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Linking species diversification to palaeo-environmental changes: A process-based modelling approach

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Abstract

Aim: The importance of quantifying the contribution of historical processes in shaping current biodiversity patterns is now recognized, but quantitative approaches that explicitly link speciation, extinction and dispersal processes to palaeo-environmental changes are currently lacking. Here, we propose a spatial diversification model of lineages through time (SPLIT) based on the reconstruction of palaeo-environments. We illustrate our approach using mangroves as a case study and evaluate whether habitat changes caused by plate tectonics explain the current biodiversity patterns of this group.

Innovations: The SPLIT model allows one to simulate the evolutionary dynamics of species ranges by spatially linking speciation, extinction and dispersal processes to habitat changes over geological time periods. The SPLIT model provides a mechanistic expectation of speciation and extinction assuming that species are ecologically identical and not interacting. The likelihood of speciation and extinction is equivalent across species and depends on two dispersal parameters interacting with habitat dynamics (d a maximum dispersal distance and ds a distance threshold beyond which gene flow is absent). Beyond classical correlative approaches, this model tracks biodiversity dynamics under palaeo-environmental changes and provides multiple expectations (i.e., α-, β-diversity, phylogenies) that can be compared to empirical patterns.

Main conclusions: The SPLIT model allows a better understanding of the origin of biodiversity by explicitly accounting for habitat changes over geological times. The simulations applied to the mangrove case study reproduced the observed longitudinal gradient in species richness, the empirical pattern of β-diversity and also provided inference on diversification rates. Future developments may include niche evolution and species interactions to evaluate the importance of non-neutral mechanisms. The method is fully implemented in the InsideDNA platform for bioinformatics analyses, and all modelling results can be accessed via interactive web links.

KEYWORDS
biodiversity dynamics, diversification, fossils, global simulation models, mangrove, marine ecosystems, palaeo-environments

1 | INTRODUCTION

Understanding how historical processes shaped large-scale biodiversity gradients is a long-standing issue in the fields of evolution, ecology and biogeography (Pyron, 20142014; Rolland, Condamine, Jiguet, & Morlon, 2014; Weir & Schluter, 2007). Investigations of the emergence of biodiversity associated with historical events have been addressed using a variety of approaches. Spatial statistical studies have highlighted the importance of proxies of past environmental changes in explaining present-day biodiversity gradients, but the processes of speciation and extinction are not modelled (e.g., Descombes et al., 2017; Pellissier et al.,

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2014; Sandel et al., 2011; Svenning et al., 2015). In parallel, rates of diversification have been associated with regional differences in palaeo-environmental conditions based on phylogenies and have highlighted how ancient Earth processes led to extant biodiversity (e.g., Condamine, Sperling, Wahlberg, Rasplus, & Kergoat, 2012; Near et al., 2012). Diversification analyses (e.g., Morlon et al., 2016) are generally not spatially explicit but summarize the dynamics of habitat configuration into a single temporal proxy (e.g., Zaffos, Finnegan, & Peters, 2017). The paucity of the fossil records and limited information on the palaeo-environments have limited the development of models integrating both spatial information and clade diversification. The latest palaeo-environmental reconstructions (e.g., Lunt et al., 2016; Müller, Sdrolias, Gaina, Steinberger, & Heine, 2008) allow the development of models linking diversification processes to species habitat changes within a spatial context to reach a mechanistic understanding of the role of historical processes in extant biodiversity (Jordan, Barraclough, & Rosindell, 2016).

The use of statistical techniques for exploring biogeographical data sets does not provide a mechanistic understanding of how historical processes have shaped current species richness, because speciation, extinction and dispersal processes are not modelled explicitly (Gotelli et al., 2009). The application of process-based models should provide a better mechanistic understanding than traditional correlative approaches (Brayard, Escarguel, & Bucher, 2005; Cabral, Valente, & Hartig, 2017; Gotelli et al., 2009; Hubert, Calcagno, Etienne, & Mouquet, 2015; Rangel, Diniz-Filho, & Colwell, 2007), which relate a specific metric to a set of environmental or static historical predictors (Descombes et al., 2017; Pellissier et al., 2014; Sandel et al., 20112011). Process-based models would typically highlight at which location and in response to which environmental changes specific events of speciation, extinction and dispersal are occurring. Spatially explicit models of species diversification inferring large-scale biodiversity patterns have recently emerged (Hellweger, van Sebille, & Fredrick, 2014; Jordan et al., 2016; Muneepeerakul et al., 2008). Process-based models integrate different levels of complexity, where either the species, the gene or the individual are the modelled unit (Melian et al., 2014; Rosindell & Phillimore, 2011). The choice of the unit depends on the hypothesis tested or the temporal scale considered when understanding intraspecific genetic structure (Yannic et al., 2013) or the diversification of entire clades (Leprieur et al., 2016). However, the common denominator of this type of model is that the probability of speciation through gene flow is modulated by the configuration of the defined landscape (Muneepeerakul et al., 2008).

Gotelli et al. (2009) proposed a species-based modelling framework that consists of tracking the presence and absence of a given species in space and time by explicitly modelling speciation and extinction processes. To capture the diversification of a clade, a general simulation model (GSM), as defined by Gotelli et al. (2009), should reach far enough back in geological times and there should be a spatio-temporal matrix of habitat distribution that defines connectivity among occupied cells (Wiens, 2015). As habitat mapping over longer time periods is generally unavailable, most examples of species diversification models consider a static habitat landscape (e.g., Hellweger et al., 2014; Muneepeerakul et al., 2008). However, landscapes are dynamic at the

time-scale of speciation, and considering a static landscape limits the inferences that can be drawn from those models (Gotelli et al., 2009). Recent efforts in palaeo-environmental reconstructions (Lunt et al., 2016; Müller et al., 2008) coupled with spatially explicit diversification models should provide a mechanistic link between the dynamic distribution of habitats through time and the speciation, extinction and dispersal of lineages (Leprieur et al., 2016; Rosindell, Cornell, Hubbell, & Etienne, 2010).

Here, we present in detail the spatial diversification model of lineages through time (SPLIT). The SPLIT model generates patterns of biodiversity dynamics under processes of allopatric speciation, extinction and dispersal in interaction with a temporally dynamic landscape (e.g., as a consequence of plate tectonics). The model provides inferences on species range dynamics, species diversity together with the expected rates of speciation and extinction through time. We first present the methodology underlying the SPLIT model. We then apply this approach to better understand the emergence of biodiversity in mangroves as a case study. We also discuss the advantages and limitations of this model in comparison to other spatial approaches of species diversification. We finally present the future development of spatial diversification models beyond neutrality.

Our case study focuses on mangrove forests, which have the particularity, together with other marine-associated clades, of expressing a particular longitudinal biodiversity pattern peaking in Southeast Asia (Ellison, Farnsworth, & Merkt, 1999; Harzhauser et al., 2007; Polidoro et al., 2010; Renema et al., 2008). Mangrove forests are composed of c. 70 species showing adaptations to saline habitats (Duke, Ball, & Ellison, 1998; Polidoro et al., 2010), and they occupy marine tropical coasts along low-depth sheltered shorelines worldwide (Chapman, 1976; Spalding, Blasco, & Field, 1997). Duke (1995) suggested that mangrove species, and their habitat, evolved and diversified because of the breakup of Gondwanaland. Mangrove biodiversity was supposed to be closely related to plate tectonics (Renema et al., 2008), but other hypotheses have been suggested, such as a higher diversification rate in the central Indo-Pacific region (centre of origin; Briggs, 1999; Ricklefs, Schwarzbach, & Renner, 2006). By combining reconstructions of palaeo-coastlines, palaeo-bathymetry and tropical latitude since the Cretaceous, we show how the SPLIT model allows the tracking of mangrove diversification and dispersal through time.

2 | METHODS

2.1 | Spatial diversification model of lineages through time (SPLIT)

Following the conceptual approach of Gotelli et al. (2009), we present the SPLIT model (Figure 1 and Supporting Information Appendix S1), which records, at any single point in space (habitat grid cell), the distribution of each species as well as genealogies (Leprieur et al., 2016). In contrast to spatial diversification models at the level of individuals (e.g., Jordan et al., 2016; Muneepeerakul et al., 2008), the modelling unit of SPLIT is the range of a species, which is defined as a grid of either presence (1) or absence (0) of the species in a habitat
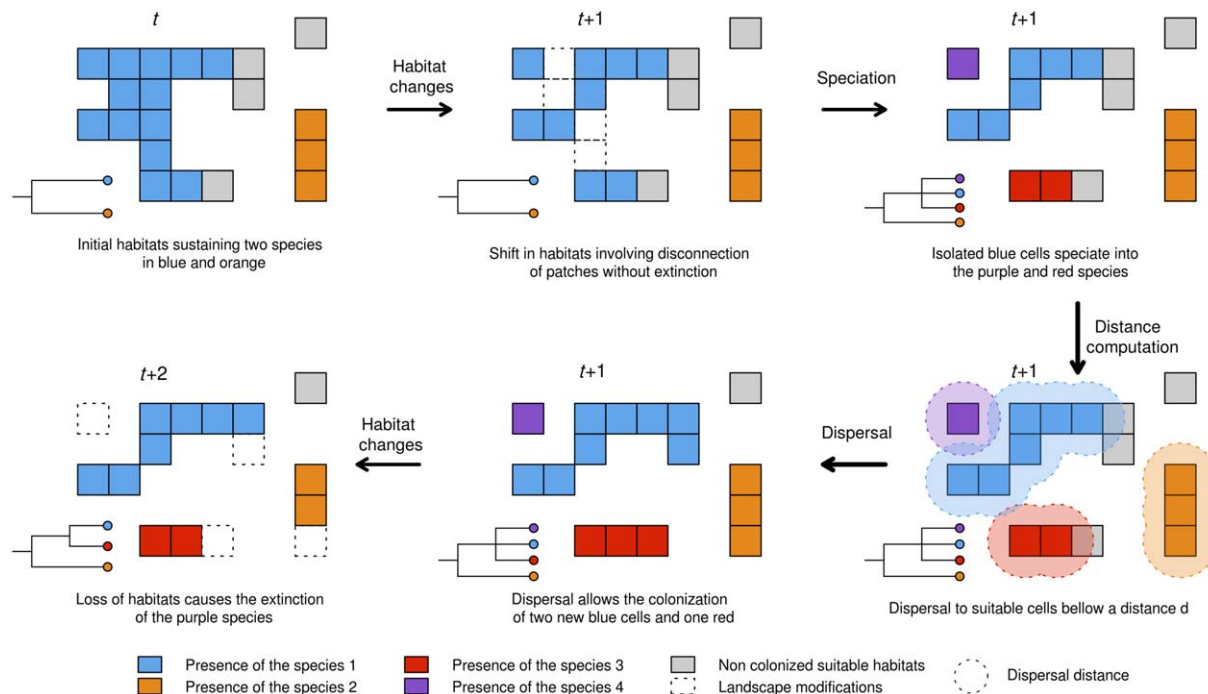
FIGURE 1 Description of the speciation, dispersal and extinction processes implemented in the spatial diversification model of lineages through time (SPLIT). The simulation starts (t) with the initialization of the landscape; here the initial habitats can sustain two species (blue and orange). At $t + 1$, some shifts in the habitats can involve disconnection and isolation of patches from the initial species distribution (the blue species in this example). Then, based on the previous configuration of habitats and on a clustering analysis controlled by a threshold distance of speciation (ds), we can determine whether the isolation between the two patches causes speciation. In our example, the species 3 and 4 (red and purple, respectively) appear as the result of a habitat loss and a consecutive isolation from species 1 (blue). The second phase of SPLIT is the dispersal phase. The maximum distance of dispersion is randomly chosen according to a Weibull distribution and the dispersion parameter of the model (d) controls the scale of the Weibull distribution. Here, the species 1 (blue) can colonize two suitable cells of habitat and the species 3 one cell, while species 2 and 4, which have no suitable available habitats, cannot colonize. Finally, the extinction occurs, based on the future suitable habitats. In this example, the species 4 will not have suitable habitats at the following time step ($t + 2$), so it will disappear from the landscape. The model records the genealogy of speciating species, hence producing a global phylogeny at the end of the simulation. Observed changes in species richness through time can be compared to empirical data based on fossils. Current biodiversity patterns can also be compared to those simulated by the SPLIT model. In addition, more complex simulated patterns can be computed, such as phylogenetic α- and β-diversity, as well as diversification rates, which can be compared to observations

grid. As in species distribution models (SDMs; Guisan & Zimmermann, 2000), the SPLIT modelled unit is a species constrained by defined environmental conditions within a particular habitat. Contrary to SDMs, all species in a simulation occupy the same habitat, and a lineage can speciate into two incipient sister lineages because of the fragmentation of occupied ranges. The major advantage of modelling species ranges instead of individuals is a large gain in processing time: a simulation over 100 time steps and maps of 65,341 cells typically takes a few hours. Computational speed is also the result of the simple model architecture. Like Hubbell's unified neutral theory of biodiversity and biogeography (Hubbell, 2001), within one simulation, all species have the same dispersal abilities and habitat preferences and they do not interact with each other. In contrast to the neutral theory, dispersal can be partially stochastic, while speciation and extinction are deterministic and depend on the spatial habitat configurations. Together, the SPLIT model provides a simple mechanistic expectation linking habitat dynamics to speciation and extinction via dispersal.

2.2 | The mechanisms of the SPLIT model

The model is run over a set of environmental maps defining the cells that are suitable or unsuitable for the species and those that can be crossed (or not) through dispersal. A simulation starts at the oldest selected time period with a fixed set of parameters (d and ds) and tracks the species dynamic forward. The parameter ds represents a distance threshold beyond which gene flow is absent, thus leading to speciation, and d represents a parameter of dispersal performance. The geographical range of the ancestral species at the oldest selected time step can be chosen according to the fossil record and/or phylogenetic dating. If unknown, it can be drawn randomly, which would require a sensitivity test of the position of the ancestral range on the simulation outputs. The model can also accommodate different starting dates and ancestral areas of a given lineage defined by a box bound by the geographical coordinates. For example, for younger clades, for example, those arising in the Miocene, it is more appropriate to start the simulation in a subregion such as the Indo-Australian Archipelago (IAA). Three

main mechanisms, speciation, dispersal and extinction, characterize the model (see Figure 1 and Supporting Information Appendix S1) and occur within each time step.

2.2.1 | Speciation

At each time step, parapatric/allopatric speciation arises for all species, whose range is split into at least two distinct areas separated by a distance ds (i.e. a distance threshold leading to speciation). Speciation was modelled as a cluster split using a cluster optimization algorithm based on the 'dbscan' function in the fpc library available in R (R Development Core Team, www.R-project.org). If the range of a lineage i is fragmented into n patches separated by a given distance threshold of ds, the lineage will separate into n incipient lineages with smaller ranges (Figure 1 and Supporting Information Appendix S1). Depending on a defined landscape matrix, the underlying mechanism of speciation is parapatric and/or allopatric, arising following the species isolation due to unsuitable habitat that drives genetic divergence over time, or parapatric, when speciation results from a limitation of gene flow due to dispersal. The model assumes that a lineage previously occupying a continuous distribution but then split into several discontinuous patches will fully speciate after one time period with no possibility of hybridization or introgression. This represents a simplification compared to more complex individual-based models that consider more detailed genetic mechanisms (e.g., Currat et al., 2016). We expect the SPLIT model to provide a suitable approximation over geological time periods.

2.2.2 | Dispersal

At each time step, all species disperse according to an identical dispersal parameter. Species in time step t are allowed to disperse to all habitat cells at time step $t + 1$ that are distant by a value lower than d. The value of d can either be a fixed dispersal distance connecting the surrounding cells and determined for each time step or the shape parameter of the dispersal kernel currently implemented as a Weibull distribution accounting for a degree of variability in effective dispersal. The Weibull distribution reproduces a shape of dispersal kernel characterized by more frequent short than long dispersal events matching empirical observations (Greene, Canham, Coates, & LePage, 2004; Uriarte, Canham, Thompson, Zimmerman, & Brokaw, 2005). This fixed parameter for the entire modelled clade is an approximation of a more complex variability of dispersal that might evolve across lineages (Larson-Johnson, 2016), but it should provide a general approximation of clade dispersal across geological time periods.

2.2.3 | Extinction

The extinction phase is a direct consequence of the dispersal phase. Indeed, if all the habitat cells inhabited by the species at time t disappear at time $t + 1$ and no other habitat cells at a dispersal distance lower than the dispersal threshold d appear at time $t + 1$, the species will become extinct (see Figure 1 and Supporting Information Appendix S1). Therefore, the model provides spatially explicit expectations on habitat-driven extinction rates.

2.3 | Evaluation of the model and parameter estimation

The SPLIT model can make inferences about assemblage properties (α-, β-diversity) through time and also about species diversification as the phylogenetic relationships between species are reconstructed during each simulation. Consequently, simulations can be compared to current species richness patterns as well as turnover in species composition between cells, reconstructed patterns of species diversity from the fossil record (Leprieur et al., 2016), diversification rates computed from fossils or phylogenies (Morlon, 2014; Silvestro, Schnitzler, Liow, Antonelli, & Salamin, 2014) and the general shape of phylogenies (Lewitus et al., 2016). Simulated and observed species diversity gradients can be compared using the mean square errors as recommended in Gotelli et al. (2009). Alternatively, a correlation between observed and predicted values can be used when the mimicking of the ranking of cells is more relevant to the research question than the absolute richness within each cell. When the simulations are compared to multiple empirical properties, the simulations are first ranked according to the performance of each of the evaluated properties, and the average ranking allows highlighting the best performing parameter set d and ds considering multiple criteria.

2.4 | Required data and applicability

The SPLIT model requires palaeo-environmental reconstructions allowing the mapping of suitable and unsuitable habitats for a given clade through time and over long time periods. The model therefore relies on habitat reconstructions of the palaeo-environment, such as palaeo-elevation or palaeo-bathymetry (Müller et al., 2008), coupled with information on palaeo-coastlines (Heine, Yeo, & Müller, 2015) or palaeo-climatic reconstructions (Lunt et al., 2016). The model is therefore applicable to any group showing a tendency for niche conservatism over time, such as the preference for tropical reefs in marine organisms (Leprieur et al., 2016).

2.5 | A case study with mangroves

We employed a plate reconstruction using an absolute plate motion model based on marine magnetic anomalies and fracture zone tracks in the crust of today's ocean basins (Müller et al., 2008). We generated synthetic palaeo-bathymetry models with 1° resolution for the past 140 Myr in 1-Myr time steps by combining oceanic palaeo-bathymetry grids derived from palaeo-oceanic crustal age grids with continental palaeo-geographical data (Leprieur et al., 2016). Since the Cretaceous, the climate has strongly fluctuated, and because many marine-dependent organisms are constrained by tropical water temperature, we reconstructed the palaeo-latitudes of the tropical ocean limits according to reef-forming coral fossil records from paleoDB (www.paleodb.org). We computed the 95th percentile of the palaeo-latitude at which corals were living to provide information on the latitudinal border of tropical oceans across time. By combining reconstructed shelfal areas with tropical limits, we generated one map per million years of tropical shallow marine habitats for the last 140 Myr.

In addition, we combined those maps with palaeo-coastlines (Heine et al., 2015) and obtained a tropical coastal habitat with a shallow sea floor suitable for mangrove establishment. We ran the SPLIT model using a Weibull distribution with a scale parameter equal to one.

To evaluate the ability of the SPLIT model to predict the current α- and β-diversity of mangroves, we computed a species assemblage matrix from the new mangrove distribution database published in Spalding, Kainuma, and Collins (2010) and available through the IUCN website (http://maps.iucnredlist.org) for 68 selected species (see list in Polidoro et al., 2010). Mangrove species are associated with tropical intertidal habitats (Polidoro et al., 2010; Tomlinson & Tomlinson, 1994). We compared observed biodiversity patterns to those expected by the SPLIT model for two of the most important mangrove clades, one mangrove lineage within the Rhizophoraceae family (18 species belonging to the *Rhizophora*, *Brugeria* and *Ceriops* genera) and another lineage within the Acanthaceae family (eight species belonging to the *Avicennia* genus).

Previous studies suggested a Tethyan origin for mangrove species (Duke, 1995; Ellison et al., 1999; Lo, Duke, & Sun, 2014). For Rhizophoraceae, we started with a unique ancestral species distributed along the continuous passive continent of the Tethys in mid-Cretaceous times (*c.* 100 Ma), corresponding to the oldest fossil pollen record for mangrove species belonging to this family (Duke, 1995). For *Avicennia*, we started a simulation at 60 Ma with a unique ancestral species distributed along the continuous passive continent of the Tethys in order to compare observed and simulated biodiversity patterns. This is supported by the fossil records dated at this period and distributed within this area (Duke, 1995; Ellison et al., 1999). To have a broad overview of the model outputs, we explored the full range of parameters of dispersal, d, and the speciation threshold, ds, as these values may depend on the taxa considered. We ran the simulation for a range of dispersal ($d \in \{1°:50°\}$) and speciation ($ds \in \{1°:50°\}$). Parameter values beyond these ranges are unrealistic, as they predict too many species (e.g., > 20,000, especially when the dispersal parameter is higher than the speciation distance parameter; see Supporting Information Appendix S2) or predict all species everywhere. Each parameter combination (d, ds) was run 10 times, given a small degree of stochastic component in the dispersal kernel.

We selected the best model (BM) predicting contemporary species richness of both lineages of mangrove, using the Pearson's correlation coefficient (r) between observed and predicted diversity values. We further evaluated the ability of the SPLIT model to reproduce the values of between-assemblage (β) diversity. We quantified the levels of the replacement of some species by others between assemblages. To quantify β-diversity, we used the turnover component (β_{jtu}) of the Jaccard dissimilarity index because this metric is independent of species richness differences (Baselga & Leprieur, 2015). We quantified the level of congruency between observed and predicted distance matrices using a simple Mantel test (r_m; 999 permutations). We ranked the performance of the model for predicting α and β and present the result for the best average ranking of the simulations.

We reconstructed past mangrove biodiversity hotspots for the mid-Eocene (50 Ma) by compiling mangrove fossil records from Ellison et al. (1999), paleoDB (www.paleodb.org) and the taxonomic list of Polidoro et al. (2010). We used fossil occurrences identified at the taxonomic genus level (i.e., 263 occurrences). Hence, this analysis is performed at coarse taxonomic resolution across all mangroves and assumes that all mangrove lineages reacted similarly to habitat changes during the last 100 Myr. For each $5° \times 5°$ cell, we summed the number of genera from the surrounding occurrences based on a $40° \times 40°$ moving window. To facilitate the comparison of the diversity maps and to highlight the diversity gradients we rescaled them between 0 and 1. We then compared the observed distribution of hotspots based on fossils at a 5° resolution to the simulated one for this specific time period.

3 | RESULTS

3.1 | Palaeoreconstruction of potential suitable habitats for mangrove species

We found that the spatial configuration of potential available suitable habitat for mangrove species inferred from coastal reconstruction, bathymetry and tropical palaeo-latitudes has shifted since the mid-Cretaceous and into the Quaternary period (see Supporting Information Appendix S3). Habitat was available at much higher latitudes in the Eocene (see Supporting Information Appendix S3), which is confirmed by the distribution of fossils observed in the Mediterranean region (see Supporting Information Appendix S4). In addition, the configuration of suitable habitats for mangrove was more complex and fragmented in the Tethys Sea of the Eocene (see Supporting Information Appendix S3).

3.2 | Spatial biodiversity gradients

The SPLIT model successfully reproduced the extant species richness gradient in mangroves (Figure 2). The best simulation for the lineage in the Rhizophoraceae ($d = 6$ and $ds = 35$) reproduced the longitudinal gradient in species richness (see Figure 2; Pearson correlation coefficient; $r = .41$, $p < .0001$) as with the best simulation ($d = 7$ and $ds = 15$) for *Avicennia* (Pearson correlation coefficient; $r = .43$, $p < .0001$). Furthermore, the best simulations provided realistic values of between-assemblage (β) diversity for both taxa (Mantel correlation; $r_m = .63$, $p < .0001$ for Rhizophoraceae and $r_m = .69$, $p < .0001$ for *Avicennia*). The agreement between observed and modelled β-diversity was mainly driven by a strong species turnover between the Atlantic and Indo-Pacific Oceans. The SPLIT model provided expected rates of speciation and extinction through time. The simulation best matching current biodiversity patterns showed a high diversification rate during the Eocene (Figure 3), underpinning the biodiversity hotspot in the central Tethys. A second diversification peak occurred in the Miocene, which matches the shaping of complex habitats in the Indo-Australian Archipelago (Figure 4 and Supporting Information Appendix S5).

3.3 | Comparison with the fossil records

Even though the modelled peak of biodiversity showed a close geographical proximity with the location of the diversity peak found in the
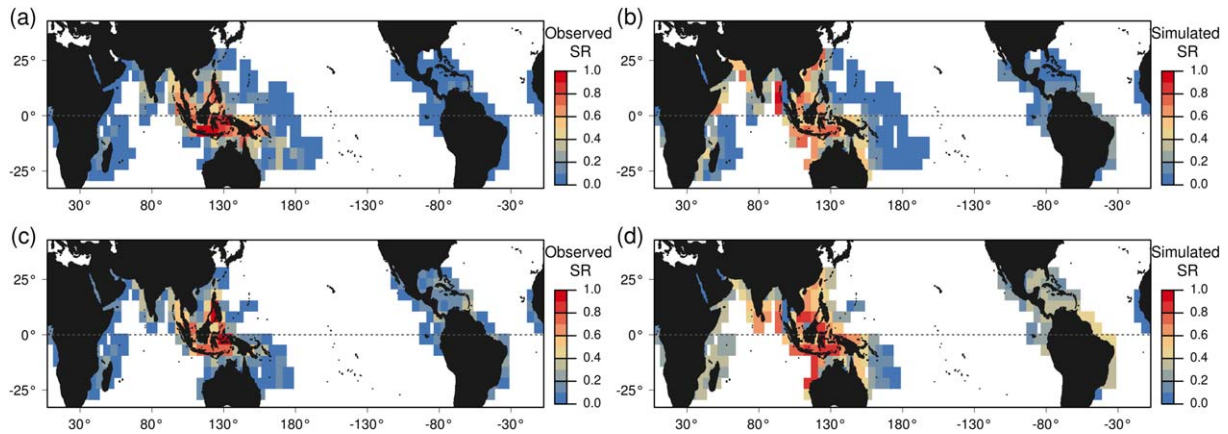
FIGURE 2 Observed species richness (SR) patterns for the Rhizophoraceae (a) and the *Avicennia* (c) mangrove lineages according to the database published in Spalding et al. (2010) and available through the IUCN website (http://maps.iucnredlist.org). Simulated species richness predicted by the spatial diversification model of lineages through time (SPLIT) according to the parapatric speciation model for the Rhizophoraceae ($d = 6$, $ds = 35$; b) and the *Avicennia* ($d = 7$, $ds = 15$; d) mangrove lineages. d = maximum dispersal distance; ds = distance threshold beyond which gene flow is absent

fossil records in the Mediterranean region, the best simulation for the Eocene (start of the simulation: 100 Ma, $d = 6$ and $ds = 35$) had a poor spatial fit to the reconstructed species richness from the fossil records for the period at 50 Ma ($r = .07$, Supporting Information Appendix S4). This low correlation is partly explained by the limited number of records of mangrove fossils in the eastern part of the Mediterranean region. The model reproduced the general pattern of a hopping hotspot of mangrove diversity from the central Tethys toward Southeast Asia (Figure 4 and Supporting Information Appendix S5), but did not strictly match species richness reconstructed from the fossil records.
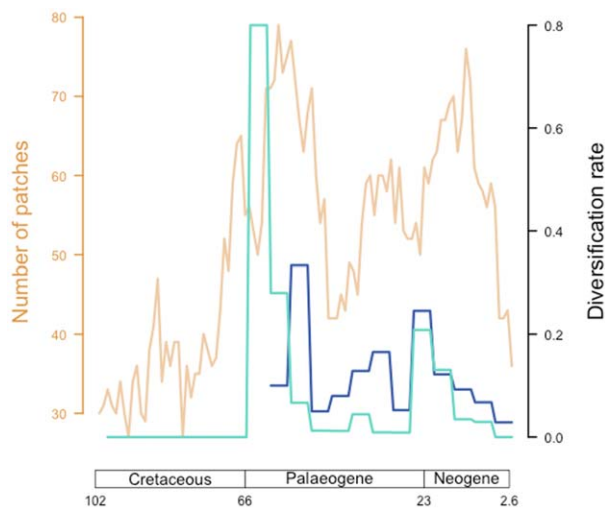

FIGURE 3 Number of mangrove habitat patches since the mid-Cretaceous and simulated diversification rate computed as speciation minus extinction through time inferred by the parapatric spatial diversification model of lineages through time (SPLIT) for the Rhizophoraceae ($d = 6$, $ds = 35$, turquoise blue) and *Avicennia* ($d = 7$, $ds = 15$, blue) lineages. According to the model, diversification was highest in the Eocene and in the Miocene. d = maximum dispersal distance; ds = distance threshold beyond which gene flow is absent

4 | DISCUSSION

Assessing the role of historical and evolutionary processes in generating biodiversity patterns is a longstanding issue in ecology and biogeography (Belmaker & Jetz, 2015; Ricklefs, 2004; Vázquez-Rivera & Currie, 2015). The development of process-based models should offer a new perspective on the multiple possible mechanisms shaping biodiversity gradients (Hubert et al., 2015; Melián et al., 2015). Here, we present a spatially explicit diversification model that allows the mapping of biodiversity patterns through geological time periods together with the production of expected speciation and extinction rates. In analogy with the unified neutral theory of biodiversity and biogeography (Hubbell, 2001), the SPLIT model considers species with identical dispersal abilities, habitat preferences and no ecological interactions. Overall, in the SPLIT model, the diversity accumulates as a direct consequence of the fragmentation of species' habitats and consequently provides expectations on the role of habitat dynamics in shaping biodiversity gradients.

4.1 | SPLIT: a spatially explicit diversification model

To understand how speciation and extinction shape biodiversity gradients, ecologists and biogeographers are increasingly using phylogenies along diversification models (Wiens & Donoghue, 2004). Goldberg, Lancaster, and Ree (2011) proposed a diversification model, the geographic state speciation and extinction model (GeoSSE), which allows one to estimate diversification parameters independently for two geographical regions. This approach relies on a reconstructed phylogeny to compute speciation and extinction rates for each area as well as dispersal rates out of each area into the other. With the GeoSSE model, changes in range availability and connectivity are therefore mapped using very simple patch connectivity matrices with a very limited number of coarse regions (Rolland et al., 2014). The inferences with partly spatial approaches are therefore limited when the main
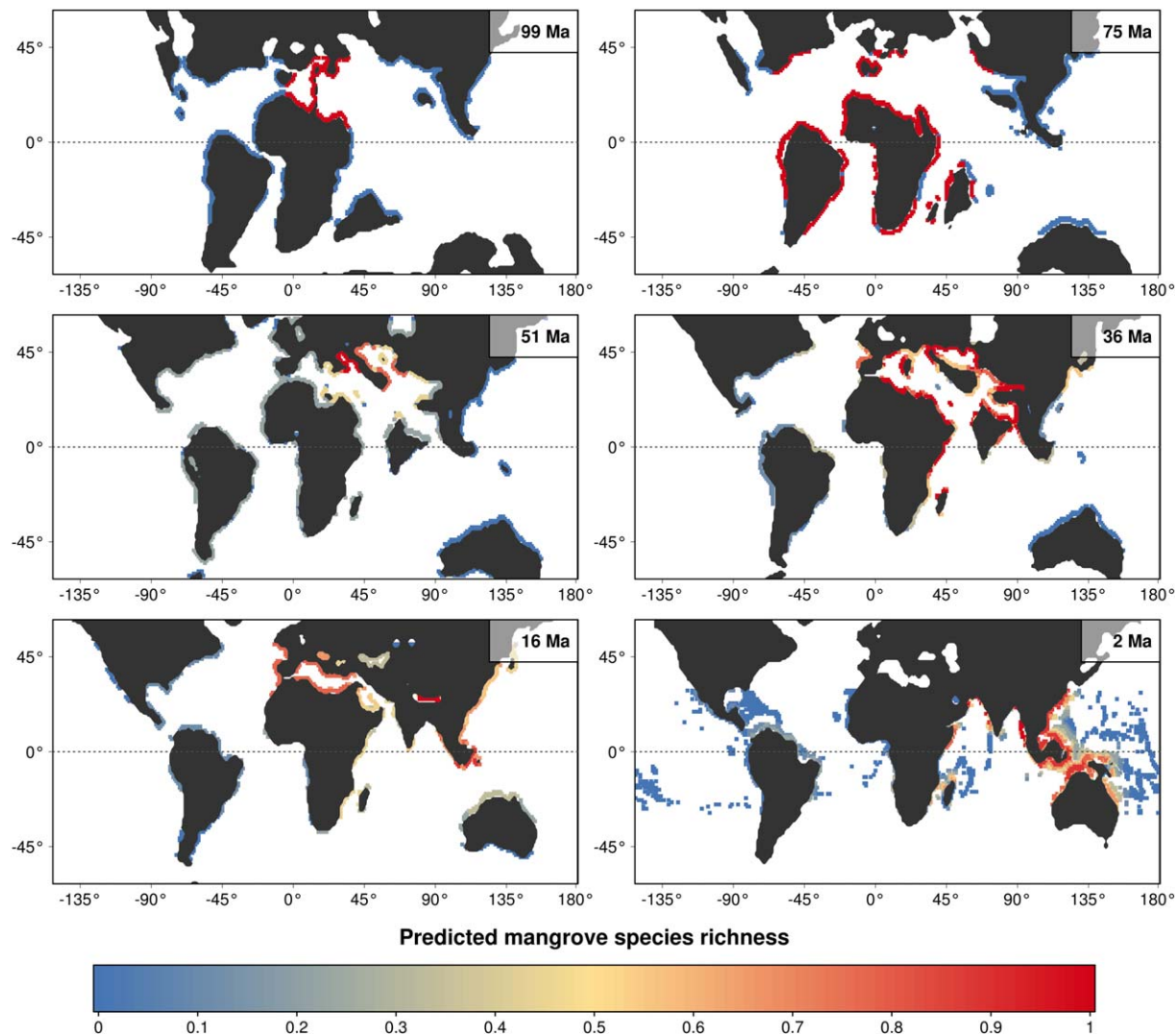
FIGURE 4 Evolution of the mangrove species richness expected by the parapatric spatial diversification model of lineages through time (SPLIT) ($d = 6$, $ds = 35$) for six time periods across the past 99 Myr. The simulation started at 100 Ma. Cells with high species richness are shown in red, while cells with low species richness are shown in blue. d = maximum dispersal distance; ds = distance threshold beyond which gene flow is absent

objective of the study is to evaluate the role of past environmental changes in shaping contemporary biodiversity patterns. It is expected that diversification models accounting for the spatial structure of habitats should provide a broader perspective on the mechanisms generating biodiversity gradients (Gotelli et al., 2009).

Several spatially explicit model of speciation have been proposed to understand the generation of species richness gradients. Brayard et al. (2005) evaluated how diversification and dispersal processes explain patterns of actual planktonic foraminifera species richness through a model generating a random clade dispersing across the Atlantic Ocean under the control of sea temperature. In the wake of the previously cited model, Rangel et al. (2007) proposed a spatial model to test whether evolutionary niche dynamics (the balance between niche conservatism and niche evolution processes) may explain current bird species richness patterns in South America. Muneepeerakul et al. (2008) used a neutral individual-based model to

evaluate the role of dispersal in the speciation of fishes in a river system, while Tittensor and Worm (2016) proposed a spatially explicit global meta-community model handling disturbance, speciation and dispersal to explore the generation of the latitude diversity gradient. The availability of palaeo-environmental maps was the main obstacle to the development of spatial diversification models, but the recent availability of palaeo-habitat reconstructions (Heine et al., 2015; Lunt et al., 2016; Müller et al., 2008) allowed new analyses. For instance, Jordan et al. (2016) quantified the role of plate tectonics in shaping terrestrial diversity using an individual-based model based on shifting distance among continents. As in Jordan et al. (2016), the SPLIT model only operates over dynamic habitats, but its architecture contrasts to previous individual-centred approaches (Muneepeerakul et al., 2008; Rosindell, Harmon, & Etienne, 2015), the SPLIT model considers species' ranges as a modelling unit, which makes it a much faster algorithm for processing many temporal environmental maps with large

spatial extent and resolution. The SPLIT model is also conceptually simpler than previous models, as it is based on a spatial cluster optimization algorithm and does not consider the evolution of ecological traits [e.g., the MBL model of Gould, Raup, Sepkoski, Schopf, and Simberloff (1977) used in Brayard et al. (2005)].

The strength of mechanistic models in general and the SPLIT model in particular is that a single simulation provides predictions for multiple properties. Here, SPLIT allows the simulation of several properties, such as species richness, β-diversity, phylogenetic diversity, speciation and extinction rates, and phylogeny shape, that can be compared to observed data (Gotelli et al., 2009). Beyond mimicking spatial diversity gradients, simulated diversification rates can be compared to those estimated from empirical phylogenies or fossil records (Leprieur et al., 2016). The shapes of the generated phylogenies themselves can be compared with observed phylogenies using metrics such as tree balance (e.g., Heard & Cox, 2007) and the lineage-branching pattern through time (e.g., Alroy, 2008; Phillimore & Price, 2008; White & Kerr, 2006). In addition, together with simulated species range, the expected phylogenetic community structure (*sensu* Webb, 2000) of taxa co-occurring in samples of spatially contiguous cells can be compared between observed and simulated data to understand the current structure of lineages within assemblages (Kissling et al., 2012; Leprieur et al., 2016).

The model is a simplification of the processes generating species diversity in nature and relies on several assumptions: the model assumes that speciation events are parapatric and are therefore contingent on both dispersal and the configuration of habitats; the model assumes that habitat changes together with dispersal limitation cause species extinctions; the model is neutral, that is, it assumes no trait variation among species, for example, their dispersal abilities. The model is also neutral in terms of species interactions, as co-occurring species are not competing with each other. In addition, the model assumes no trait or niche evolution across the time frame considered. A modelled clade retains a constant dispersal ability and habitat preference through time as determined for the ancestral species. Therefore, like Hubbell's neutral model (2001), species are equivalent in birth rates, death rates, dispersal rates and speciation rates, which depends only on habitat dynamics; Finally, because of the architecture of the model, it requires that sufficient time elapses across every time step to allow a full speciation event between disconnected patches (e.g., 1 Myr). The SPLIT model provides simple expectations under allopatric or parapatric speciation, to which more complex non-neutral models and those with more complex modes of speciation can be compared. Despite its apparent simplicity, the SPLIT model provides a realistic expectation of the biodiversity dynamics through time, as shown for coral reefs (Leprieur et al., 2016) and mangrove systems.

4.2 | Case study: The global biogeography of mangroves

In mangrove taxa, there is a unique longitudinal pattern of species richness from the Atlantic to the central Indo-Pacific region that is thought to be related to ancient anomalies in diversification rates across the world's oceans (Ellison et al., 1999; Ricklefs et al., 2006). Many different hypotheses have been proposed to explain such longitudinal diversity unbalance, including species immigration from outside the Indo-Pacific (Ellison et al., 1999), in situ diversification (Briggs, 1999) or a combination of both (Ricklefs et al., 2006). Yet, no conclusive evidence exists given the paucity of fossil records (Plaziat, Cavagnetto, Koeniguer, & Baltzer, 2001).

Our model suggests that the observed peak of mangrove diversity in the IAA results from two main sources, immigration from the Tethys and in situ diversification in the IAA (see Supporting Information Appendix S5). Diversification showed a peak in the Eocene (Figure 3), when the habitat patch configuration in the central Tethys Sea was most favourable for diversification. According to the plate tectonics reconstruction, the closing Tethys of the Miocene was well connected to favourable habitat in South Asia. In addition, during the same period, the Sunda and Sahul shelves entered into collision and generated a complex archipelago that, according to the model, promoted parapatric speciation and the formation of new lineages. In accordance with our model outputs, Ricklefs et al. (2006) proposed that the high mangrove diversity in the Indian western Pacific region is due to the presence of large areas of continental shelf islands scattered among shallow tropical seas, initially along the Tethyan border, including parts of actual Europe, and later in the region of the Sunda Shelf of Malaysia and Indonesia. Our results concur with this and the hypothesis of McCoy and Heck (1976) that many modern mangrove genera arose on the shores of the central Tethys Sea. Subsequent continental drift resulted in disjunctive distributions of species within genera in the Atlantic and Indo-Pacific Oceans (McCoy & Heck 1976). Finally, in situ diversification of these genera in Southeast Asia likely led to the modern-day mangrove diversity anomaly.

A few mangrove genera occur both in the Atlantic and Indo-Pacific Oceans, and several hypotheses have been proposed to explain this pattern, including colonization from the eastern Tethys to the Atlantic Ocean (Ricklefs et al., 2006) or ancient vicariance (Ellison et al., 1999). Using the SPLIT model, we predict that after a period of high diversification in the central Tethys during the Eocene, the closure forming the current Mediterranean Sea led to the disconnection of the western and eastern ranges and the vicariance of lineages. The model inferences agree with previous expectations from fossil records (Ellison et al., 1999). Also, Ricklefs et al. (2006) showed that mangrove lineages occurring in both the Indo-Pacific and Atlantic oceans (e.g., Rhizophoraceae, *Avicennia*) tend to be older, suggesting ancient exchanges before the closure of the Tethys Sea (Ricklefs & Latham, 1993). For example, the earliest fossils of the New World *Pelliciera* genus originate from southern Europe, indicating a Tethyan origin for these lineages with subsequent spread to the Atlantic coasts (Ellison et al., 1999; Saenger, 1998). Finally, our results are also in accordance with a recent study based on a dated molecular phylogeny for *Rhizophora* species (Lo et al., 2014). This study dated the deep split between the Old and New World lineages to the early Eocene based on fossil calibration, which corresponds to the diversification peak inferred from the SPLIT model (see Figure 3). Finally, according to the model, a distance of $ds = 35$ and $ds = 15$ is necessary for two populations to separate after a time

window of 1 Myr for Rhizophoraceae and *Avicennia*, respectively. As mangroves have long dispersal strategies, such large speciation distances are biologically realistic. For instance, the flotation time of propagules can vary from a few days to several months and even a year (Duke et al., 1998; Triest, 2008). Consequently, a large distance is required to limit gene flow and allow speciation in the case of mangroves.

4.3 | Future directions

The SPLIT model allows the assessment of the role of diversification and dispersal processes constrained by past environmental changes in shaping current biodiversity patterns (Leprieur et al., 2016). However, as for any model, several aspects can be improved in the future. First, the model can only accommodate habitat changes that occurred over large temporal scales, as full speciation needs to be assumed if the population range becomes disconnected during a given time step. While this assumption is valid for processes unfolding over large temporal scales, such as plate tectonics, the model is currently unsuitable for habitat changes that have occurred over millennia, such as the Quaternary glaciations (Pellissier et al., 2014). Considering the spatial clusters as populations instead of species as a modelling unit might allow the model to be applied to periods of faster temporal habitat shifts. In addition, the model is purely neutral, meaning that all species are considered equivalent and there is no carrying capacity associated with a given cell related to, for instance, environmental conditions or species interactions. For example, a more advanced model could integrate ecological interactions among species modulated by traits that could evolve through time (Pellissier et al. 2015). Finally, the model as presented here currently only includes allopatric or parapatric speciation, which are expected to be the most common forms of speciation (Mayr, 1969).

Future collaborative works among the fields of biogeography, palaeobiology and geology are needed to develop process-based models incorporating palaeo-environmental changes. Currently, the SPLIT model has only been applied to the marine realm (Leprieur et al., 2016, and this study), because the reconstruction of shallow tropical reef habitats is straightforward due to the availability of accurate data on palaeo-bathymetry (Müller et al., 2008) and extensive coral fossil records to distinguish between tropical and temperate climates. For example, to apply the model to the diversification of terrestrial clades, more effort should be invested in the palaeo-modelling of temperatures and precipitations for land surface at regular time steps (e.g., Sepulchre et al., 2006). For terrestrial life, one of the key boundary conditions is the availability of robust palaeo-elevation models in regularly spaced intervals. A recent study used palaeo-elevation to map ancient climates at regular time intervals since the Cretaceous (Lunt et al., 2016), which can be used to constrain vegetation models (Sepulchre et al., 2006). Efforts should be invested in such open access reconstruction to produce a benchmark data set to model terrestrial biodiversity dynamics. Finally, in the same way that hindcasts of species distribution models are sensitive to palaeo-climate reconstructions for the Last Glacial Maximum (Schmatz, Luterbacher, Zimmermann, & Pearman, 2015), our

model depends on accurate palaeo-habitat reconstructions for the past. In the future, the use of several independent palaeo-habitat reconstructions is warranted.

5 | CONCLUSION

Decades of research in the field of macroecology have been devoted to identifying the broad-scale organization of biodiversity using statistical models and to bringing out general macroecological patterns, such as the decrease of assemblage dissimilarity with geographical distance (Smith, Lyons, Ernest, & Brown, 2008). Brown (1999) noted that the challenge for future macroecological studies was no longer to identify these patterns but to build and evaluate mechanistic models that can explain macroecological patterns in terms of established physical and biological principles. In line with this objective, the SPLIT model allows one to quantify the role of history in explaining current biodiversity patterns, and it is applicable to any taxonomic group whose habitat has been mapped at regular intervals for deep time periods. Related to the long-standing debate about Hubbell's neutral theory (Wennekes, Rosindell, & Etienne, 2012), the fact that a process-based model fits a specific empirical pattern does not necessarily prove a causal link between the mechanism and the natural order. Rather than fitting a single empirical parameter, the SPLIT model can simultaneously predict present and past diversity gradients, diversification rates and phylogenies. Such an integrative comparison of mechanisms and nature should provide more detailed knowledge of the degree to which biodiversity gradients are explained by the direct effect of palaeo-habitat dynamics or the non-neutral evolution of ecological functions to tolerate new environments and co-occurring species.

AUTHOR CONTRIBUTIONS

P.D., T.G., F.L. and L.P. designed the study; P.D., T.G., C.A. and C.H. conducted the analyses; C.A., T.G. and L.P. wrote the R code; and L.P. and F.L. led the writing of the manuscript with the help of all co-authors.

DATA AVAILABILITY

The R code (R Development Core Team, https://www.R-project.org) detailing the step-by-step procedure of the model is available online, and our approach is implemented as a web service in the new InsideDNA cloud platform for reproducible bioinformatics analyses (https://insidedna.me). InsideDNA allows one to publish, search and run bioinformatics tools, store and analyse genomic data, and share results of analysis via interactive methods (iMethods). iMethod is an executable bundle comprising a bioinformatics tool, tool settings and

data stored under a permanent web url. The R code for the SPLIT model can be either downloaded as a Docker container or run directly via an interface from InsideDNA (https://insidedna.me/app#/tools/100859/edit). An iMethod link for the analysis described above is accessible via https://insidedna.me/link/MQQo.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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