reef fish biodiversity. *Glob. Ecol. Biogeogr.* **25**, 1466–1476. (doi:10.1111/geb.12506)

24. Buckley LB *et al.* 2010 Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proc. R. Soc. B* **277**, 2131–2138. (doi:10.1098/rspb.2010.0179)

25. Lehtonen S *et al.* 2017 Environmentally driven extinction and opportunistic origination explain fern diversification patterns. *Sci. Rep.* **7**, 4831. (doi:10.1038/s41598-017-05263-7)

26. Pellissier L, Heine C, Rosauer DF, Albouy C. 2018 Are global hotspots of endemic richness shaped by plate tectonics? *Biol. J. Linn. Soc.* **123**, 247–261. (doi:10.1111/brv.12366)

27. Albert JS, Schoolmaster DR, Tagliacollo V, Duke-Sylvester SM. 2017 Barrier displacement on a neutral landscape: toward a theory of continental biogeography. *Syst. Biol.* **66**, 167–182. (doi:10.1093/sysbio/syw080)

28. Janzen DH. 1967 Why mountain passes are higher in the tropics? *Am. Nat.* **101**, 233–249. (doi:10.1086/282487)

29. Jordan SMR, Barraclough TG, Rosindell J. 2016 Quantifying the effects of the break up of Pangaea on global terrestrial diversification with neutral theory. *Phil. Trans. R. Soc. B* **371**, 20150221. (doi:10.1098/rstb.2015.0221)

30. Rangel TF *et al.* 2018 Modeling the ecology and evolution of biodiversity: biogeographical cradles,

31. museums, and graves. *Science* **361**, eaar5452. (doi:10.1126/science.aar5452)

31. Bellwood DR, Hughes TP, Connolly SR, Tanner J. 2005 Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecol. Lett.* **8**, 643–651. (doi:10.1111/j.1461-0248.2005.00763.x)

32. Price SA, Claverie T, Near TJ, Wainwright PC. 2015 Phylogenetic insights into the history and diversification of fishes on reefs. *Coral Reefs* **34**, 997–1009. (doi:10.1007/s00338-015-1326-7)

33. Müller RD, Sdrolias M, Gaina C, Steinberger B, Heine C. 2008 Long-term sea-level fluctuations driven by ocean basin dynamics. *Science* **319**, 1357–1362. (doi:10.1126/science.1151540)

34. Poyato-Ariza FJ. 1996 A revision of Rubiesichthys gregalis Wenz 1984 (Ostariophysi, Gonorynchiformes), from the Early Cretaceous of Spain. *Syst. Paleoecol.* **1984**, 329–348.

35. Baselga A. 2010 Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* **19**, 134–143. (doi:10.1111/j.1466-8238.2009.00490.x)

36. Baselga A, Orme CDL. 2012 Betapart: an R package for the study of beta diversity. *Methods Ecol. Evol.* **3**, 808–812. (doi:10.1111/j.2041-210X.2012.00224.x)

37. Lichstein JW. 2006 Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecol.* **188**, 117–131. (doi:10.1007/s11258-006-9126-3)

38. Muggeo VM. 2008 Segmented: an R package to fit regression models with broken-line relationships. *R News* **20–25**, 1–73.

39. R Core Team. 2019 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.r-project.org.

40. Ricklefs RE. 1987 Community diversity: relative roles of local and regional processes. *Science* **235**, 167–171. (doi:10.1126/science.235.4785.167)

41. Schluter D, Pennell MW. 2017 Speciation gradients and the distribution of biodiversity. *Nature* **546**, 48–55. (doi:10.1038/nature22897)

42. Gotelli NJ *et al.* 2009 Patterns and causes of species richness: a general simulation model for macroecology. *Ecol. Lett.* **12**, 873–886. (doi:10.1111/j.1461-0248.2009.01353.x)

43. Renema W *et al.* 2008 Hopping hotspots: global shifts in marine biodiversity. *Science* **321**, 654–657. (doi:10.1126/science.1155674)

44. Descombes P, Leprieur F, Albouy C, Heine C, Pellissier L. 2017 Spatial imprints of plate tectonics on extant richness of terrestrial vertebrates. *J. Biogeogr.* **44**, 1185–1197. (doi:10.1111/jbi.12959)

45. Mazel F, Wüest RO, Lessard J-P, Renaud J, Ficetola GF, Lavergne S, Thuiller W. 2017 Global patterns of β-diversity along the phylogenetic time-scale: the role of climate and plate tectonics. *Glob. Ecol. Biogeogr.* **26**, 1211–1221. (doi:10.1111/geb.12632)

46. Fine PVA, Ree RH. 2006 Evidence for a time-integrated species-area effect on the latitudinal

10

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gradient in tree diversity. *Am. Nat.* **168**, 796–804. (doi:10.1086/508635)

47. Jablonski D, Kaustuv R, Valentine JW. 2006 Out of the tropics: evolutionary diversity gradient. *Science* **314**, 102–106. (doi:10.1126/science.1130880)

48. Cowman PF, Parravicini V, Kulbicki M, Floeter SR. 2017 The biogeography of tropical reef fishes: endemism and provinciality through time. *Biol. Rev.* **92**, 2112–2130. (doi:10.1111/brv.12323)

49. Miller EC, Hayashi KT, Song D, Wiens JJ. 2018 Explaining the ocean's richest biodiversity hotspot and global patterns of fish diversity. *Proc. R. Soc. B* **285**, 20181314. (doi:10.1098/rspb.2018.1314)

50. Mannion PD, Upchurch P, Benson RBJ, Goswami A. 2014 The latitudinal biodiversity gradient through deep time. *Trends Ecol. Evol.* **29**, 42–50. (doi:10.1016/j.tree.2013.09.012)

51. Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Berghe EV, Worm B. 2010 Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**, 1098–1101. (doi:10.1038/nature09329)

52. Crame JA. 2001 Taxonomic diversity gradients through geological time. *Divers. Distrib.* **7**, 175–189. (doi:10.1046/j.1472-4642.2001.00106.x)

53. Fenton IS, Pearson PN, Jones TD, Farnsworth A, Lunt DJ, Markwick P, Purvis A. 2016 The impact of Cenozoic cooling on assemblage diversity in planktonic foraminifera. *Phil. Trans. R. Soc. B* **371**, 20150224. (doi:10.1098/rstb.2015.0224)

54. Kergoat GJ *et al.* 2014 Cretaceous environmental changes led to high extinction rates in a hyperdiverse beetle family. *BMC Evol. Biol.* **14**, 220. (doi:10.1186/s12862-014-0220-1)

55. Machac A, Graham CH. 2017 Regional diversity and diversification in mammals. *Am. Nat.* **189**, E1–E13. (doi:10.1086/689398)

56. Tomašových A, Jablonski D. 2017 Decoupling of latitudinal gradients in species and genus geographic range size: a signature of clade range expansion. *Glob. Ecol. Biogeogr.* **26**, 288–303. (doi:10.1111/geb.12533)

57. Edinger EN, Burr GS, Pandolfi JM, Ortiz JC. 2007 Age accuracy and resolution of Quaternary corals used as proxies for sea level. *Earth Planet. Sci. Lett.* **253**, 37–49. (doi:10.1016/j.epsl.2006.10.014)

58. Stebbins GL. 1974 *Flowering plants: evolution above the species level*, 480 p. Cambridge, MA: Belknap Press.

59. Huang S, Roy K, Jablonski D. 2014 Do past climate states influence diversity dynamics and the present-day latitudinal diversity gradient? *Glob. Ecol. Biogeogr.* **23**, 530–540. (doi:10.1111/geb.12153)

60. Pontarp M *et al.* 2018 The latitudinal diversity gradient: novel understanding through mechanistic eco-evolutionary models. *Trends Ecol. Evol.* **24**, P211–223. (doi:10.1016/j.tree.2018.11.009)

61. Gaboriau T, Albouy C, Descombes P, Mouillot D, Pellissier L, Leprieur F. 2019 Data from: Ecological constraints coupled with deep-time habitat dynamics predict the latitudinal diversity gradient in reef fishes. Dryad Digital Repository. (http://doi.org/10.5061/dryad.0r852nm)