

Are global hotspots of endemic richness shaped by plate tectonics?

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The geology of the earth has shown profound changes in the position, connectivity and topography of continents during the last 100 Myr, which could have shaped the diversification of lineages and thus the current distribution of biodiversity. Here, we evaluate the association between plate tectonics and the current location of hotspots of endemic richness across the globe. We used palaeogeographies in a model that quantifies, through time and for each geographic cell, the potential dispersal between disconnected habitat areas. We expected that rare dispersal events across barriers of unsuitable habitat allow species colonization, but a subsequent absence of gene flow could lead to *in situ* speciation. We evaluated whether this process could pinpoint the locations of hotspots of endemic richness computed from the ranges of 181 603 species across 14 taxonomic groups. The significant spatial congruence between the model and the endemic richness of several clades provides evidence of the contribution of plate tectonics in shaping global biodiversity gradients. The signal of plate tectonics was independent from those of the Quaternary glaciation, topographical heterogeneity and contemporary productivity and was stronger for terrestrial than freshwater and marine taxa. Regions with high tectonic complexity, predominantly located at the confluence of major lithospheric plates such as the Mediterranean basin, Mesoamerica, Madagascar and South East Asia, probably provided favourable circumstances for allopatric speciation and the emergence of new species across straits. Further efforts should be made to disentangle the effect of past diversification relative to current ecological interactions in shaping global patterns in species diversity.

ADDITIONAL KEYWORDS: allopatric speciation – biodiversity – continental drift – dispersal – species richness.

INTRODUCTION

Biodiversity on Earth is the result of the radiation of lineages in interaction with relentless changes in their environment and is sustained by extant ecological conditions. Convergence of ecological and evolutionary

theories stems from the recognition that the uneven spatial distribution of biodiversity is the product of both contemporary and historical factors (Ricklefs & Latham, 1993; Mittelbach *et al.*, 2007). The emergence and maintenance of biodiversity have been investigated using a variety of approaches. Based on phylogenies, rates of diversification have been ascribed to regional differences in palaeoenvironmental conditions, highlighting how ancient Earth processes may shape

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extant biodiversity (e.g. [Condamine *et al.*, 2012](#); [Near *et al.*, 2012](#)). In particular, plate tectonics have been shown to foster species diversification in geologically active regions ([Magri *et al.*, 2007](#); [Li *et al.*, 2013](#); [Bagley & Johnson, 2014](#); [Richardson *et al.*, 2014](#)). However, macroevolutionary models are based on a very limited number of regions (e.g. low latitude vs. high latitude [Pyron, 2014](#); [Pulido-Santacruz & Weir, 2016](#)), and their power to explain complex spatial gradients is limited. Spatial statistical models provide an alternative approach to explain spatial gradients of biodiversity. Yet, in these models, contemporary factors have more frequently been investigated (e.g. climate or energy; [Currie, 1991](#); [Hawkins *et al.*, 2003](#); [Kreft & Jetz, 2007](#)) than historical proxies (e.g. latitude; [Kerckhoff, Moriarty & Weiser, 2014](#)), and those that have been considered rarely extend beyond the Quaternary ([Peter & Axelrod, 1975](#); [Graham, Moritz & Williams, 2006](#); [Sandel *et al.*, 2011](#); [Pellissier *et al.*, 2014](#)). Thus, while plate tectonics is recognized to have shaped past and extant biogeographical patterns, in practice, ancient geomorphological dynamics are rarely considered to explain current biodiversity ([Descombes *et al.*, 2017](#)). Hence, correlative ecological models may currently underestimate the influence of historical factors on extant biodiversity patterns ([Rahbek *et al.*, 2007](#)).

Using spatial statistical models, patterns in the large-scale distribution of biodiversity across the globe have been associated with a multitude of variables ([Mittelbach *et al.*, 2007](#)). The most commonly proposed driver of biodiversity is energy, in the form of either temperature ([Currie, 1991](#); [Hawkins *et al.*, 2003](#)) or primary productivity ([Kay *et al.*, 1997](#); [Waide *et al.*, 1999](#); [Jetz *et al.*, 2012](#)), where higher energy should sustain more complex food chains ([Briand & Cohen, 1987](#)). Other extant environmental conditions, including water availability ([Qian *et al.*, 2007](#)) or habitat area ([Hawkins *et al.*, 2003](#); [Bellwood *et al.*, 2005](#)), show correlations with extant species diversity. Most historical studies investigate whether species distributions are in disequilibrium with extant climate as a legacy of the last glaciations ([Graham *et al.*, 2006](#); [Sandel *et al.*, 2011](#); [Pellissier *et al.*, 2014](#)). Yet phylogeographical and palaeontological evidence suggests that geomorphological dynamics reshaped species distributions in the past ([Li *et al.*, 2013](#); [Bagley & Johnson, 2014](#); [Richardson *et al.*, 2014](#)). The legacy of plate tectonics should be detectable today in the diversity of species ([Craw *et al.*, 2016](#)). Areas where geomorphological processes have promoted the diversification of lineages in the past should have inherited a comparatively larger number of extant species ([Leprieur *et al.*, 2016](#); [Descombes *et al.*, 2017](#)). The association between species richness and topography ([Davies *et al.*, 2007](#)), heterogeneity ([Stein, Gerstner & Kreft, 2014](#)) or plate boundaries ([Keith *et al.*, 2013](#)) suggests that older processes, for example associated with

orogeny, also represented biodiversity pumps ([Badgley, 2010](#)). The quest to fully understand the spatial distribution of extant biodiversity must better integrate more ancient processes, which acted concomitantly with the phases of diversification of extant species, usually millions of years old ([Hodge & Bellwood, 2016](#)).

Beyond the overarching gradient of biodiversity with latitude, particular regions of the globe form hotspots, hosting a disproportionately large fraction of extant biodiversity. For instance, at comparable latitudes and climates, Asia is considerably more diverse than the Americas or Africa for plants ([Ricklefs, 2004](#); [Couvreur, 2015](#)). Similarly, the biodiversity of the Neotropics is thought to have largely emerged from geological activities, for example associated with orogeny ([Hoorn *et al.*, 2010](#)). Within the last ~100 Myr, diversification gave rise to most modern lineages, including within birds ([Barker *et al.*, 2004](#)), mammals ([Meredith *et al.*, 2011](#)) and higher plants ([Magallón & Castillo, 2009](#)). During this period of diversification, plate tectonics dramatically remodelled the structure of terrestrial landscapes and near-shore marine habitats and should have left a legacy on current diversity ([Renema *et al.*, 2008](#); [Leprieur *et al.*, 2016](#)). Evidence suggests that the emergence of biodiversity is linked to geology for both marine and terrestrial organisms ([Briggs, 1987](#); [Morley, 1998](#)). Among the geological processes shaping biodiversity, the convergence of tectonic plates promotes environmental heterogeneity through building of topography. Temporal changes in convergence kinematics along subduction zones (such as the Andes) can generate significant vertical crustal motions. Towards the end of a Wilson cycle, collision of continental plates generates Alpine-Himalayan type mountain chains, which enhance the diversification of organisms, for example plant ([Hoorn *et al.*, 2010](#)) and animal lineages ([Toussaint *et al.*, 2014](#)). Other geological processes, such as the emergence of islands associated with volcanism, are also expected to contribute to species diversification through allopatric speciation ([Briggs, 2003](#); [Bidegaray-Batista & Arnedo, 2011](#)). By isolating populations with oceanic gateways, fuelled by sporadic events of dispersal across straits ([Lavergne, Hampe & Arroyo, 2013](#)), plate divergence may represent a further major catalyst of speciation ([Steeman *et al.*, 2009](#)). Nevertheless, the processes of plate tectonics are rarely considered when modelling the current spatial distribution of biodiversity.

Biodiversity has many facets, and the signal of history may be stronger in some than others ([Sandel *et al.*, 2011](#)). For instance, species with large range size are generally associated with high dispersal abilities ([Bowman, Jaeger & Fahrig, 2002](#); [Lester *et al.*, 2007](#)). Hence, the extant distribution of these species can

extend far from their origin, eroding the signal of the historical process that led to their diversification. In contrast, endemic species – at least those not resulting from range contractions – are more frequently found in their specific locations of origin (e.g. [Vetaas & Grytnes, 2002](#); [Barluenga *et al.*, 2006](#)). The level of endemism may thus show a stronger association with regional geological processes. Biogeographical analyses have already shown a congruence between pan-biogeographical nodes of geological origin and areas of endemism ([Contreras-Medina, Morrone & Lunz Vega, 2001](#); [Luna-Vega & Contreras-Medina, 2010](#)). For instance, high endemic richness in Madagascar is associated with a long history of geological separation of the island ([Ali & Huber, 2010](#)). However, novel mechanistic modelling approaches are required to test for a more general link between plate tectonics and endemism at a global scale.

Here, we evaluate the congruence between the dynamics of plate tectonics and current hotspots of species endemism. We used a spatial model that quantifies dynamically the role of plate movements in providing opportunities to generate biodiversity at the margins of continental plates. Allopatry is thought to be the dominant force of speciation ([Futuyma & Mayer, 1980](#); [Gastauer *et al.*, 2015](#)), and this mechanism may generate a higher diversity of species endemic to regions subject to plate divergence ([Raven & Axelrod, 1974](#); [Molina-Venegas *et al.*, 2015](#)). Since it is less subject to diffusion after diversification, endemic richness should provide a stronger signal than species richness ([Descombes *et al.*, 2017](#)). We identified locations, where high diversity is expected from a speciation process linked to plate movements, and compared these locations to the distribution of ‘hotspots’, the cells with the highest endemic richness worldwide in a data set of 181 603 species across 14 taxonomic groups in marine, freshwater and terrestrial environments. We had the following expectations:

1. Regions of highest endemic richness should be congruent with regions of plate divergence or convergence, which fostered dispersal and ultimately speciation among patches separated by unsuitable habitat.
2. The relationship between plate tectonics and endemic richness should be independent of other historical factors associated with the glaciations of the Quaternary and independent of contemporary factors, including topographical heterogeneity and productivity.

Together, we expect that the availability of palaeo-habitat reconstructions mapping of the potential speciation generated by plate movement should provide

the missing link between past tectonic activity and its consequences on the current global distribution of endemic richness.

MATERIAL AND METHODS

SPECIES DATA AND ENDEMIC RICHNESS

We mapped endemic richness globally using an indicator that combines information on species endemism and species richness ([Kier *et al.*, 2009](#)), by calculating the sum of the inverse range sizes of all species occurring in each grid cell. This metric was calculated from gridded species distributions for 181 603 species in terrestrial, freshwater and marine ecosystems, consisting of (1) 154 507 terrestrial species (6309 amphibians, 5289 mammals, 128 565 plants, 4278 reptiles, 10 066 birds); (2) 9597 freshwater species (1277 crabs, 1887 molluscs, 135 plants, 6298 fishes); and (3) 17 499 marine species (844 corals, 632 cone snails, 369 sea cucumbers, 61 sea snakes, 15 593 fishes). Each species range size was measured as the number of grid cells in which a species occurs across the globe using an equal-area projection.

For most species (amphibians, mammals, reptiles, corals, cone snails, sea cucumbers, crabs, molluscs, freshwater plants and freshwater fishes), distribution data were obtained from the IUCN web site (accession date: 30 November 2016). Bird distribution maps were obtained from BirdLife International ([BirdLife International & NatureServe, 2015](#)). For the scale and resolution of the current study, IUCN and BirdLife polygons represent the distribution of species with sufficient accuracy, and such data have been used in many analyses in macroecology (e.g. [Hurlbert & Jetz, 2007](#); [Marin & Hedges, 2016](#)). For the plants, we used regional species checklists of all families present in the Kew Checklist database from the Taxonomic Databases Working Group (TDWG). We used checklists corresponding to the most detailed ‘Level 3’ TDWG polygons (<http://www.tdwg.org/>, <http://www.kew.org/science-conservation/research-data/resources/gis-unit/tdwg-world>). Polygons generally correspond to countries, although larger countries are often subdivided into states, or islands, for example in South East Asia.

Fish species data were obtained from the Ocean Biogeographic Information System (OBIS; <http://www.iobis.org>). We inventoried 16 238 200 occurrence records. We cleaned the data by identifying synonyms, misspellings and rare species (only one occurrence). Synonyms were replaced with accepted names. This resulted in a set of 11 503 257 occurrences for 11 345 fish species around the world. We reconstructed distribution maps for each species, defined

as the convex polygon surrounding the area where each species was observed. The resulting polygon was divided into four parts across the world to integrate possible discontinuity between the two hemispheres and the Atlantic and Pacific Oceans. For instance, anti-tropical species are distributed in the northern and southern hemisphere, but show a range discontinuity near the tropics (Briggs, 1987), and a polygon division allows this to be accounted for. We refined each species distribution map by removing areas where depths did not include the known depth range of the species from FishBase. As the OBIS database did not represent well the tropical assemblage of fish, we merged it with the Gaspar database that encompasses 6316 coral reef species (Pellissier *et al.*, 2014). We obtained a world database containing 15 593 fish species. We transformed individual species shapefiles into equal-area raster grids. All maps of endemic richness were then projected into global longitude–latitude projection 1°-resolution grids to match environmental variables.

As a complement to endemic richness, phylogenetic endemism can pinpoint areas where substantial components of phylogenetic diversity are restricted (Rosauer *et al.*, 2009). Phylogenetic endemism can show associations with both contemporary and historical variables such as Wallace's Line (Rosauer & Jetz, 2015). The geographic range is calculated for each branch in the tree, including the union of the ranges of all descendant taxa in a clade, such that overlapping areas were counted only once. Data are available for mammals, allowing a comparison of the metric of endemic richness and phylogenetic endemism (Rosauer & Jetz, 2015). We evaluated the correlation between endemic richness and phylogenetic endemism for the analysed clade to evaluate the congruence of the two metrics.

PLATE TECTONIC RECONSTRUCTION

Reconstructions of palaeoenvironments are needed to understand which regions were historically the most likely to promote the emergence of biodiversity (Svenning *et al.*, 2015). Here, we used palaeoreconstructions of the position of continents, coastlines and palaeobathymetry (Müller *et al.*, 2008; Heine, Yeo & Müller, 2015) from the Early Cretaceous (140 Mya) to the present in 1 Myr steps as boundary conditions for our models. We used the GPLates open source software (<http://www.gplates.org>) in conjunction with a set of digital palaeoshoreline positions (Heine *et al.*, 2015) and a model of global plate motion to generate gridded, individual palaeogeographic reconstructions for land surface area at any given time step. While there are uncertainties, the palaeogeography of Heine *et al.* (2015) is a detailed open access global data set providing reconstructions at regular time steps of 1 Myr. We

focused on the period spanning the last 140 Myr, which was characterized by significant changes in the position of the tectonic plates across the globe, for example from the breaking of the Gondwana supercontinent, followed by the rapid northward motion of India and Australia. This period also represents the time window during which many extant clades diversified (Meredith *et al.*, 2011; Jetz *et al.*, 2012) possibly under the influence of plate tectonics. Nonetheless, because the peak of diversification of some of the groups occurred more recently, for example in the Miocene (Santos *et al.*, 2009), we ran a sensitivity analysis that considered different starting dates for the simulations (100, 80, 60 and 40 Mya).

MODELLING THE POTENTIAL FOR SPECIATION

We developed a model based on habitat dynamics, which quantifies the amount of potential dispersal into each cell from disconnected patches separated by unsuitable areas (i.e. of sea for terrestrial species or deep sea and land for marine species; Fig. 1; Supporting Information, Figs S1, S2). Rare dispersal across geographic barriers should allow the establishment of new populations, but gene flow is subsequently almost non-existent, leading to *in situ* speciation. Classical examples of colonization of remote areas such as islands (e.g. Guzmán & Vargas, 2009; Gillespie & Roderick, 2014) followed by local speciation support the possibility of dispersal across straits on geological time scales (Cowie & Holland, 2006). Our model records for each point in time and for each cell, the number of cells from disconnected patches from which it can receive dispersers, which would potentially give rise to a new species. During each million-year time slice, the simulation first defines the patches separated by at least one cell of unsuitable area using an algorithm of cluster splits implemented in the 'dbscan' function in the fpc library in R. The model then quantifies for each cell, the number of surrounding cells from disconnected patches within a dispersal distance d . A higher number of possible donor cells are assumed to increase the chance of dispersal across a barrier. To accommodate the movement of the continents, the cell values at time t added to the value of potential incoming dispersal are transferred to the closest cell at time $t + 1$. Areas with the greatest potential incoming dispersal across barriers for an extended duration are expected to have the highest potential for allopatric speciation, shaping species richness and endemism across barriers. We tested a range of values of dispersal d [5, 10, 15, 20, 25, 30 (°)] for both terrestrial and marine ecosystems (Supporting Information, Figs S4, S6).

The previous proxy only covers a mechanism for the generation of new species, but fails to account for extinction. Extinction is thought to be associated with the more intense climatic fluctuation towards the poles

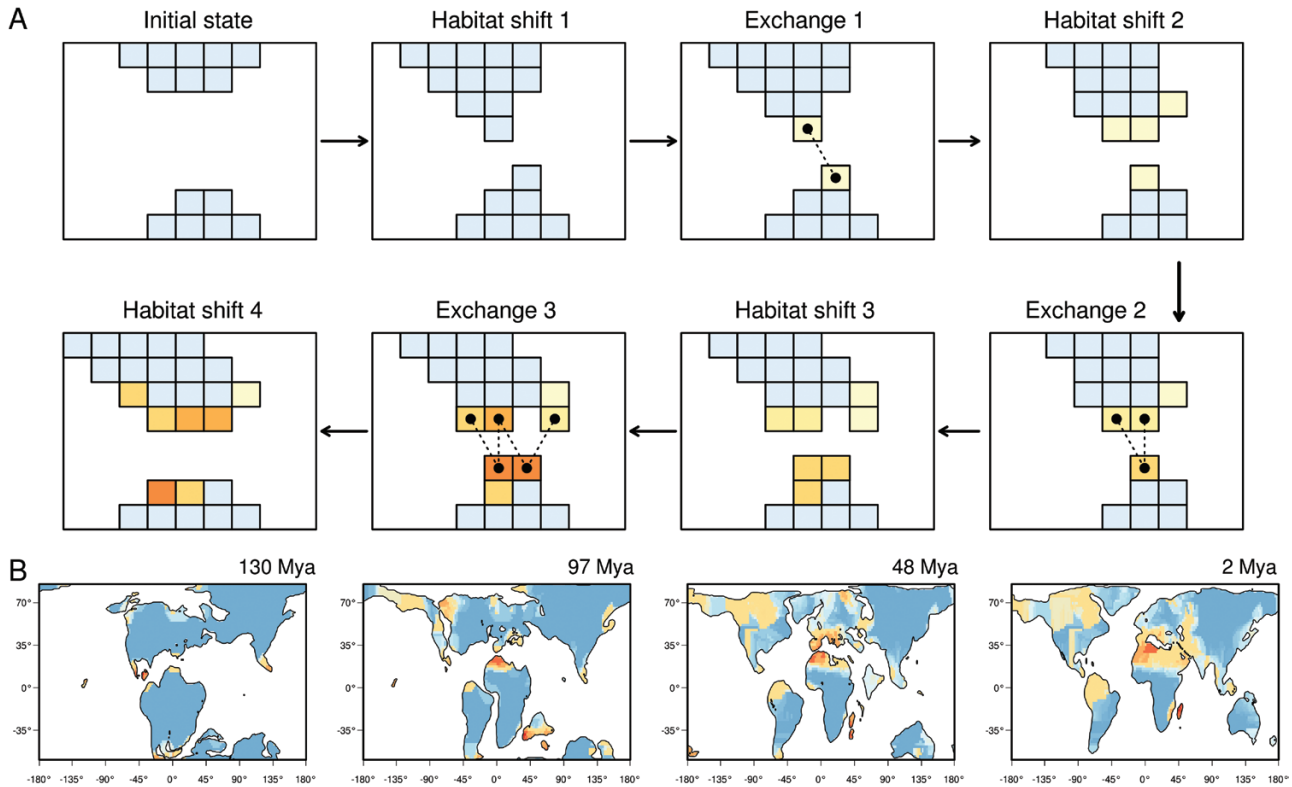


Figure 1. A, illustration of the mechanism used to produce the spatial proxy of speciation potential due to plate tectonics, including from left to right, alternating phases of (1) habitat change and (2) exchange among cells. During each million-year time slice, the simulation first defines the patches separated by at least one cell of unsuitable habitat. The model identifies for each cell, the number of surrounding ‘donor’ cells from disconnected habitat patches below a dispersal distance d (linked by dashed lines). A higher number of possible donor cells are assumed to increase the chance of long-distance dispersal across a barrier (intensity of shading). To accommodate the movement of the continents, the cell values at time t are transferred to the closest new cells at time $t + 1$. B, examples of four palaeogeographies showing the terrestrial locations with high potential for speciation across straits for 130, 97, 48 and 2 Mya.

(Dynesius, Jansson & Fischer, 2000). To account for a gradient in extinction rate associated with latitude and better highlight the locations of biodiversity hotspots, we created filters assuming that survival decreases linearly (or with a Gaussian shape see Supporting Information, Figs S5, S7 for results) either with latitude with an X -intercept at 0 and a Y -intercept corresponding to the maximum number in the potential for allopatric speciation. We computed the difference between the maps of the potential for allopatric speciation and the potential filtering effect of extinction to further refine the locations of biodiversity hotspots.

ADDITIONAL ENVIRONMENTAL VARIABLES

To evaluate whether plate tectonics provide independent information compared to other influential environmental factors, we assembled maps of extant productivity, topographical heterogeneity and climate change velocity during the glaciations of the Quaternary. For the

terrestrial environment, we considered annual net primary productivity ($g\ C/m^2/year$) as computed by Imhoff & Bounoua (2006), elevation heterogeneity computed as in Descombes *et al.* (2017) and climate change velocity during the Quaternary (Sandel *et al.*, 2011). Climate velocity is an indicator of the distance that species had to move each year to track suitable conditions during the Quaternary climate fluctuations. For the marine environment, we considered primary productivity (<http://gmed.auckland.ac.nz/data.html>), bathymetric heterogeneity computed as in Descombes *et al.* (2017) and Quaternary climate change velocity. Velocity of climate change during the glaciations was computed from reconstructed temperature at the last glacial maximum (LGM) from the MARSPEC layers (Sbrocco & Barber, 2013). We computed past climate change velocity by comparing current and past sea surface temperature at the LGM, calculated as the distance between a cell and the closest cell with the same temperature (rounded in °C) during the LGM.

SPATIAL CONGRUENCE ANALYSIS

We tested whether there is a significant spatial congruence between the regions of endemism predicted by the model and the observed endemic richness. For each comparison between observed and predicted maps, we evaluated the spatial match between the cells with the highest endemic richness and those with the highest expected value predicted by the model. To assess whether the observed number of overlapping cells is significantly different from that obtained by chance, we used a randomization procedure as in Mouillot *et al.* (2011). We randomly redistributed the value of expected diversity 999 times within the grid and counted the number of overlapping cells for each. We computed the *P*-values by counting the number of times for which the match of the randomized data with the observed endemic richness was as good as or better than that of the prediction from the model. We tested the sensitivity of this analysis to the selection of the threshold by successively using 2.5, 5, 7.5, 10, 12.5 and 15% thresholds to classify what was regarded as the highest values of richness.

SPATIAL AUTOREGRESSIVE MODEL

We related endemic richness to the variable derived from plate tectonics together with Quaternary climate change velocity, topographical heterogeneity and contemporary productivity, using a spatial autoregressive (SAR) model (Kissling & Carl, 2008). To provide conservative results and since the effect of glaciation is accounted for by the variable of climatic velocity, we used the variable from plate tectonics without the extinction filter. For each taxonomic group, we used the variable of speciation potential due to plate tectonics with the dispersal distance parameter that yielded the highest spatial congruence with levels of endemism in the analysis described above. The SAR model incorporates a spatially dependent error term to adjust for spatial autocorrelation. We used a spatial weight matrix with neighbourhoods defined as all cells within 200 km of the focal cell. Variables were standardized to allow direct comparison of their respective slopes in the SAR models.

RESULTS

CONGRUENCE ANALYSIS

Our model simulating a mechanism of speciation associated with plate tectonics pinpoints several regions with high potential for speciation, namely Meso-America, the circum-Mediterranean basin, Madagascar and the Sundaland region of South East Asia (Fig. 2). Two additional regions at higher latitude

in the archipelago of Northern Canada and between Patagonia and Antarctica are also apparent, but their general influence is attenuated once the extinction is considered (Supporting Information, Figs S11, S12). Terrestrial regions that have undergone significant tectonic deformation potentially generating species across straits showed a significant match with the hotspots of endemic richness, with 29% of common grid cells (47% when accounting for extinction) for land organisms and 27% (25% with the extinction filter) for terrestrial freshwater organisms (Table 1). Among the multiple clades investigated, the congruence was the highest for freshwater vascular plants with 40% (46% with the extinction filter, Supporting Information, Tables S1, S2) mainly due to their more pronounced match in the Mediterranean area. Applied to the marine realm, the model showed broader areas with high expected diversity, including the Indo-Australian archipelago, the region of Madagascar, the circum-Mediterranean Sea and the Southern Atlantic. In contrast to terrestrial clades, the congruence of the expectations of the model and the regions of high endemic richness was low, with only 12% of matching cells (25% with extinction). The highest level of congruence was found for sea cucumbers with 18% of overlap (33% with extinction). Results with different thresholds were very similar, so we only present those using a 10% threshold for the definition of hotspots in the main manuscript (see Supporting Information, Table S3 for results using other values). We found a strong correlation between endemic richness and phylogenetic endemism for mammals (Pearson's correlation = 0.88; Supporting Information, Fig. S10), suggesting that species endemism is spatially associated with the endemism of lineages. The sensitivity analysis using different starting dates to generate the predictor of the effect of geomorphological dynamics provided similar distributions of expected diversity as the full simulation starting at 140 Mya (Supporting Information, Fig. S1).

SPATIAL AUTOREGRESSIVE MODEL

The relationship between endemic richness and geodynamics received strong support in the SAR models considering historical and contemporary variables for terrestrial (SAR model: slope = 0.105, $P < 0.001$; Table 2), marginal support for freshwater (SAR model: slope = 0.073, $P < 0.1$) and no support for marine (SAR model: slope = -0.001, $P > 0.1$) taxonomic groups. All the terrestrial taxonomic groups with the exception of birds showed a significant relationship with the proxy of plate tectonics, while only molluscs among freshwater groups and cone snails among marine groups showed a significant relationship once the other environmental factors were accounted for in the SAR

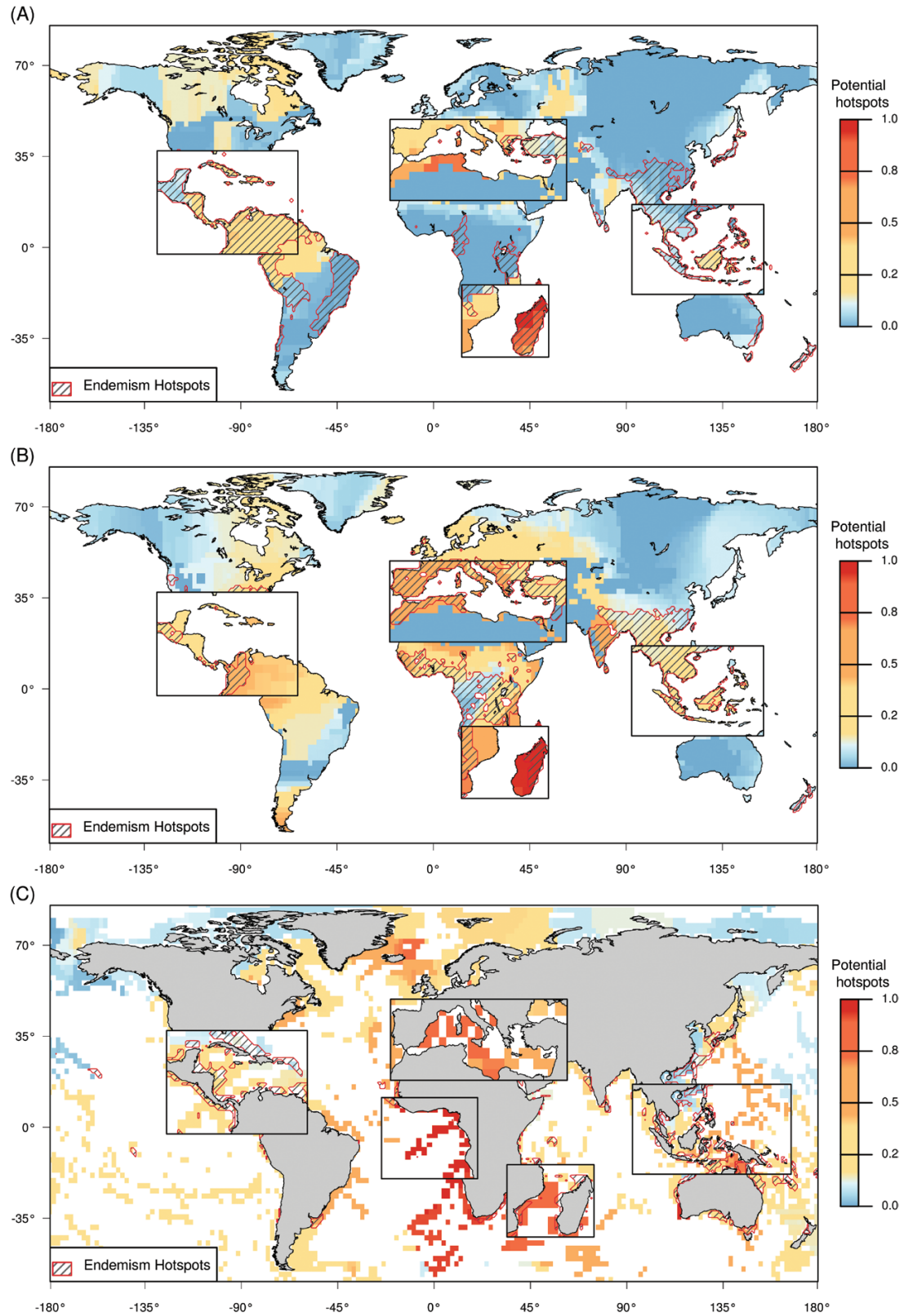


Figure 2. Map of the proxy of the potential for speciation associated with plate tectonics for the (A) terrestrial, (B) freshwater and (C) marine species ($d = 10$ for A and C; $d = 25$ for B). The most important areas that provided favourable circumstances

Table 1. Statistical tests of congruence between simulated and observed endemic richness hotspots for terrestrial, freshwater and marine species

	<i>d</i>	Number of common cells	Expected overlap	<i>P</i> -value	Percent of common hotspots
Total terrestrial	10	435	154.47	0.001	28.79
Amphibians	30	395	151.27	0.001	26.14
Mammals	30	349	151.27	0.001	23.10
Reptiles	20	385	151.27	0.001	25.48
Plants	30	438	152.37	0.001	28.99
Birds	10	449	154.47	0.001	29.72
Total freshwater	25	407	151.27	0.001	26.94
Crabs	30	440	151.57	0.001	29.12
Molluscs	20	571	151.27	0.001	37.79
Plants	25	606	151.27	0.001	40.11
Fishes	25	335	151.27	0.001	22.17
Total marine	10	117	101.26	0.042	11.65
Corals	15	132	100.56	0.001	13.15
Cone snails	15	128	100.86	0.002	12.75
Sea snakes	10	55	101.46	1	5.48
Sea cucumbers	25	181	100.66	0.001	18.03
Fishes	10	123	101.26	0.011	12.25

The endemic richness was calculated as the sum of the inverse range sizes of all species occurring in a given grid cell. Results are shown for the value of dispersal distance (*d*) in the simulation that resulted in the greatest congruence with observed endemism. The number of common cells indicates the number of overlapping cells among the 10% of the highest values of endemic richness and in the simulation. The expected overlap corresponds to the mean number of overlapping cells expected from the randomization of the simulated data 999 times.

models. In contrast, heterogeneity and primary productivity were associated with endemic richness for terrestrial, freshwater and marine taxonomic groups overall and for many individual groups (Table 2).

DISCUSSION

The current climate constrains the number of species that can survive at a given place, for instance through processes of environmental filtering along latitude (Sommer *et al.*, 2014). It is, however, not sufficient to explain the full regional variability of species diversity across the globe (Ricklefs, 2004; Ricklefs & He, 2016). In addition to ecological factors such as productivity (Waide *et al.*, 1999; Jetz *et al.*, 2012), biodiversity gradients can be related to historical events of speciation and extinction, the intensity of which varied across regions (Pellissier *et al.*, 2014; Svenning *et al.*, 2015). Interestingly, many regions recognized for their high diversity or degree of endemism, such as Mesoamerica, Madagascar or South East Asia, are situated in

proximity to continental plate margins, where previously joined continental crust was either rifted apart or is converging, providing clues to the role of plate tectonics in shaping biodiversity hotspots. Here, we provide evidence of congruence between a spatial proxy for the effect of plate tectonics on species diversification and global patterns of endemic richness for terrestrial clades. Our results suggest that, in agreement with many phylogeographical or palaeontological analyses, deep time historical factors should be considered to explain the current distribution of biodiversity.

CONGRUENCE BETWEEN PLATE TECTONICS AND ENDEMIC RICHNESS

The model, which quantifies the amount of potential dispersal into each cell from disconnected patches under plate tectonics, was congruent with the observed distribution of endemic richness of several clades and showed significant correlations independent of other relevant variables. The dynamics of continental separation and the formation of narrow, deep water oceanic basins

for speciation are highlighted by the enlarged insets. These correspond, for the terrestrial taxa, to the Mediterranean basin, Central America, Madagascar and South East Asia. The distributions of cells with the highest 10% of values of endemic richness are represented by hatched regions.

Table 2. Results of the statistical analyses of spatial autoregressive models for total terrestrial, marine and freshwater organisms and for each taxonomic group separately

Terrestrial			Marine			Freshwater		
Group	Variable	Estimate	Group	Variable	Estimate	Group	Variable	Estimate
Total terrestrial	NPP	0.334***	Total marine	NPP	0.224***	Total freshwater	NPP	0.060***
<i>d</i> = 10	Heter	0.074***	<i>d</i> = 10	Heter	0.042***	<i>d</i> = 25	Heter	0.028***
	Velocity	-0.077***		Velocity	0.006		Velocity	-0.020
	LBE	0.105***		LBE	-0.001		LBE	0.073(*)
Amphibians	NPP	0.166***	Corals	NPP	0.0184(*)	Crabs	NPP	0.067***
<i>d</i> = 30	Heter	0.166***	<i>d</i> = 15	Heter	0.003	<i>d</i> = 30	Heter	0.039***
	Velocity	-0.04*		Velocity	-0.035**		Velocity	-0.021
	LBE	0.10***		LBE	0.020		LBE	0.037
Mammals	NPP	0.25***	Cone snails	NPP	0.052***	Molluscs	NPP	0.060***
<i>d</i> = 30	Heter	0.124***	<i>d</i> = 15	Heter	0.051***	<i>d</i> = 20	Heter	0.012
	Velocity	-0.07***		Velocity	0.024		Velocity	-0.039*
	LBE	0.118***		LBE	0.036*		LBE	0.081***
Reptiles	NPP	0.137***	Sea snakes	NPP	0.102***	Plants	NPP	0.021**
<i>d</i> = 20	Heter	0.114***	<i>d</i> = 10	Heter	-0.008	<i>d</i> = 25	Heter	0.008*
	Velocity	-0.045**		Velocity	-0.116***		Velocity	0.004
	LBE	0.212***		LBE	-0.0001		LBE	0.05
Plants	NPP	0.306***	Sea cucumbers	NPP	0.050***	Fishes	NPP	0.011
<i>d</i> = 30	Heter	0.059***	<i>d</i> = 25	Heter	0.010(*)	<i>d</i> = 25	Heter	0.03***
	Velocity	-0.070***		Velocity	0.020		Velocity	-0.009
	LBE	0.086***		LBE	0.037		LBE	0.001
Birds	NPP	0.146***	Fishes	NPP	0.0115			
<i>d</i> = 10	Heter	0.108***	<i>d</i> = 10	Heter	0.030***			
	Velocity	-0.027*		Velocity	-0.009			
	LBE	0.018		LBE	0.001			

The slopes of the relationship between endemic richness and each variable are shown. Values for *d* are those selected according to the statistical tests of congruence between simulated and observed endemic richness hotspots (see Table 1). NPP, net primary productivity; Heter, topographical heterogeneity; velocity, climate change velocity.
 (*)*P* < 0.1, **P* < 0.05, ***P* < 0.01, ****P* < 0.001.

probably permitted rare events of dispersal followed by allopatric speciation (Xiang & Soltis, 2001; Lavergne *et al.*, 2013) and corroborates the idea that plate tectonic processes over time and space shaped regions of exceptional endemic richness (Gillespie & Roderick, 2014; Couvreur, 2015). For instance, phylogeographical inferences suggest that dispersal from eastern Asia to insular areas in South East Asia coincides with the timing of major tectonic activity and the collision between the Sunda and Sahul shelves, which caused continental fragments to be rearranged throughout the region (Bacon *et al.*, 2013). When populations are established after dispersal across oceanic gateways, isolation prompts the emergence of disparate gene pools, which

ultimately leads to speciation (Ali & Aitchison, 2014). The model highlighted some of the regions of the globe with the highest levels of endemic richness, including the Mediterranean basin, Mesoamerica, Madagascar and South East Asia (Fig. 2). In agreement with our model, evidence suggests that periodic dispersal events between land masses triggered species diversification, with known examples being those between the North, Central and South American plates (Bagley & Johnson, 2014), across the Iberian, Adriatic and African tectonic plates in the Mediterranean basin (Lavergne *et al.*, 2013) or in the Indo-Australian archipelago (Warren *et al.*, 2010). Similarly, the early separation of Madagascar followed by asymmetrical exchanges with the coast of

Africa probably enhanced speciation and promoted a high level of endemism on the island (Ali & Huber, 2010). Moreover, a palaeostrait at Cape Horn putatively shaped high diversity in the South America–Antarctic Peninsula region, which has revealed an exceptional fossil plant diversity in the Eocene (Wilf *et al.*, 2005).

Overall, the model showed a good match with observations for the land, but a lower match for the marine realm (Table 1). We hypothesize that deep water oceanic gateways between shallow shelf areas are probably much more permeable for marine organisms than are shallow epicontinental sea straits for terrestrial taxa (Palumbi, 1994). The separation of shallower reefs by areas of deep water is not necessarily associated with speciation since larvae of marine species can disperse over large distances (Luiz *et al.*, 2013), which would explain the discrepancy between the model and observations (Fig. 1). As further evidence of variation in speciation mechanisms among ecosystems, the model pinpointed different values of d for the marine compared to the terrestrial ecosystem and only showed significant effects in the SAR models for terrestrial taxa. Our results support the idea that the marine realm is more permeable to the movement of organisms (Palumbi, 1994). We also found differences among the terrestrial taxa in both the dispersal values and the slope of the relationship with geomorphological dynamics in the SAR model. For instance, birds, which have higher dispersal abilities than other vertebrate groups, showed values of endemic richness that were not related to plate tectonics when other variables were considered, paralleling differential taxonomic responses to the glaciations of the Quaternary (Sandel *et al.*, 2011).

Because phylogenies were not available for most of the taxonomic groups considered, we investigated endemic richness instead of phylogenetic endemism (Rosauer *et al.*, 2009). However, the extant species analysed are younger than many of the geological events considered in the plate tectonic model. Nevertheless, as lineages accumulate in specific regions, so does species number, generating a spatial congruence between endemic richness and phylogenetic endemism (Supporting Information, Fig. S6). While we only compared endemic richness to phylogenetic endemism in mammals, we expect that the congruence between these metrics is general. Hence, the dynamics of plate tectonics that occurred more than a few million years ago may have catalysed allopatric speciation of the hypothetical ancestors of the species that we can recognize nowadays, but this too increased the eventual number of species in the region. Future comparisons of spatial diversification models with empirical data should directly compare genealogies inferred from models to the structure of phylogenies of clades (Descombes *et al.*, 2017).

UNEXPLAINED VARIATION AND LIMITATIONS OF THE STUDY

Most of the species for which the distribution was modelled have evolved relatively recently and other factors (e.g. Quaternary climate, availability of habitats and habitat types) have contributed to their current distributional patterns. The congruence between the geodynamics and endemic richness ranged from 20 up to 46%, indicating considerable unexplained variation. The SAR models showed a significant effect of productivity and heterogeneity in most of the investigated taxonomic groups, while the effect of the velocity of Quaternary climate change was especially pronounced for terrestrial taxa. Hence, despite an association with geodynamics, other historical and contemporary factors are likely to have shaped the distribution of endemism (Sandel *et al.*, 2011). The SAR models also indicated a consistent relationship between topographical heterogeneity and endemic richness. One of the main drawbacks of the current approach is that it does not integrate orogeny, thus failing to consider how mountain-building contributes to speciation. Improving the details of tectonic and palaeoelevation reconstructions will allow a better quantification of how plate tectonics shaped the extant spatial gradients of biodiversity. Our model has further limitations linked to the coarseness of the continental reconstructions used in our analyses. For example, the potential for allopatric speciation is likely to be underestimated in South East Asia because the patchiness of small islands is not well represented in our global model. In addition, the continental plate reconstruction only includes the formation of large islands caused by massive hot spot volcanism (e.g. Kerguelen, Ontong–Java) but not smaller volcanic islands or island arc chains due to subduction processes, which are also expected to have promoted exceptional biodiversity hotspots. Finally, islands also provide stepping stones that allow colonization or gene flow among areas (Harbaugh *et al.*, 2009) and influence the regional potential for speciation. Islands are extremely difficult to model and future palaeogeographic reconstructions should integrate them with greater accuracy. Improvement in the reconstruction of past habitats should provide better constraints for dynamic biodiversity models.

TOWARDS BETTER PALAEOENVIRONMENTAL RECONSTRUCTIONS

In recent years, significant progress has been made in reconstructing the bathymetric evolution of ocean basins over the past 230 Myr (Müller *et al.*, 2008, 2016), along with advances in assimilating global data sets on the distribution of palaeoshorelines (Heine *et al.*, 2015). These palaeobathymetric reconstructions

have been used to model the diversification of marine organisms (Leprieur *et al.*, 2016). For terrestrial life, one of the key boundary conditions is the availability of robust palaeoelevation models in regularly spaced intervals. While such models have been assembled for proprietary studies in industry-research consortiums, for instance to reconstruct elevation-dependant temperatures (Lunt *et al.*, 2016) and thus constrain vegetation models (Sepulchre *et al.*, 2006), they are currently not freely available for academic research. Furthermore, reconstructions of palaeotopography are inherently biased by the fact that sedimentary basins record the subsidence of the Earth's crust in relatively great detail, while erosion destroys significant information on the temporal dynamics in the extent and height of mountain ranges. The availability of global and regional crustal-scale data sets (e.g. Pasyanos *et al.*, 2014), along with improved computational tools, creates potential avenues to construct palaeoelevation models. These can be further augmented with more detailed regional estimates of palaeoelevation in existing databases including thermochronology (e.g. Barnes *et al.*, 2012) and isotopes studies (e.g. Campani *et al.*, 2012). Effort should be invested in such open access reconstruction to produce a benchmark data set to model terrestrial biodiversity dynamics.

CONCLUSIONS

The goal of the present analysis is to encourage research that bridges palaeobiology with macroecology using palaeogeographies. Accounting for deep time geomorphological events in spatial models of extant biodiversity is not straightforward, and even if our study proposes a first illustrative approach, it should motivate further development. A new generation of biodiversity models could explicitly model species diversification from the spatio-temporal sequence of environmental conditions (Gotelli *et al.*, 2009). Based on reconstructed palaeohabitats, spatial diversification models may track the distribution of lineages in grid cells, as well as their genealogy, which can be compared with multiple sources of empirical evidence, including biodiversity metrics. Leprieur *et al.* (2016) showed the interest of such an approach to understand tropical marine diversification, which can be compared to current patterns and the fossil records. To this aim, more effort should be invested in producing openly accessible palaeoenvironmental maps that can be coupled with mechanistic models to understand the spatial dynamics of species diversification. As stated by Myers & Giller (1988), 'To progress, biogeography must attempt to integrate divergent interests and determine how speciation, adaptation and ecological processes interact with one another and with

geology and climate to produce distributional patterns of the world's biota'. We now have the tools to realize this research agenda and quantify the role of historical habitat dynamics within a fully spatial framework. Acknowledging the limitations of the present model, we stress the need for further research into the influence of past habitat dynamics associated with plate tectonics on the spatial distribution of current biodiversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

Figure S1. Maps of the terrestrial areas predicted by the model under an allopatric speciation hypothesis and dispersal across sea straits, for different values of the dispersal distance parameter.

Figure S2. Maps of the terrestrial areas favourable for allopatric speciation predicted by the model for several values of the dispersal distance parameter and incorporating extinction, as a linearly decreasing function from the pole to the equator.

Figures S3. Maps of the coastal marine areas favourable for allopatric speciation predicted by the model for several values of the dispersal distance parameter.

Figures S4. Maps of the coastal marine areas favourable for allopatric speciation predicted by the model for several values of the dispersal distance parameter and incorporation extinction, as a linearly decreasing function from the pole to the equator.

Figure S5. Map of the potential hotspots for allopatric speciation across sea straits for the terrestrial (A) and freshwater species (B) and across reef separated by deep water for marine species (C).

Figure S6. Map of the potential hotspots for allopatric speciation across sea straits for the terrestrial (A) and freshwater species (B) and across reefs separated by deep water for marine species (C), with extinction incorporated as a decreasing Gaussian function from the pole to the equator.

Figure S7. Map of the terrestrial endemic richness calculated as the sum of the inverse range size of all species occurring in a given cell for terrestrial groups.

Figure S8. Map of the freshwater endemic richness calculated as the sum of the inverse range size of all species occurring in a given cell for freshwater groups.

Figure S9. Map of the marine endemic richness calculated as the sum of the inverse range size of all species occurring in a given cell for marine groups.

Figure S10. Map of endemic richness compared to the map of phylogenetic endemism for mammals.