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ECOGRAPHY

Research

A process-based model supports an association between dispersal and the prevalence of species traits in tropical reef fish assemblages

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Habitat dynamics interacting with species dispersal abilities could generate gradients in species diversity and prevalence of species traits when the latter are associated with species dispersal potential. Using a process-based model of diversification constrained by a dispersal parameter, we simulated the interplay between reef habitat dynamics during the past 140 million years and dispersal, shaping lineage diversification history and assemblage composition globally. The emerging patterns from the simulations were compared to current prevalence of species traits related to dispersal for 6315 tropical reef fish species. We found a significant spatial congruence between the prevalence of simulated low dispersal values and areas with a large proportion of species characterized by small adult body size, narrow home range mobility behaviour, pelagic larval duration shorter than 21 days and diurnal activity. Species characterized by such traits were found predominantly in the Indo-Australian Archipelago and the Caribbean Sea. Furthermore, the frequency distribution of the dispersal parameter was found to match empirical distributions for body size, PLD and home range mobility behaviour. Also, the dispersal parameter in the simulations was associated to diversification rates and resulted in trait frequency matching empirical distributions. Overall, our findings suggest that past habitat dynamics, in conjunction with dispersal processes, influenced diversification in tropical reef fishes, which may explain the present-day geography of species traits.

Keywords: biodiversity, dispersal, diversification, mechanistic models, reef fish, traits



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Introduction

Specific regions of the globe host a disproportionately large fraction of extant biodiversity. Many hypotheses have been proposed to explain the global imbalance in species richness along latitude (Mittelbach et al. 2007), continents or oceans (Qian and Ricklefs 2000, Renema et al. 2008, Couvreur et al. 2015). Biogeographic hypotheses assume that paleoenvironmental dynamics shaped current diversity patterns (Fine 2015) through the interactions with species ecological characteristics (Givnish et al. 2014). During the last ~100 million years, when many extant clades diversified, the continents and ocean basins position, topography and climatic conditions changed, influencing biodiversity dynamics (Leprieur et al. 2016, Chalmandrier et al. 2018, Rolland and Condamine 2019). Some regions, typically those at high latitude (Dynesius and Jansson 2000) or across different continents or marine basins (Pellissier et al. 2014), suffered larger environmental changes, while others were more stable, thereby shaping speciation and extinction rates (Weir and Schluter 2007). For example, Leprieur et al. (2016) showed how the dynamics of shallow reefs influenced the diversification of tropical marine organisms in space and time. However, while research has largely focused on gradients in species richness (Mittelbach et al. 2007), biodiversity also integrates trait or phylogenetic diversity components in assemblages, which are not always spatially congruent (Devictor et al. 2010). The drivers underlying the global variation in species trait composition within assemblages are only starting to be explored and may not always correspond to those of species richness (Blonder et al. 2018). Therefore, there is growing interest to assess whether processes that have shaped species richness have also influenced the spatial distribution of species traits.

The mechanisms explaining the emergence of geographic contrasts in species richness may also lead to spatial gradients in species trait prevalence within assemblages. Such mechanisms can be associated with the processes of speciation and extinction modulated by dispersal (Chown and Gaston 2000, Ricklefs 2006). In particular, the traits enabling dispersal influence 1) speciation, through the modulation of gene flow; 2) extinction, through the ability to access a new suitable patch during a phase of strong habitat dynamics; and 3) the colonisation of newly created distant habitats. Limited dispersal ability in animal and plants resulting from a combination of traits is thought to prevent the persistence of gene flow among populations (Loveless and Hamrick 1984, Bradbury et al. 2008, Huyghe and Kochzius 2017) and ultimately lead to speciation (Kisel and Barraclough 2010, Riginos 2014, Tedesco et al. 2017). Further, to survive over geological time, populations facing important environmental changes need not only a connected network of habitats, but also a sufficient dispersal ability to track shifting suitable habitats through time (Cowen and Sponaugle 2009, Almany et al. 2017). Lastly, when new remote habitats are made available, such as oceanic islands (Cowie and Holland 2006), high dispersal facilitates their

colonisation (Luiz et al. 2013, Alzate et al. 2019a). Due to these processes, species-poor areas that have been historically disturbed or isolated for a long time should display a higher proportion of species with high dispersal ability (Stier et al. 2014, Ottimofiore et al. 2017). In contrast, species-rich areas with stable and connected habitats should display a higher proportion of species with traits associated with low dispersal ability (Mora and Robertson 2005, Ottimofiore et al. 2017). While similar mechanisms responsible for species richness could explain global trait patterns (Loreau et al. 2001), this association remains to be quantified at large spatial scales.

Evaluating whether there is a link between species traits related to dispersal, diversification and species richness gradients is a methodological challenge. The association between species traits and clade diversity has mostly been documented using non-spatial phylogenetic approaches (Magallón and Sanderson 2001, FitzJohn et al. 2009, Morlon et al. 2016, Tedesco et al. 2017) and generally restricted by the ability to integrate substantial historical information due to the lack of phylogenetic tree resolution linked to the paucity of the fossil record, especially in the marine realm. Moreover, in marine fishes, a variety of adult and larval traits are expected to reflect dispersal ability, thereby influencing gene flow, speciation and as a consequence species richness (Table 1), but those associations remain to be evaluated. In particular, it is generally accepted that the pelagic larval phase favours, dispersal among populations over long distances (Cowen and Sponaugle 2009), and that the Pelagic Larval Duration (hereafter 'PLD') trait can determine the rate of speciation (Mora et al. 2003). Additional traits, such as those related to the adult stage (e.g. home range mobility behaviour and adult body size among others) may also be associated with dispersal and geographic range expansion (Luiz et al. 2012, 2013, Alzate et al. 2019a). Although dispersal is a spatial process, the study of species diversification rarely considers external constraints that may vary among regions, such as dispersal dynamics through geological time (Pellissier et al. 2017). While ancestral range reconstruction models such as BioGeoBEARS (Matzke et al. 2013) provide significant insight to the historical biogeography of clades (Toussaint et al. 2017, Klaus and Matzke 2019), those models can only take into account a limited number of regions, and hence partially represent the complexity of habitat dynamics over geological time. An alternative to this limitation would be to simulate the evolution of species ranges constrained by past habitat dynamics and a parameter of dispersal ability (Leprieur et al. 2016, Descombes et al. 2018, Rangel et al. 2018). Outcomes based on such a framework would provide valuable insights on how dispersal processes have shaped the current biogeographic distribution of species traits possibly linked to dispersal.

Pattern-oriented modelling aims to determine parsimonious eco-evolutionary mechanisms governing the behaviour of a system and to explore how emerging patterns match observations (Grimm et al. 2005). Such modelling approach relies on the development of a structurally logical

Table 1. Ecological traits and their possible association with dispersal and habitat dynamics. Dispersal includes multiple range-shift processes, such as emigration, movement and settlement (Travis et al. 2012). We explored five traits that we hypothesise to be linked to dispersal as documented here below.

| Trait | Description | Range-shift processes and relationship with dispersal | Relationship to habitat dynamics |
|-----------------|--------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Adult body size | Total length (cm) | Adult body size is negatively related to predation risk and positively related to competitive ability, ecological generality as well as enhanced survival and growth of rafting juveniles (e.g. juveniles of large species tend to grow faster and be larger). All aspects which favour settlement success in new suitable habitats, including flotsam (Munday et al. 1998, Luiz et al. 2012, 2013, 2015, Feary 2014). | Adult body size is expected to facilitate the ability to track suitable habitats. Thus, larger-bodied species should be found in higher proportion in distant and less stable reef habitats (Luiz et al. 2012, 2013, 2015, Stier et al. 2014, Barneche et al. 2019). |
| Home range | Mobility behaviour | A highly mobile home range behaviour indicates broad habitat use and is positively related to ecological generality, favouring dispersal and settlement in a broad range of suitable habitats (Stobutzki and Bellwood 1997, Luiz et al. 2013, Alzate et al. 2019a). | A wide home range is expected to enhance species ability to track suitable habitats. Species moving between reefs in short time period, should be found in higher proportion in distant and less stable locations (Nash et al. 2015). |
| PLD | Pelagic Larval Duration (days) | PLD indicates the duration to which larvae are exposed to currents. Longer PLDs imply a longer period of movement after emigration, increasing chances of colonization of remote and isolated reefs (Stier et al. 2014). Positive relationships were found between PLD and dispersal distances (Shanks et al. 2003, Siegel et al. 2003, Bradbury et al. 2008). | Species with long PLD are expected to be present in higher proportion in distant and less stable habitats. (Stier et al. 2014). |
| Activity | Circadian activity | Nocturnal activity emerged as a primary determinant of successful geographic range extension (McCauley et al. 2012, Luiz et al. 2013). Morphological and behavioural features associated with nocturnal activity were found to be consistent with reduced predation risk (Helfman 1993) favouring population establishment and persistence. By reducing the exposure to predators, nocturnal activity could favour chances of propagule establishment in novel areas (Hobson and Chess 1978, Helfman 1993). | Nocturnal activity is expected to be present in higher proportion in novel suitable reef areas (Luiz et al. 2013). |
| Schooling | School size | Benefits from schooling include reduction of predation risk (Pitcher et al. 1993), increased mating and resource accessibilities (Cushing et al. 1968, Robertson et al. 1976), and provides hydrodynamical advantages (Weihs 1973). Altogether such factors could favour dispersal in newly colonised areas (Luiz et al. 2013). | Large schooling is expected to be present in higher proportion in distant and newly colonised reef areas (Luiz et al. 2013). |

and parsimonious process-based model that captures the bottom-level mechanisms of a system acting on a defined agent (Grimm and Railsback 2012). In the context of biodiversity, the agents are the species, the bottom-level mechanisms may include speciation, dispersal and extinction (Gotelli et al. 2009, Descombes et al. 2018), while the emerging patterns are, for example, species diversity gradients, geographical range size (Alzate et al. 2019b) or the prevalence of traits in species assemblages. Spatial mechanistic models can simultaneously reproduce patterns of species diversity and diversification rates (Leprieur et al. 2016, Rangel et al. 2018), but require the integration of paleo-environmental reconstruction (Leprieur et al. 2016, Rangel et al. 2018). The advantage of a spatial approach for studying diversification over a traditional phylogenetic one is that the influence of past habitat dynamics on species dispersal, and hence on species diversification, is considered explicitly (Gotelli et al. 2009, Descombes et al. 2018). As an alternative to phylogenetic approaches, spatial simulations can provide a process-based

understanding of how dispersal might influence species diversification and, in turn, large-scale biodiversity and ecological gradients. However, to date, the understanding of whether past habitat dynamics left an imprint on the current distribution of species traits related to dispersal remains elusive.

In this study, we use a mechanistic model of diversification constrained by dispersal and paleo-habitat dynamics (SPLIT, see Leprieur et al. 2016, Descombes et al. 2018) to evaluate the link between historical habitat dynamics, dispersal and the distribution of species traits in tropical reef fishes globally. We compared simulated to observed patterns of trait prevalence for species traits that are expected to be related to dispersal ability in tropical reef fishes (Table 1), namely adult body size, home range mobility behaviour, PLD, schooling and circadian activity. We expect a spatial correspondence between simulations run with low values of the dispersal parameter and the geographic prevalence of small-bodied species with narrower home range mobility

behaviour, shortest PLD, of diurnal activity and not engaging in large schools. Further, we expect a greater proportion of small-bodied species to be found in the less isolated reef habitats such as those of the Indo-Australian Archipelago and the Caribbean regions (Stier et al. 2014, Barneche et al. 2019). Conversely, we expect that simulations run with high values of the dispersal parameter should correspond to those species characterized by larger adult body sizes, highly mobile home range behaviour, longer PLD, rather nocturnal and engaging in larger and cohesive schools. The correspondence between the simulations and empirical patterns would support a link between historical habitat dynamics, dispersal abilities, species diversification and the spatial gradient in species diversity and trait prevalence.

Material and methods

Reconstruction of the ancient marine environment

Spatial process-based models of diversification require paleo-habitat reconstructions covering long time periods (Descombes et al. 2018). Plate reconstructions were carried out 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 paleo-topographic models with a 1° resolution for the past 140 My, for each My until the present, by combining oceanic paleo-bathymetry grids derived from paleo-oceanic crustal age grids with paleo-geographic data on continents and volcanic islands (Clouard et al. 2005). In addition, we combined these maps with coastline positions to obtain coastal tropical habitat with a shallow sea floor suitable for tropical reef fish establishment. To constrain tropical habitats, we computed the 95th percentile of the paleo-latitude at which corals were living to calculate the latitudinal border of tropical oceans across time. By combining reconstructed shelf areas with tropical limits, we generated one map per My. Grid cells were defined as habitat that is either suitable or unsuitable for tropical reef fish species: we assumed that suitable habitats lie within the tropical borders and between 0 and 200 m depth from the ocean's surface.

A process-based model of speciation, extinction and dispersal

The simulations from the different sub-models over a static or dynamic landscapes produce – independently from the biological data – emerging patterns. Through the comparison with empirical patterns, models can be evaluated in their ability to reproduce empirical patterns (Grimm and Railsback 2012). We used a spatial diversification model (SPLIT) that provides a parsimonious mechanistic expectation linking past habitat dynamics to speciation and extinction via dispersal. The method is described fully in Descombes et al. (2018). At any single point in space (i.e. a habitat grid cell), the model reports the distribution of every species, as well as their

genealogies. The modelling unit is the species range (i.e. the habitat grid cell), which is defined as a grid of either presence (1) or absence (0) of a species. Three main mechanisms, i.e. speciation, dispersal and extinction, characterise the model (see Descombes et al. 2018: Fig. 1, Supplementary material Appendix 1 Fig. A1, A2) and occur within each time step. The model starts with an ancestral species occupying a continuous range of 1° resolution cells in the early Cretaceous (~140 Myr ago). In the SPLIT model, the only process driving the split of lineages is the succession of disconnection and reconnection of habitat patches. A species becomes extinct if all suitable cells inhabited by the species at time t disappear at time $t+1$, with no colonisation possibilities. Therefore, the model also provides spatially explicit predictions of habitat-driven extinction rates.

The result of a given simulation run is determined by one parameter of dispersal d . At each time step within a simulation, species disperse according to this parameter d . Species at time step t are allowed to disperse to all habitat cells at time step $t+1$ that are distant by a value less than d . The value of d determines a dispersal kernel, implemented as a Weibull distribution that accounts for a degree of variability in effective dispersal. The Weibull distribution reproduces a shape of dispersal kernel characterised by more short dispersal events, rather than long events, matching empirical observations (Kinlan et al. 2005). New species occur when the species range is split into at least two distinct areas separated by a sea distance ds (speciation distance). We assumed a cubic relationship between ds and d because higher dispersal abilities require a larger distance to attenuate gene flow sufficiently to promote speciation, and thus $ds > d$. We ran a set of simulations starting with a minimum dispersal value, where each species is able to colonise each adjacent cell, and ending with the value of d for which all the extant habitats, including the most remote Pacific islands, have been colonised ($d \in [1.75^\circ: 5.45^\circ]$). By stacking the outputs of the different simulations, we obtained an expected assemblage structure from a range of dispersal abilities. The predicted assemblages are fully independent from fish species richness and trait data. Expectations from simulations can be compared to empirical patterns in particular spatial diversity gradients and geographic prevalence of ecological traits. To evaluate the emerging mechanistic link between dispersal and diversification rates in the model, we computed the simulated diversification rates for low dispersal (d below the 10th percentile of the dispersal parameters) and high dispersal (d above the 90th percentile of the dispersal parameters) simulations.

Species distribution data

The species distribution data set included global-scale distribution along with life-history and ecological trait information on tropical reef fish species, gathered from the General Approach to Species Abundance Relationships (GASPAR) database (Kulbicki et al. 2013, Parravicini et al. 2013), FishBase and Luiz et al. (2013) for the PLD

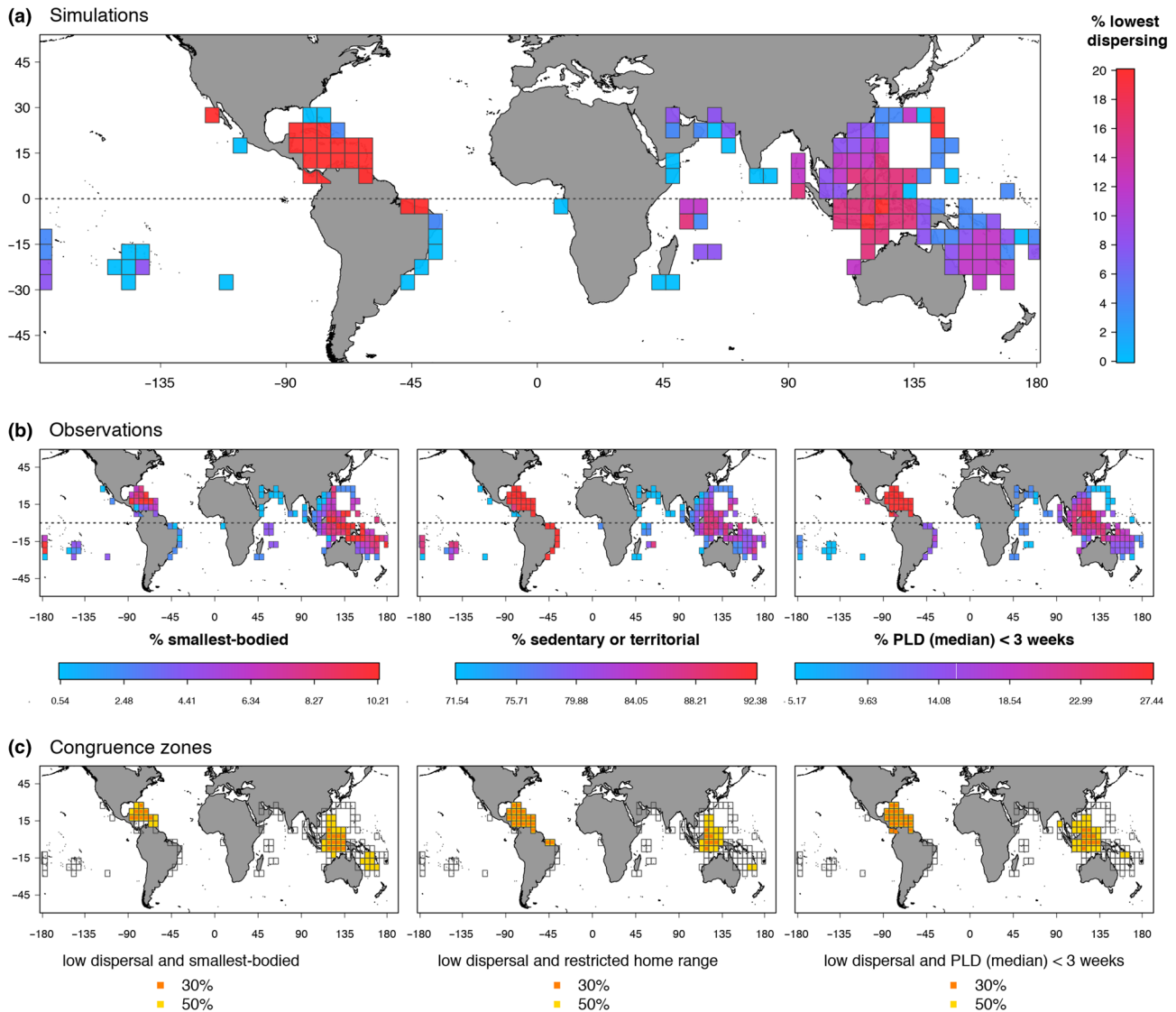


Figure 1. Global distribution maps for tropical reef fishes showing proportions of species richness for (a) low-dispersal parameter simulations (b) observed dispersal-related traits and (c) congruence zones between (a) and (b). The observed dispersal-related traits mapped are: smallest adult body sizes (left), sedentary or territorial behaviour (centre) and PLD shorter than three weeks (right). Congruence maps show overlapping zones (matching cells) between the highest proportions of low-dispersal parameter simulations and low-dispersal-related trait observations, for 30% (orange) and 50% (yellow) thresholds of hotspot congruence.

information. We obtained information on presence/absence for 6316 reef fishes in grid cells of $5 \times 5^\circ$, corresponding to circa 555×555 km at the Equator (see Parravicini et al. 2013, Leprieur et al. 2016 for more details). From this species occurrence database, we mapped the prevalence of five species traits (see below) to investigate their spatial distribution patterns globally.

Species traits data

We considered the following traits possibly related to dispersal abilities in tropical reef fishes (Table 1): 1) adult body size, measured as the maximal Total Length (TL) in centimetres;

2) home range mobility behaviour, coded as sedentary or territorial (both considered as ‘narrow home range’) and mobile or highly mobile between reefs (both considered as ‘wide home range’) (Chapman and Kramer 2000), 3) the Pelagic Larval Duration (PLD), measured in days gathered from Luiz et al. (2013). We reported the results with three sets of PLD data, which we hereafter refer as ‘raw’, ‘median’ and ‘resampled’. We reported the ‘raw’ PLD results when considering the values of Luiz et al. (2013) alone ($n = 571$); for species with missing PLD information, we estimated it by calculating the median PLD value at the genus level (‘median’) ($n = 2908$), and by drawing the value randomly within the known range of PLD in the genus (‘resampled’) ($n = 2908$),

- 4) circadian activity, coded as ‘diurnal’ and ‘nocturnal’ and
- 5) schooling behaviour was coded as solitary, pairing, small (3–20 individuals), medium (20–50 individuals) and large (> 50 individuals).

Spatial congruence of simulations and observations

We evaluated the spatial congruence following Mouillot et al. (2011), in terms of matching cells ($5 \times 5^\circ$), between the geographic distribution of the areas where predominantly low dispersing or high dispersing species were expected based on the simulations and the ones where low or high-dispersal-related trait values were observed for the five investigated traits. We summed species richness values resulting from the simulations of low dispersal parameters, i.e. those within the 10th percentile of the lowest dispersal parameter values. We proceeded similarly for the simulations of high dispersal parameters, where we summed species richness values resulting from the simulations above the 90th percentile of the parameter d ($d \in [1.75^\circ: 5.45^\circ]$). Likewise, for the observed adult body size, we defined the cells where the smallest-bodied species were present (i.e. 10th percentile of fish body size, hereafter ‘small-bodied’) and those where the largest-bodied species were present (i.e. 90th percentile of fish body size, hereafter ‘large-bodied’). For home range behaviour, relative to the overall species composition per grid cell, we defined cells’ proportions in terms of sedentary or territorial (i.e. ‘narrow home range’) and mobile-highly mobile (i.e. ‘wide home range’), respectively. For PLD we used the 20th and the 80th percentiles, corresponding to a PLD shorter than three weeks and longer than six weeks (Taylor and Hellberg 2003). For circadian activity, relative to the overall species composition per grid cell, we defined cells’ proportions in terms of ‘diurnal’ and ‘nocturnal’ activity. Similarly, for schooling, we defined cells’ proportions in terms of ‘solitary’ to ‘pairing’ (that reflect the lowest schooling aggregations) and, at the opposite extreme, the cluster of ‘medium’ to ‘large’ schools (that reflect the highest schooling aggregations). We compared the spatial hotspot overlap at 30% and 50% thresholds between observed and simulated areas compared to the null model. That is, for each pairwise comparison, we calculated the number of cells having a specific trait pattern for both the observation and the simulation; the independence between the two areas ensembles was determined and the significance was tested using 999 randomisations. We finally compared the frequency distribution of the dispersal parameter considered in the simulations to those observed in the empirical trait data.

Data deposition

The R codes (R Development Core Team, <www.R-project.org>) and data are available online on EnviDat: doi:10.16904/envidat.85.

Results

Biogeographic difference in the dominance of dispersal-related traits

Species richness differed across the major biogeographic regions, with one of the most evident contrasts observed between the Indo-Australian Archipelago (IAA), hosting simultaneously on average 1844 ± 331 distinct species and the Caribbean with ca. four fold less observed species richness (536 ± 56 ; Supplementary material Appendix 1 Fig. A3). Furthermore, for the investigated traits, their prevalence across the major biogeographic regions also differed (Fig. 1, 2, Supplementary material Appendix 1 Fig. A1, A2). While we found some agreement between species richness and trait patterns, such as with adult body size in the IAA, this geographic distribution was not fully congruent with species richness. Small-bodied species were more prevalent in both the Caribbean and the IAA compared with the Western Indian Ocean, the Eastern Pacific and the Eastern Indo-Pacific, but those regions also had a highly contrasted level of species richness (Fig. 1, Supplementary material Appendix 1 Fig. A3).

Spatial mechanistic model of speciation, extinction and dispersal

The simulations provided expectations of the spatio-temporal biodiversity dynamics for low and high dispersal parameter values (Fig. 1, 2). At the end of the simulations, the Caribbean Sea and the IAA were found to harbour the highest number of species (Fig. 1, Supplementary material Appendix 1 Fig. A3). We found that altogether the stacked simulations within the range of theoretical values tended to reproduce the longitudinal gradient of tropical reef fish richness (Pearson correlation coefficient $r_p = 0.49$, $p < 0.001$), with strong differences between the Indo-Pacific and the Atlantic regions (Supplementary material Appendix 1 Fig. A3). Furthermore, we found concordant results, expressed as a percentage of matching cells (%), between the prevalence of low dispersal species in the simulations and the prevalence of empirical traits (Table 2, Supplementary material Appendix 1 Table A1): small adult body size (62.5%, $p = 0.002$; Table 2), narrow home range mobility behaviour (59.7%, $p = 0.005$; Table 2), PLD shorter than 3 weeks (70.8%, $p = 0.001$; Table 2, Supplementary material Appendix 1 Table A1) and diurnal activity (58.3%, $p = 0.019$; Supplementary material Appendix 1 Table A1). Areas of congruence were predominantly observed in the IAA as well as the Caribbean Sea (Fig. 1, Supplementary material Appendix 1 Fig. A1, A5). Regarding the prevalence of high dispersal-related traits, the simulations were found to be significantly congruent with observed prevalence patterns of PLD longer than six weeks (69.4%, $p = 0.001$; Table 2, Fig. 2) and wide home range mobility (56.9%, $p = 0.045$; Table 2, Fig. 2). We also found a consensus between high dispersal parameter values and observed

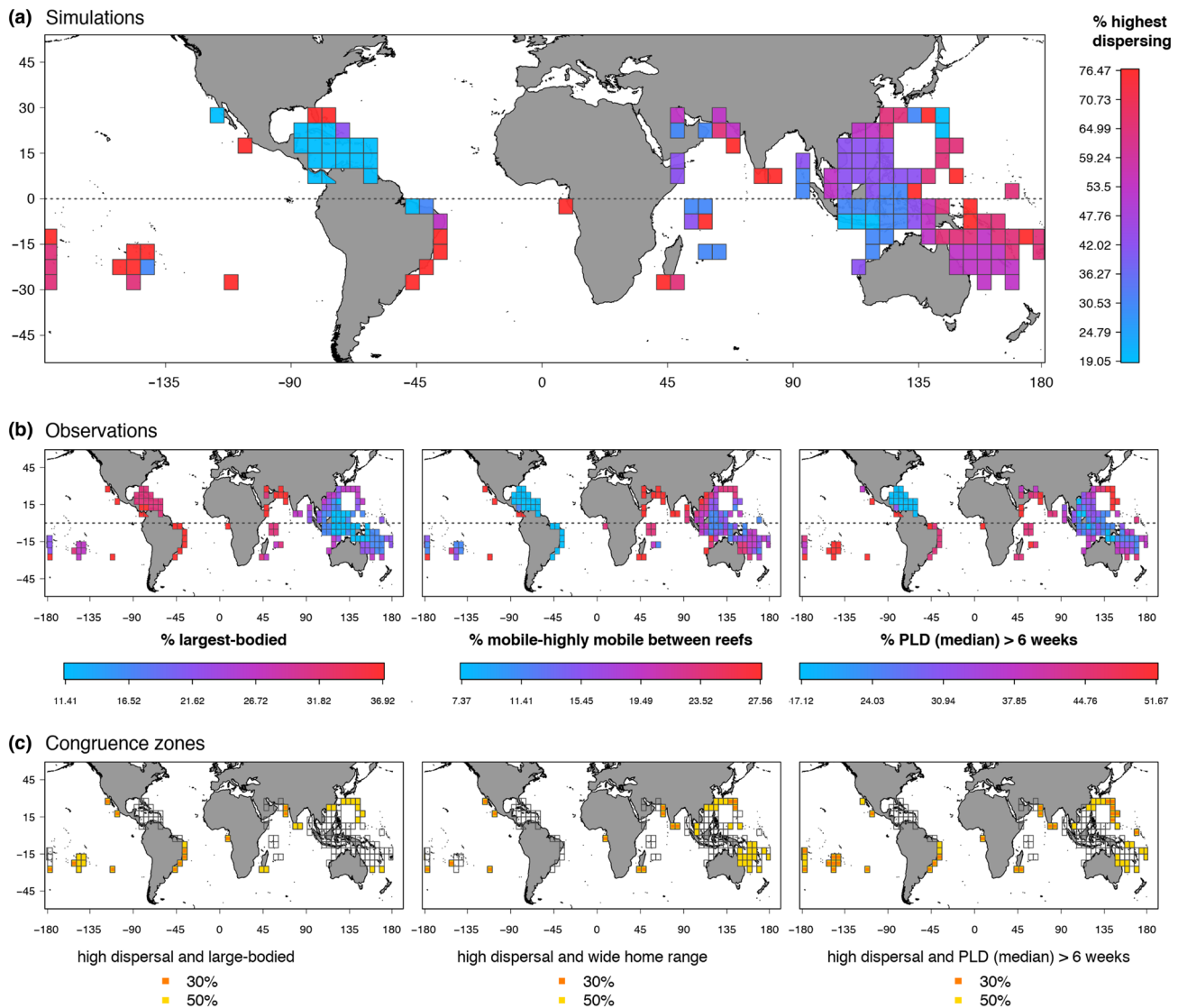


Figure 2. Global distribution maps for tropical reef fishes showing proportions of species richness for (a) high-dispersal parameter simulations (b) observed dispersal-related traits and (c) congruence zones between (a) and (b). The observed dispersal-related traits mapped are: the largest adult-body sizes (left), highly mobile behaviour (centre), and PLD longer than six weeks (right). Congruence maps show overlapping zones (matching cells) between the highest proportions of high-dispersal parameter simulations and high-dispersal-related trait observations, for 30% (orange) and 50% (yellow) thresholds of hotspot congruence.

large-bodied species distributions, where species characterized by a large body size were observed over the remotest reef structures, such as those of the Pacific islands (Fig. 2).

Further, our results indicated that the frequency distribution of the dispersal parameter d matched the observed body size, PLD and home range mobility behaviour frequency

Table 2. Spatial congruence test of overlap between simulated proportions of low and high dispersal and observed low- and high-dispersal-related traits in assemblages (50% threshold).

| Dispersal proxies _(observed) | Low dispersal _(simulated) | | | | High dispersal _(simulated) | | | |
|-----------------------------------------|--------------------------------------|----|------|--------------|---------------------------------------|----|------|--------------|
| | Category | Oo | Oe | p-value | Category | Oo | Oe | p-value |
| Adult body size | smallest-bodied | 45 | 35.5 | 0.002 | largest-bodied | 33 | 35.5 | 0.842 |
| Home range | sedentary or territorial | 43 | 35.5 | 0.005 | highly mobile | 41 | 35.5 | 0.054 |
| PLD (median) | < 3 weeks | 51 | 35.5 | 0.001 | > 6 weeks | 50 | 35.5 | 0.001 |

Adult body size, smallest-bodied (< 10th quantile, TL) and largest-bodied (> 90th quantile, TL); Home range, sedentary or territorial (restricted within reef movements) and highly mobile (between reef movements); PLD (median) (n=2908), short (< 3 weeks) and long (> 6 weeks) Pelagic Larval Duration; Oo, observed number of overlaps (i.e. number of cells that are recorded as a hotspot for both variables); Oe, expected number of overlaps (i.e. the independence between the two hotspot ensembles).

distributions for tropical reef fishes (Fig. 3), in the form of a positively skewed distributions, with the highest frequencies of low dispersal values matching the smallest adult body sizes, the shortest PLDs, as well as the sedentary home range behaviour amounts. Finally, the model revealed an association between dispersal and diversification rate. That is, simulations based on low values of the dispersal parameter (d below the 10th quantile; Supplementary material Appendix 1 Fig. A4) predicted higher net diversification rates than those based on high values of the dispersal parameter (d above the 90th quantile; Supplementary material Appendix 1 Fig. A4).

Discussion

Our findings provide evidence that historical reef habitat dynamics, which have influenced the diversification of lineages and their dispersal through geological time, can explain the current geographic prevalence of multiple species traits possibly linked to dispersal ability in tropical reef fishes (Fig. 1, 2, Supplementary material Appendix 1 Fig. A1, A2). Further, in support of the hypothesis that certain species traits might affect speciation and extinction, and thereby shape lineage diversification (Tedesco et al. 2017), we found

that the frequency distribution of the dispersal parameter matched empirical distributions for body size, PLD and home range mobility behaviour (Fig. 3). Simulations based on low values of the dispersal parameter were also found to produce the highest net diversification rates (Supplementary material Appendix 1 Fig. A4).

Our findings show that the observed distributions of species traits match those predicted by the simulations, predominantly in the Indo-Australian Archipelago and in the Caribbean region (Fig. 1, Supplementary material Appendix 1 Fig. A1). Indeed, both are recognized as the biogeographic regions of the world with the most stable shallow reefs over geological time (Leprieur et al. 2016, Bellwood et al. 2017). Therefore, species characterised by low dispersal ability, such as for example, small adult body size, highly sedentary or territorial home range behaviour, shortest PLDs and/or diurnal activity, most likely have been able to persist and accumulate in those regions, despite their relatively low dispersal ability. In contrast, in agreement with Luiz et al. (2013) and Barneche et al. (2019), distant and species-poor reefs, such as those in the eastern Pacific and southern Atlantic, were found to be predominantly inhabited by species with longer PLD and larger body sizes (Fig. 2, Supplementary material Appendix 1 Fig. A6). Also,

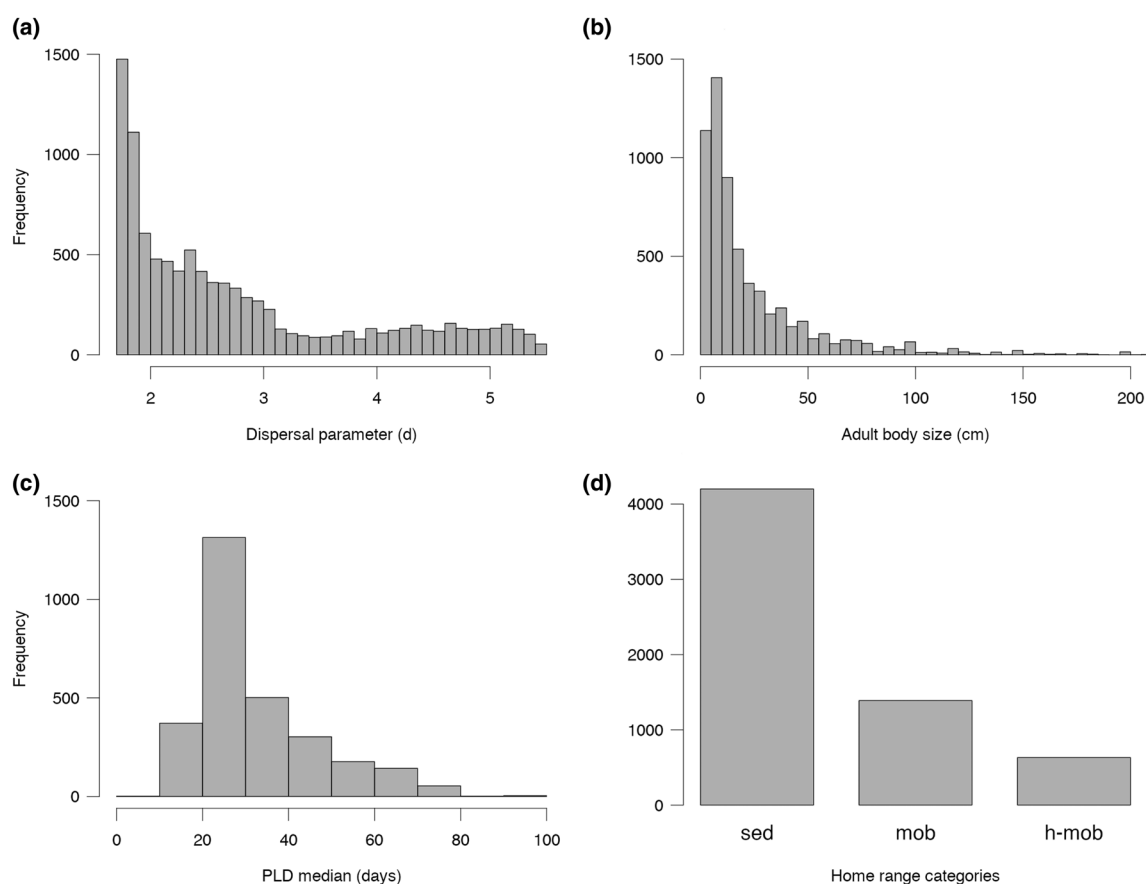


Figure 3. Frequency distribution of the dispersal parameter considered in the simulations (a) and observed frequency distribution for adult body size (b), median PLD (c) and home range category (d). The number of species is biased toward more smaller species, with lower median PLD and of sedentary home range, which correspond to the higher frequency of simulated species with lower dispersal.

our results are consistent with a recent study employing a Bayesian modelling approach to relate species richness of tropical reef fishes at different spatial scales to several predictors such as body size, temperature, reef areas, isolation and anthropogenic impacts (Barneche et al. 2019). In particular, the authors found that body size distribution was one of the major predictor of species richness across scales (i.e. from sites to biogeographic provinces), with accumulation of species across space being strongly associated with smaller body sizes. Our simulations not only generated emerging patterns in agreement with the empirical distribution of traits (Fig. 3), but also highlighted a possible link between trait distribution patterns and diversification rates (Fig. 1, Supplementary material Appendix 1 Fig. A4). Our model suggests that species with low dispersal traits should be more frequent than with high dispersal traits, which correspond to observations: small-bodied species are found to be more frequent than large-bodied species, while short PLD species are more frequent than long PLD species (Fig. 3). Due to their comparatively lower ability to disperse, smaller-bodied species with short PLD may more frequently face barriers to gene flow, thereby increasing speciation incidence compared with that of large-bodied species. Similar findings were presented by Tedesco et al. (2017), who argued that fishes of small body sizes result in limited dispersal abilities, causing smaller and more easily fragmented habitat ranges. This may facilitate reproductive isolation and promote speciation as found in terrestrial taxa (Wollenberg et al. 2011). Thus, our results suggest that dispersal-related traits not only influence the extant distribution of species through the interaction with past habitat dynamics, but could also explain diversification through dispersal and its association with gene flow.

Phylogenetic-based studies have supported a major role of species traits linked to dispersal ability in explaining differences in species diversity among clades for mammals (Machac and Graham 2017), birds (Claramunt et al. 2012, McGuire et al. 2014), squamates (Feldman et al. 2016) and fishes (Tedesco et al. 2017). Our process-based model suggests a mechanistic link between past habitat dynamics, dispersal traits and lineage diversification. Nevertheless, the validation of simulated diversification rates with empirical data accounting for traits and geography remains challenging. It is for instance difficult to integrate phylogenetic estimation of diversification rates for clades with complex geographic structures (Sukumaran and Knowles 2018). Therefore, in complement to our study, future research could be directed towards the investigation of the influence of the traits highlighted in this study on lineage diversification of tropical reef fishes within different biogeographic regions. For example, the future development of trait-dependent diversification models (e.g. QuaSSE for continuous traits, FitzJohn (2010) or BiSSE for binary characters (Maddison et al. 2007)), that relies on well-resolved dated phylogenies (Inostroza-Michael et al. 2018) should provide valuable comparisons to our process-based model approach.

While our process-based approach presents the advantage to couple species speciation, extinction and dispersal to paleo-environmental reconstructions, it nevertheless presents a set of assumptions and limitations. We generally operated under the assumption that the understanding of the causes of a phenomenon is the ability to build a simulation model from first principles and to reproduce realistic higher-level empirical patterns (Leprieur et al. 2016, Pontarp and Wiens 2017, Rangel et al. 2018). We voluntarily adopted a parsimonious model with a limited number of rules regulating speciation, extinction and dispersal, acknowledging that ecological and evolutionary processes regulating marine biodiversity represent more complex processes. The development of process-based models represent a simplification of the reality (DeAngelis and Mooij 2005, Grimm et al. 2005) and our simulations were done along three main lines of abstraction: 1) of the agent (i.e. the species), where we model cells as homogeneous populations, but do not integrate underlying genetic differences among cells of the same species (Melian et al. 2010), 2) the bottom-level mechanisms, which neglect important processes including competition among species of a cell and position in the food-web (Albouy et al. 2019) or trait evolution through time (Fitzjohn et al. 2010) and 3) the landscape dynamic, where the reef reconstruction represents a simplification of ecological conditions experienced by a species. For example, the temperature in a given cell might increase the rate of differentiation among populations, the rate of phenotypic trait evolution, or determine interaction strength (Allen et al. 2006). Together, the implementation of process-based models should seek consistency and be consolidated to capture what is currently accepted as plausible explanation, or explanations with higher potential to integrate alternative hypotheses (Cabral et al. 2017). For simplification and running the model over large and realistic landscapes, we decided not to simulate all the evolutionary process including drift, selection, sex/recombination and the process of mutation fixation when implementing the model. Finally, even if the process-based models are able to reproduce emerging patterns that correspond to the observed data, this approach does not demonstrate a causal link but remains correlative. Future developments in the field of biogeography should aim to integrate more realistic ecological and evolutionary processes into spatial models of diversification (Gotelli et al. 2009, Rangel et al. 2018).

Together, our study supports a link between past habitat dynamics, dispersal and the spatial distribution of species traits in tropical reef fishes globally. Owing to the coarse resolution of the reef reconstruction over geological time (i.e. 1° cell resolution with a large expected uncertainty), the spatial diversification model only reproduced the major speciation events occurring between large reef patches and over large spatial distances. Future studies may benefit from finer paleo-environmental reconstructions, accounting, for example, for the influence of the Quaternary glaciations in addition to plate tectonics (Pellissier et al. 2014). Nevertheless, our study provides new insights regarding the processes

shaping large-scale diversity patterns of tropical reef fishes' and more particularly the contrasted distribution of species traits among regions. Overall, we argue that a deeper understanding of complex biological patterns, such as the current distribution of different facets of biodiversity benefits from a process-based approach: speciation and extinction processes mediated by dispersal, which are responsible for the generation of new biodiversity, depend not only on species traits characteristics but also on the habitat configuration, which is dynamic through time.

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Supplementary material (available online as Appendix ecog-04537 at <www.ecography.org/appendix/ecog-04537>). Appendix 1.