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Evolutionary processes underlying latitudinal differences in reef fish biodiversity

Alexandre C. Siqueira^{1*}, Luiz Gustavo R. Oliveira-Santos², Peter F. Cowman^{3,4} and Sergio R. Floeter¹

¹Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, SC, Brazil, ²Departamento de Ecologia, Universidade Federal do Mato Grosso do Sul, Campo Grande, MS, Brazil, ³Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA, ⁴Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Qld, Australia

ABSTRACT

Aim To examine the dynamics among the processes of speciation, extinction and dispersal in marine environments using phylogenies to reveal the evolutionary mechanisms that promote latitudinal differences in biodiversity. Using phylogenetic comparative methods we assess whether tropical reef fish lineages show higher diversification rates and whether the majority of extratropical reef fish lineages have originated from tropical areas.

Location Shallow water tropical and extratropical reefs globally.

Methods Using fossil-calibrated phylogenies for four reef-associated fish families (Chaetodontidae, Labridae, Pomacentridae and Sparidae) we apply evolutionary models (GeoSSE and HiSSE) that allow the estimation of speciation, extinction and dispersal rates associated with geographical ranges and explore potential biases from unsampled characters.

Results We found that tropical lineages show higher rates of speciation and tended to have lower extinction rates. Overall, we identify higher net diversification rates for tropical lineages compared with those in extratropical regions in all four families. Rates of dispersal tended to be higher for lineages with tropical origins expanding into extratropical regions. Within the family Labridae, two tropical lineages were found to exhibit higher net diversification rates, above that expected from latitudinal differences.

Main conclusions Our results offer support for the predictions of the ‘out of the tropics’ and ‘evolutionary speed’ models of evolution, both of which highlight the marine tropics as an important evolutionary engine promoting latitudinal differences in reef fish biodiversity. Moreover, we find that two tropical labrid lineages are undergoing exceptional diversification associated with additional traits, possibly linked with the extreme sexual dichromatism observed in both clades.

Keywords

Dispersal, diversification, extinction, models of evolution, speciation, species richness.

*Correspondence: Alexandre C. Siqueira, Marine Macroecology and Biogeography Lab, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, SC, 88040-970, Brazil. E-mail: alesixbio@gmail.com

INTRODUCTION

Although it is the most widespread macroecological pattern in the world, the latitudinal diversity gradient (LDG) remains poorly understood with respect to the processes that generate it (Hillebrand, 2004). This limited understanding stems from

a lack of focus on the historical and evolutionary factors driving this pervasive pattern of biodiversity. The uneven distribution of tropical and extratropical lineages in phylogenetic trees is an evolutionary property that arises from the LDG and depends on the dynamics between speciation and

extinction (Mittelbach *et al.*, 2007). In addition, the phylogenetic component of the LDG depends on the process of lineage dispersal between different ecological zones (Ricklefs, 2006). Thus, every evolutionary hypotheses concerning the LDG must take into account at least one of these three fundamental processes that alter species richness: speciation, extinction and dispersal (Dowle *et al.*, 2013).

Considering these processes, there are four main hypotheses to explain the phylogenetic properties arising from the LDG. **1.** The 'evolutionary time' hypothesis (Fischer, 1960) considers that tropical lineages have had more time to diversify because tropical environments have remained more stable throughout geological time. According to this hypothesis, evolutionary rates would be equal among geographical regions, however, tropical lineages would be older than extratropical ones, leading to more extant species in the tropics. **2.** The 'tropical niche conservatism' hypothesis (Wiens & Donoghue, 2004) assumes that species that share common ancestry tend to share niche affinities. It proposes that most lineages would have originated in the tropics because tropical areas had greater geographical extent in the recent geological past and that the transition to extratropical zones would be rare. In terms of evolutionary rates, speciation and extinction were supposed to be equal among geographical regions and dispersal would be more frequent from extratropical zones to the tropics. **3.** The 'out of the tropics' (Jablonski *et al.*, 2006) is an explicit hypothesis about differences in all evolutionary rates. It suggests that lineage origination is higher in the tropics, extinction rates are higher or equal in the extratropics compared with the tropics, and that tropical lineages disperse to the extratropics more frequently than the reverse. **4.** Finally, the 'evolutionary speed' hypothesis (Rohde, 1992) proposes that speciation rates would be higher in tropical environments, mainly due to increased rates of molecular evolution in the tropics (reviewed in Dowle *et al.*, 2013). Thus, this hypothesis considers that extinction and dispersal rates would not vary among geographical regions.

Recent studies are helping to disentangle these evolutionary processes by using time-calibrated phylogenies to make explicit tests of speciation, extinction and dispersal rates between tropical and extratropical lineages (Pyron & Wiens, 2013; Pyron, 2014; Rolland *et al.*, 2014). Their main results suggest higher speciation rates for tropical lineages in amphibians and

mammals (Pyron & Wiens, 2013; Rolland *et al.*, 2014) but not in squamate reptiles (Pyron, 2014), while higher extinction rates have been reported for extratropical lineages in all groups. As for dispersal rates, these studies showed more lineage dispersal from the extratropics to the tropics in amphibians and squamate reptiles, while mammals follow the opposite pattern. These results reinforce the idiosyncratic nature of evolutionary processes among taxonomic groups, yet they have focused on terrestrial organisms. It is still unclear which processes have been important in marine systems for generating latitudinal patterns of biodiversity.

Although many marine groups exhibit a strong LDG (Hillebrand, 2004), there remains a gap in our knowledge of the underlying phylogenetic component, especially in diverse systems like coral reefs. These environments tend to occupy tropical latitudinal bands, but peripheral extratropical conditions may also permit the establishment of complex, non-coral-dominated reef communities (Ebeling & Hixon, 1991; Fig. 1). It is the transition from tropical coral-dominated reef to extratropical rocky reef and kelp forest systems that forms the LDG for reef-associated organisms. Coral reef environments are recognized as important promoters of lineage diversification, in particular for associated fishes, where they have acted as refugia for biodiversity in periods of elevated extinction (Cowman & Bellwood, 2011; Pellissier *et al.*, 2014). Reef fishes not only exhibit a marked latitudinal gradient with more species in the tropics but also a striking longitudinal gradient with species richness peaking in the Indo-Australian Archipelago (Mora *et al.*, 2003). Much effort has been devoted to understanding the present-day factors that influences these patterns (e.g. Bellwood *et al.*, 2005; Tittensor *et al.*, 2010), with geometric (reef area and costal length) and biogeographical variables identified as powerful predictors of reef fish species richness (Parravicini *et al.*, 2013). However, so far, no study has attempted to quantify the roles played by processes of speciation, extinction and dispersal in large-scale patterns of reef fish richness among tropical and extratropical regions.

Here, we employed phylogenetic comparative methods to test predictions of the evolutionary hypotheses concerning latitudinal differences in reef fish biodiversity. We used time-calibrated phylogenies of four families that are known to have representatives in both tropical and extratropical reefs to test for differences in speciation, extinction and dispersal

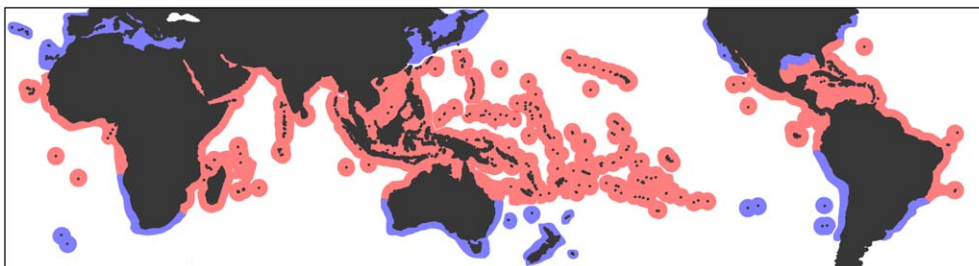


Figure 1 Map showing tropical (red/dark grey) and extratropical (blue/lighter grey) reef locations around the world defined by the isocrym of 20 °C, which is considered the latitudinal distribution limit for tropical marine fauna (Briggs, 1974).

Table 1 Absolute number of species represented in phylogenies and the respective proportion in relation to all recognized species by family in each character state: widespread (Wide), tropical (Trop), extratropical (Extra).

Family	Chaetodontidae			Labridae			Pomacentridae			Sparidae		
	Wide	Trop	Extra	Wide	Trop	Extra	Wide	Trop	Extra	Wide	Trop	Extra
Species	32	58	5	80	169	54	25	174	7	33	24	34
% in phylogeny	0.89	0.71	0.56	0.62	0.44	0.67	0.57	0.56	0.33	0.83	0.59	0.79

rates among lineages. Although these three processes have not been tested for reef fishes in the context of the LDG, they are recognized as important drivers of present-day species richness patterns for this system (Mora *et al.*, 2003). Specifically, we assessed which evolutionary hypothesis ('evolutionary time', 'tropical niche conservatism', 'out of the tropics' or 'evolutionary speed') drives the formation and maintenance of higher reef fish diversity in the tropics.

METHODS

Reef fish evolutionary relationships

We examined four percomorph families with high phylogenetic resolution known to be associated with both tropical and extratropical reef environments (Bellwood & Wainwright, 2002): Chaetodontidae, Labridae, Pomacentridae and Sparidae. The Chaetodontidae, Labridae and Pomacentridae are among the most species-rich families in reef environments and have a good phylogenetic resolution. However, they are predominantly associated with tropical coral reefs. To capture good representativeness both in terms of species richness and variation in occupation of tropical versus extratropical environments we also included the family Sparidae, which is characteristic of extratropical reefs (Bellwood & Wainwright, 2002). For our phylogenetic comparative methods, we used recent published chronograms for each family.

The Chaetodontidae phylogeny was reconstructed with Bayesian inferences using four mitochondrial genes and four nuclear genes (see Cowman & Bellwood, 2011). It was calibrated using fossil data and included 96 species from all nominal genera for the family.

The labrid phylogeny from Cowman & Bellwood (2011) was combined with the parrotfish phylogeny of Choat *et al.* (2012). This was accomplished by grafting the parrotfish clade into the labrid tree at the appropriate node using the 'ape' package (Paradis *et al.*, 2004) in R (R Core Team, 2014). This larger phylogeny included 303 species from 70 genera.

For the Pomacentridae we employed the chronogram of Frédéric *et al.* (2013). This represents the most recent molecular and phylogenetic analysis of the family with Bayesian inferences using three nuclear and four mitochondrial genes. This chronogram also used fossil data and comprised 206 species from 28 of 29 recognized genera for the family.

For the Sparidae, we used the most well-sampled phylogeny to date (Santini *et al.*, 2014). This fossil-calibrated phylogeny was built with three mitochondrial and two nuclear genes, and included 91 species with representatives from all recognized genera for the family (see Santini *et al.*, 2014).

Geographical data

We assessed the geographical ranges of all nominal species in each family through four different sources: published data in books and papers (e.g. Allen, 1991; Randall, 2005; Kuiter, 2010), *Catalog of Fishes* (Eschmeyer, 2014), the IUCN Red List (IUCN, 2014) and FishBase (Froese & Pauly, 2014). The range data for each species were cross-checked between these four sources to avoid any probable large-scale geographical error. We then categorized each species according to its presence or absence in tropical and extratropical regions, leading to three discrete geographical states: tropical, extratropical and widespread. This categorization was made considering the isocryme of 20 °C (Fig. 1) – mean sea surface temperature for the coldest month – as a latitudinal distribution limit for tropical marine fauna (Briggs, 1974). We also calculated the proportion of species in each of the three geographical states that were present in the phylogeny of each family (Table 1).

Phylogenetic comparative methods

To test for differences in speciation, extinction and dispersal rates between tropical and extratropical regions, we used the geographic state speciation and extinction model (GeoSSE; Goldberg *et al.*, 2011), implemented in the R package 'diversitree' (FitzJohn, 2012). This is a phylogenetic comparative method that uses a similar mathematical formulation as the BiSSE (binary state speciation and extinction) model, but enables tests of evolutionary rates associated with geographical states rather than with discrete character states. Recent concerns have been raised about BiSSE and related methods (Rabosky & Goldberg, 2015) with regard to the possibility of phylogenetic pseudoreplication and high Type I error rates associated with speciation estimates. To mitigate these potential biases we employed three approaches: (1) we replicate the GeoSSE models across families of varying size and tip state ratio (Table 1); (2) we built models using the hidden state speciation and extinction (HiSSE) framework (Beaulieu & O'Meara, 2016), a new approach which considers that unmeasured characters ('hidden traits') related to the ones in

the model might be influencing diversification estimates; (3) we run simulation models to explicitly assess the Type I error rates associated with GeoSSE model in our data. By assessing models across multiple reef fish families we can identify robust patterns, and with the implementation of HiSSE we can explore the potential effects of unsampled character traits to deal with the problem of phylogenetic pseudoreplication. Simulation tests help to ensure that our results are not examples of mistaken inferences by the models (Rabosky & Goldberg, 2015).

The GeoSSE model included three speciation parameters: s_{Trop} and s_{Ex} representing the divergence of an 'endemic' (restricted to a tropical or an extratropical range) ancestral species producing two daughters in the same geographical state, or a widespread lineage giving rise to tropical or extratropical endemic lineages; and s_{Btw} representing the divergence of a widespread lineage between regions producing two daughter lineages, one in each geographical state. The parameters included in the model associated with extinction are x_{Trop} and x_{Ex} representing global lineage extinction or range contraction of a widespread lineage. The model also includes the dispersal parameter d_{Trop} , representing range expansion of tropical lineages, and d_{Ex} , representing range expansion of extratropical lineages. During model construction, all these parameters can be constrained or allowed to vary freely between regions.

We used the four chronograms to test several models that were built according to the predictions of each evolutionary hypothesis proposed to explain the LDG. First, we built unconstrained (full) models in which the seven parameters were allowed to vary freely, representing the notation of the 'out of the tropics' model of evolution that predicts differences in all rates. We also built models by constraining all rates to be equal among regions, representing the 'evolutionary time' hypothesis that predicts no difference in evolutionary rates. To represent the 'evolutionary speed' hypothesis, we built models in which only speciation rates varied geographically, constraining extinction and dispersal rates to be equal among regions. Finally, we constrained speciation and extinction to fit the 'niche conservatism' hypothesis, which predicts higher dispersal rates from the extratropics to the tropical regions. As it is not possible to constrain the direction of parameter values when fitting our models, consistency with an evolutionary hypothesis depends on a superior fit and finding the correct parameter direction. From the four evolutionary models, we built four other submodels by constraining the parameter s_{Btw} to be equal to zero to assess the effect of between-region speciation mode in each family. These combinations resulted in a set of eight models varying from the fully unconstrained ('out of the tropics') model with seven parameters to the totally constrained ('evolutionary time') model with only three parameters (Table S1 in Appendix S1 in the Supporting Information).

For the modelling process we implemented a searching procedure throughout the parameter space with 50 different combinations of initial parameters to ensure that we reached

the maximum likelihood (global optimum). After that, we used one of these convergent results as starting values to run our models. We then compared our set of models using the Akaike Information Criterion (AIC), choosing the best-fit model by the lowest delta AIC score ($\Delta\text{AIC} = 0$). To assess the power in model selection for our original data, we also used a Monte Carlo approach described by Boettiger *et al.* (2012). We simulated 100 phylogenies with parameters estimated under GeoSSE for each model ('out of the tropics', 'evolutionary speed', 'evolutionary time' and 'niche conservatism'), which resulted in four sets of 100 simulated phylogenies. Then, we assessed the distribution of likelihood ratio statistic (δ) values for each set of simulated phylogenies by re-estimating and comparing model fit for the most complex model ('out of the tropics') against each respective simpler model ('evolutionary speed', 'evolutionary time' and 'niche conservatism'). Considerable overlap among δ -value distributions reflects a lack of information for adequately distinguishing between models (Boettiger *et al.*, 2012).

After model selection, we estimated the parameters for the best-fit model in each family and sampled their posterior probability distributions using Markov Chain Monte Carlo (MCMC) to account for estimate uncertainty. The MCMC was run for 1000 generations using exponential priors from the initial likelihood function. With the resulting samples from MCMC runs we calculated the net diversification rates of each family by subtracting extinction rates from speciation rates. Within the GeoSSE model it is possible to account for incomplete sampling by including the percentage of species from each geographical state that are present in the trees. We performed the modelling procedure as described above including the percentage of sampling species for each family's phylogeny (Table 1). For a better visualization of changes through time in geographical states, we also performed a simple marginal ancestral state reconstruction with GeoSSE's initial likelihood function (Figs S1–S4 in Appendix S2).

We compared the regular time-constant GeoSSE model with a recently modified version of this model that allows the incorporation of time dependency in evolutionary rates with a function developed by Rolland *et al.* (2014). This function was created to avoid a potential bias of time variance in the estimation of evolutionary rates. For our four trees we implemented the time-variable model as in Rolland *et al.* (2014) by assuming speciation rates to vary linearly as a function of time, $s(t) = s_0 + rt$, where s_0 is the current speciation, r is the component associated with the variation in speciation rate through time and t is the interval of time from the present to the past. As we were interested in the effect of variation in speciation rates with time, dispersal and extinction rates were considered constant in the time-variable model. The results of the best-fit time-constant model were compared with the correspondent time-variable model using AIC scores to investigate the robustness of the observed patterns.

As the HiSSE method only deals with binary character states, we reclassified the widespread species as tropical or

extratropical according to the predominant geographical range for each species. Since our GeoSSE models showed a higher diversification rate for tropical lineages (see Results), we built, for each family, a character-dependent model (BiSSE equivalent) and a character-independent model in which we associated a ‘hidden’ character state with the tropical state using the HiSSE notation. All models also included the percentage of species from each measured character state that were present in the phylogenies to deal with incomplete sampling. These models were compared using AIC scores to assess if the higher tropical diversification rates were indeed associated with the geographical character or if it is likely that other unmeasured character could account for the differences observed. We implemented these analyses in the R package ‘hisse’ (Beaulieu & O’Meara, 2016).

We assessed the Type I error rates associated with the GeoSSE model for our four families by building models with simulated neutral traits. By using the package ‘diversitree’, we simulated 100 phylogenies with initial parameters estimated from our totally constrained model (‘evolutionary time’) of the empirical GeoSSE model and with respective numbers of tips for each family. For each of these neutral trees, we estimated parameters from an unconstrained GeoSSE likelihood function and assessed the posterior distribution of estimated parameters using MCMC for 1000 generations. These distributions of likelihood ratios for each parameter were compared to check if there were differences among regions, and the Type I error rates were calculated based on the proportion of neutral trees in which the estimated parameters differed among geographical regions. As suggested by Rabosky & Goldberg (2015), we employed the results from the simulations to adjust the critical value of significance by dividing the threshold of 0.05 by the growth rate of spurious results (Type I error rates/0.05) for each parameter in the four families with the empirical dataset. For those parameters in which the Type I error rates were below the threshold of 0.05, we kept this value as the critical significance level.

RESULTS

The families Chaetodontidae, Labridae and Pomacentridae contain predominantly tropical species, while the Sparidae has more extratropical than tropical species (Table 1). The set of best-supported GeoSSE models showed that tropical lineages have higher speciation rates in all families (Fig. 2, Table 2). However, the results for extinction and dispersal rates varied among families.

For Chaetodontidae, the best supported model was the ‘out of the tropics’ model that prohibits between-region speciation (Table 2). Within this model, the extinction rate was higher for extratropical lineages (Fig. 2A, Table 2). The dispersal rate was higher for tropical lineages expanding ranges into extratropical regions rather than the reverse (Fig. 2A, Table 2). Considering that the speciation rate was higher in the tropics, we found that the net diversification rate was negative for extratropical lineages (-0.446 lineages Myr^{-1})

and positive for tropical lineages (0.132 lineages Myr^{-1} ; Fig. 2A).

The best-fit model for Labridae was also the ‘out of the tropics’ model prohibiting between-region speciation (Table 2). The estimate for extinction rate in this model was higher for extratropical lineages (Fig. 2B, Table 2), and the dispersal rate was found to be higher for tropical lineages expanding ranges into the extratropics (Fig. 2B, Table 2). Based on speciation and extinction estimates, we found positive diversification rates for both tropical (0.123 lineages Myr^{-1}) and extratropical lineages (0.026 lineages Myr^{-1}), although tropical net diversification was almost five times higher (Fig. 2B).

For Pomacentridae the best-fit model was the ‘evolutionary speed’ model permitting between-region speciation (Fig. 2C, Table 2). The estimated value for between-region speciation was similar to that estimated for extratropical speciation. The extinction rate was low for both tropical and extratropical lineages, causing the difference found for the speciation rates to be the major influence in the observed difference in diversification rate among regions. We found a higher tropical net diversification rate (0.108 lineages Myr^{-1}) compared with the extratropics (0.029 lineages Myr^{-1} ; Fig. 2C).

Within the Sparidae, the best supported model was also the ‘out of the tropics’ model, but permitting between-region speciation (Fig. 2D, Table 2). The estimated between-region speciation was lower than the extratropical and tropical speciation rates in this model. The dispersal rate was higher for tropical lineages expanding ranges into the extratropics rather than in the opposite direction (Fig. 2D, Table 2). As in the Pomacentridae, the estimated extinction rate for Sparidae was low for both regions, which resulted in a higher tropical net diversification rate (0.062 lineages Myr^{-1}) compared with the extratropics (0.033 lineages Myr^{-1} ; Fig. 2D).

Although the AIC results supported ‘out of the tropics’ as the best model for Chaetodontidae, Labridae and Sparidae (Table 2), our simulations for model selection showed that, given the available phylogenetic data, it is not possible to discriminate this model from the ‘evolutionary speed’ in all four families (Fig. S5). Therefore, we can consider that these two models fit our data equally. These results do not change the overall picture, since the speciation rates estimated under the ‘evolutionary speed’ model were still higher for tropical lineages in all families (Table 2), but it limits our inferences about the roles of extinction and dispersal.

When we considered time variation in evolutionary rates, the models received little support compared with time-constant models in Pomacentridae and Sparidae (Table S2), indicating little variation in rates through time. For Chaetodontidae and Labridae, the time-variable model received support against the time-constant model, indicating that evolutionary rates varied through time in these families. However, the differences among tropical and extratropical rates showed the same pattern as in the time-constant models (Table S2), which highlights the robustness of the predicted differences among regions in the these models.

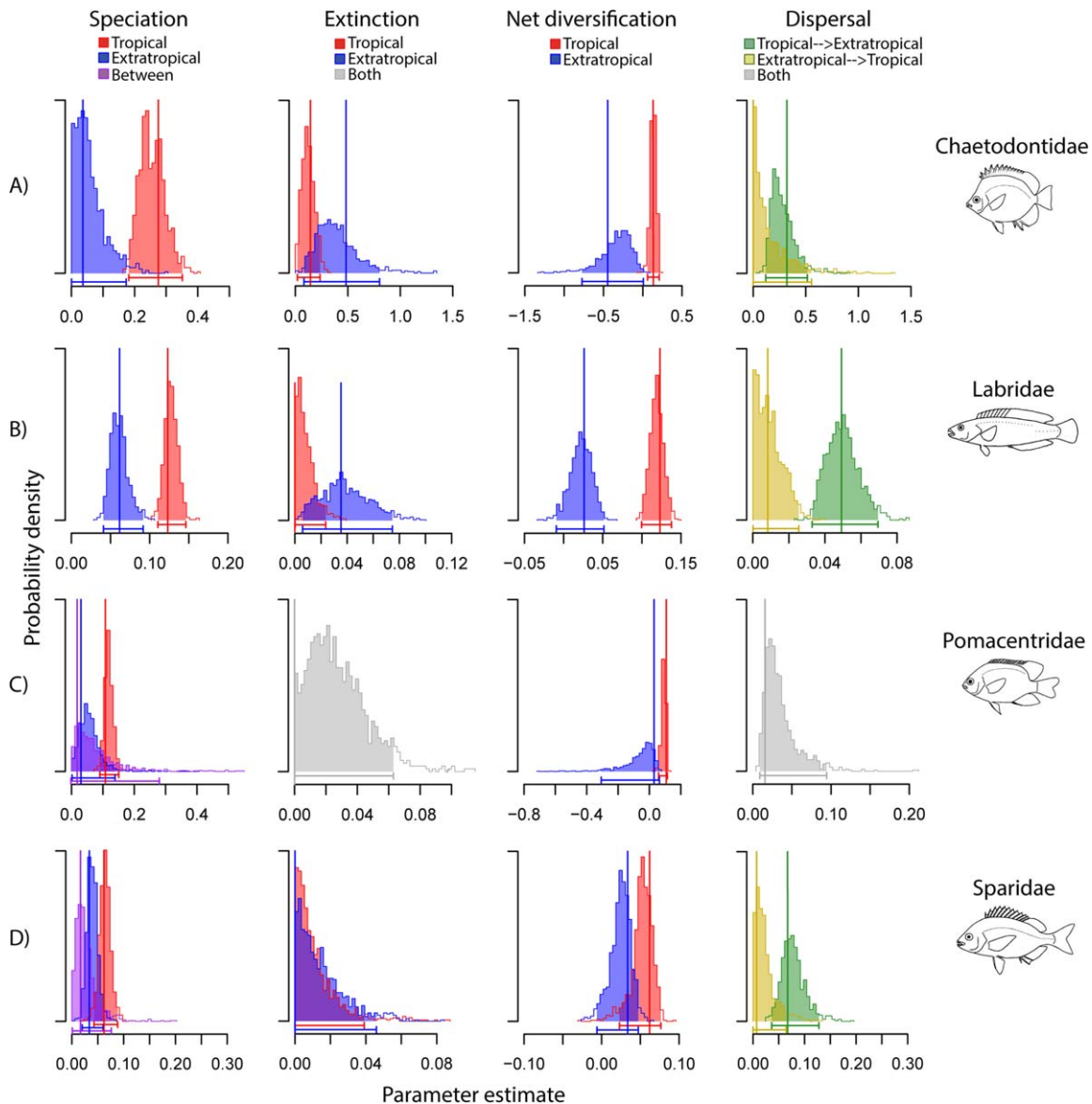


Figure 2 Rates of speciation, extinction and net diversification (speciation minus extinction) for tropical and extratropical lineages of four reef fish families. Dispersal rates are also shown with tropical lineages expanding ranges into extratropical environments and extratropical lineages expanding ranges into the tropics. Probability density plots are based on 1000 Markov Chain Monte Carlo samples of the best-fit model for each family under geographic state speciation and extinction (GeoSSE). Vertical lines represent parameter estimates based on maximum likelihood of the best-fit GeoSSE model for each family. Credibility intervals were adjusted by the Type I error rates calculated for each parameter using the results from GeoSSE simulations in each family. For Pomacentridae and Sparidae the best-fit model permitted the between-region speciation parameter to be > 0 . For Pomacentridae, dispersal and extinction were found to be equal for both tropical and extratropical lineages ('Both' in the Extinction and Dispersal columns).

The comparison of character-dependent (BiSSE equivalent) and character-independent (HiSSE) models showed that for the Chaetodontidae, Pomacentridae and Sparidae the presence of unmeasured characters could not account for rate differences, since the character-dependent model received more support (Table S3). The pattern of higher tropical diversification rates was maintained in the character-dependent model for these families, which is consistent with GeoSSE results. However, for Labridae, the character-independent model received more support (Table S3),

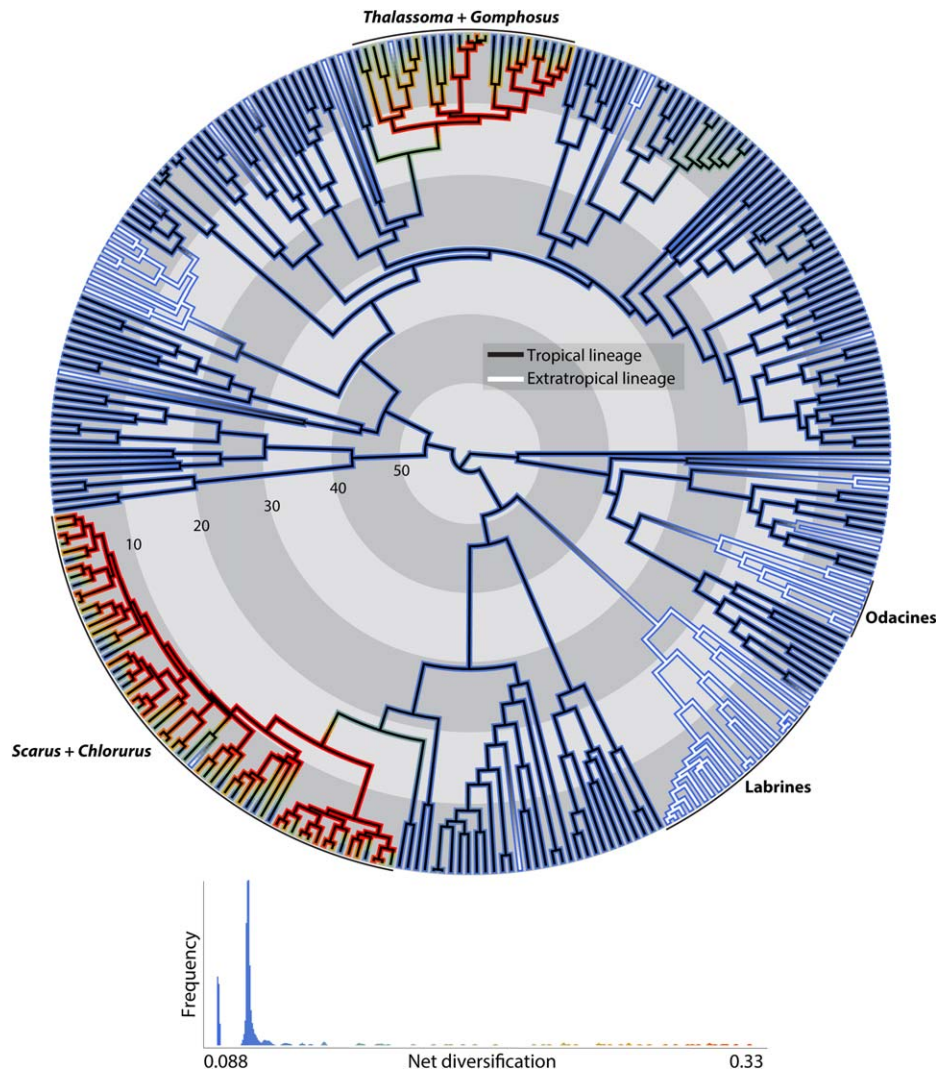
indicating that some unmeasured character might be driving the pattern of higher tropical diversification. When we plotted the net diversification along the labrid phylogeny, we detected higher rates associated with the tropical clade that includes the genus *Thalassoma* + *Gomphosus* and the tropical clade including the genus *Scarus* + *Chlorurus* (Fig. 3). These results do not invalidate the GeoSSE results as extratropical lineages were still associated with lower net diversification rates, however, they show that most tropical lineages had intermediate diversification rates, while two tropical clades

Table 2 Comparison between models constructed under geographic state speciation and extinction (GeoSSE) for each family ordered by ΔAIC , with respective degrees of freedom (d.f.), log-likelihood (lnL) and Akaike Information Criterion (AIC).

Models	d.f.	lnL	AIC	ΔAIC	s_{Trop}^*	s_{Ext}^*	s_{Btw}^*	x_{Trop}^*	x_{Ext}^*	d_{Trop}^*	d_{Ext}^*
Chaetodontidae											
Out of the tropics ($s_{Btw} = 0$)	6	-332.9	677.9	0	2.7×10^{-1}	3.6×10^{-2}	-	1.4×10^{-1}	4.8×10^{-1}	3.2×10^{-1}	3.9×10^{-8}
Out of the tropics	7	-332.9	679.9	2.0	2.7×10^{-1}	3.5×10^{-2}	2.4×10^{-10}	1.4×10^{-1}	4.8×10^{-1}	3.2×10^{-1}	2.3×10^{-8}
Evolutionary speed ($s_{Btw} = 0$)	4	-336.0	680.1	2.2	2.8×10^{-1}	3.5×10^{-2}	-	1.5×10^{-1}	-	1.5×10^{-1}	-
Evolutionary speed	5	-336.0	682.1	4.2	2.8×10^{-1}	3.5×10^{-2}	1.5×10^{-8}	1.5×10^{-1}	-	1.5×10^{-1}	-
Niche conservatism	5	-336.3	682.7	4.8	1.2×10^{-1}	-	5.3×10^{-1}	2.9×10^{-1}	-	1.7×10^{-1}	3.0
Niche conservatism ($s_{Btw} = 0$)	4	-337.4	682.9	5.0	2.4×10^{-1}	-	-	2.9×10^{-1}	-	1.0×10^{-1}	1.6
Evolutionary time ($s_{Btw} = 0$)	3	-347.1	700.3	22.4	1.9×10^{-1}	-	-	7.0×10^{-2}	-	9.5×10^{-2}	-
Evolutionary time	4	-347.1	702.3	24.4	1.9×10^{-1}	-	8.4×10^{-9}	7.0×10^{-2}	-	9.5×10^{-2}	-
Labridae											
Out of the tropics ($s_{Btw} = 0$)	6	-1279.6	2571.2	0	1.2×10^{-1}	6.1×10^{-2}	-	5.6×10^{-7}	3.5×10^{-2}	4.9×10^{-2}	8.2×10^{-3}
Out of the tropics	7	-1279.6	2573.4	2.2	1.2×10^{-1}	5.9×10^{-2}	3.3×10^{-6}	3.8×10^{-7}	4.2×10^{-2}	5.2×10^{-2}	4.5×10^{-6}
Evolutionary speed ($s_{Btw} = 0$)	4	-1284.7	2577.4	6.2	1.3×10^{-1}	2.3×10^{-2}	-	7.1×10^{-3}	-	3.3×10^{-2}	-
Evolutionary speed	5	-1284.7	2579.4	8.2	1.3×10^{-1}	5.3×10^{-2}	6.3×10^{-9}	7.1×10^{-3}	-	3.3×10^{-2}	-
Evolutionary time ($s_{Btw} = 0$)	3	-1306.5	2619.0	48.2	1.0×10^{-1}	-	-	9.2×10^{-3}	-	3.0×10^{-2}	-
Niche conservatism ($s_{Btw} = 0$)	4	-1305.7	2619.4	48.6	1.0×10^{-1}	-	-	8.1×10^{-3}	-	3.3×10^{-2}	7.4×10^{-7}
Evolutionary time	4	-1306.5	2621.0	50.2	1.0×10^{-1}	-	8.1×10^{-7}	9.1×10^{-3}	-	3.0×10^{-2}	-
Niche conservatism	5	-1305.7	2621.4	50.6	1.0×10^{-1}	-	1.2×10^{-6}	8.2×10^{-3}	-	3.3×10^{-2}	6.2×10^{-6}
Pomacentridae											
Evolutionary speed	5	-813.7	1637.5	0	1.0×10^{-1}	2.9×10^{-2}	-	5.8×10^{-9}	-	1.5×10^{-2}	-
Evolutionary speed ($s_{Btw} = 0$)	4	-815.7	1639.5	2	1.1×10^{-1}	3.7×10^{-2}	-	8.9×10^{-3}	-	1.5×10^{-2}	-
Out of the tropics	7	-813.6	1641.2	3.7	1.0×10^{-1}	3.6×10^{-2}	1.7×10^{-2}	5.2×10^{-10}	2.0×10^{-2}	1.8×10^{-2}	1.0×10^{-2}
Out of the tropics ($s_{Btw} = 0$)	6	-815.0	1642.1	4.6	1.0×10^{-1}	5.5×10^{-2}	-	3.6×10^{-7}	4.9×10^{-2}	2.1×10^{-2}	7.9×10^{-3}
Niche conservatism ($s_{Btw} = 0$)	4	-821.1	1650.2	12.7	1.0×10^{-1}	-	-	9.4×10^{-3}	-	1.1×10^{-2}	6.6×10^{-2}
Niche conservatism	5	-820.1	1650.3	12.8	1.0×10^{-1}	-	1.7×10^{-2}	3.9×10^{-3}	-	1.1×10^{-2}	7.7×10^{-2}
Evolutionary time ($s_{Btw} = 0$)	3	-822.3	1650.7	13.2	1.0×10^{-1}	-	-	4.8×10^{-3}	-	1.3×10^{-2}	-
Evolutionary time	4	-821.6	1651.3	13.8	1.0×10^{-1}	-	1.0×10^{-2}	1.8×10^{-3}	-	1.3×10^{-2}	-
Sparidae											
Out of the tropics	7	-429.3	872.7	0	6.2×10^{-2}	3.3×10^{-2}	1.6×10^{-2}	2.3×10^{-7}	2.4×10^{-7}	6.7×10^{-2}	7.1×10^{-3}
Evolutionary speed	5	-433.5	877.0	4.3	1.6×10^{-2}	2.8×10^{-7}	2.2×10^{-1}	2.8×10^{-3}	-	1.2×10^{-1}	-
Out of the tropics ($s_{Btw} = 0$)	6	-432.5	877.1	4.4	6.6×10^{-2}	4.2×10^{-2}	-	4.5×10^{-3}	1.4×10^{-2}	7.6×10^{-2}	5.4×10^{-3}
Evolutionary time ($s_{Btw} = 0$)	4	-435.3	878.6	5.9	8.4×10^{-3}	-	2.2×10^{-1}	4.1×10^{-3}	-	1.2×10^{-1}	-
Niche conservatism ($s_{Btw} = 0$)	4	-435.4	878.8	6.1	5.4×10^{-2}	-	-	8.1×10^{-3}	-	6.0×10^{-2}	1.9×10^{-2}
Evolutionary time	3	-436.8	879.7	7.0	5.5×10^{-2}	-	-	1.0×10^{-2}	-	4.0×10^{-2}	-
Niche conservatism	5	-435.2	880.4	7.7	8.8×10^{-3}	-	2.1×10^{-1}	3.6×10^{-3}	-	1.3×10^{-1}	1.1×10^{-1}
Evolutionary speed ($s_{Btw} = 0$)	4	-436.6	881.3	8.6	6.0×10^{-2}	5.2×10^{-2}	-	9.8×10^{-3}	-	3.9×10^{-2}	-

Parameter estimates are: tropical speciation (s_{Trop}^*), extratropical speciation (s_{Ext}^*), between-region speciation (s_{Btw}^*), tropical extinction (x_{Trop}^*), extratropical extinction (x_{Ext}^*), dispersal from the tropics (d_{Trop}^*), dispersal from the extratropics (d_{Ext}^*).

Figure 3 Labridae phylogeny built under hidden state speciation and extinction (HiSSE) notation, showing tropical lineages and extratropical lineages, with respective net diversification rates (colour/shade gradient from lower diversification to higher diversification). Four clades are highlighted, being two tropical clades with high net diversification rates (*Scarus + Chlorurus* and *Thalassoma + Gomphosus*), and two extratropical clades with low net diversification rates (Labrines and Odacines). The graph shows the frequency of net diversification rates on the tips of the phylogeny, highlighting that there are few lineages with high rates and more lineages with lower to intermediate rates.



displayed exceptionally higher net diversification (Fig. 3, Table S3).

The simulation results showed that the Type I error rates of the GeoSSE model are moderate to low. For speciation rates, the maximum error rates were 0.1 in Chaetodontidae, while for net diversification we detected an error rate of 0.11 in the Labridae (Table S4). For all other parameters, the GeoSSE model performed well in all families and we found Type I error rates of around 0.06 and 0.09, with some remaining below the 0.05 threshold. By using these values to adjust the critical significance value for the empirical dataset, we found no differences in results of parameter comparisons among geographical regions (Fig. 2).

DISCUSSION

We found marked differences in tropical and extratropical evolutionary rates, with tropical lineages showing higher diversification, mainly driven by greater speciation in the tropics. In addition, we report a tendency of higher dispersal rates for tropical lineages expanding ranges into the

extratropics. This suggests that the majority of extratropical lineages have arisen from tropical ones. These results support the predictions of the ‘out of the tropics’ model of evolution (Jablonski *et al.*, 2006), although we also found support for the ‘evolutionary speed’ hypothesis (Rohde, 1992). Our results confirm the tropics as an important evolutionary engine for marine environments (Briggs, 2003), and highlight the complementarity of the predictions concerning the evolutionary dynamics behind latitudinal differences in biodiversity for reef fishes. Moreover, we find that two tropical Labridae lineages exhibit much higher diversification than that expected from latitudinal differences alone.

Most reef fishes depend on available coral reef habitats, so geological climatic changes that affected these environments might have also had a negative influence in their persistence (Cowman & Bellwood, 2011; Pellissier *et al.*, 2014). The areas in which coral reef habitats remained stable over geological time served as refugia from extinction during periods of drastic climatic fluctuations, such as the Pleistocene glacial cycles (Pellissier *et al.*, 2014). Even though habitat loss resulting from climatic oscillations and tectonic activity is likely to

have caused extinctions in tropical fish and other reef-associated lineages in the past (Renema *et al.*, 2008), fracturing and isolation of refugia may also have increased the potential for speciation in some tropical regions (Pellissier *et al.*, 2014). Our results show that this effect might be less pronounced for extratropical lineages, with the lack of fragmented or stable extratropical refugia resulting in lower rates of speciation. Peripheral extratropical reefs may have acted historically as reef fish biodiversity sinks. For Chaetodontidae in particular the estimated negative net diversification indicates that the extratropics might be a recipient of lineages through speciation and dispersal from the tropics with little subsequent speciation to counteract the higher rate of extinction in the extratropics.

Patterns of diversification have previously been examined for several reef fish groups, with reef association linked to higher clade diversity (Alfaro *et al.*, 2007; Cowman & Bellwood, 2011). Here, we show that patterns of reef fish diversification also follow a clear geographical trend of higher diversification rates for tropical lineages compared with extratropical ones. Our estimated values for tropical net diversification in Chaetodontidae, Labridae and Pomacentridae are very similar to whole family estimates calculated by Cowman & Bellwood (2011), reflecting the predominance of tropical species within these families. As for Sparidae, our finding of higher tropical lineage diversification is a surprising result considering that most of the current species within this family are associated with extratropical environments. This suggests that the actual distribution of species richness within this family might be greatly influenced by lineage dispersal. By comparing our results with other works that used a similar approach but different taxa (Pyron & Wiens, 2013; Pyron, 2014; Rolland *et al.*, 2014), it is possible to infer that higher tropical net diversification might be a general pattern for vertebrates across different phylogenetic scales and in both terrestrial and marine environments.

In addition to the geographical results, we show that exceptionally high rates of lineage diversification are associated with two predominantly tropical clades in the family Labridae. Similar rate shifts in the Labridae have been reported previously (Alfaro *et al.*, 2009), associated with the tribe Julidines and a clade containing *Scarus* + *Chlorurus*. Here, we show that the rate shifts previously reported to be associated with the Julidines might represent a trickle-down effect driven by the subclade including *Thalassoma* + *Gomphosus* (Fig. 3). In the case of *Scarus* + *Chlorurus*, the previously identified shift in diversification rate was associated with their pronounced dichromatism and other social and behavioural characters related to sexual selection (Alfaro *et al.*, 2009; Kazancioglu *et al.*, 2009). It is possible that this same trait might also explain the elevated diversification rate in the clade *Thalassoma* + *Gomphosus*, since species within this group also display extreme sexual dichromatism (Kuitert, 2010). If true, then these two tropical clades might have undergone a sequential pattern of diversification (Streelman & Danley, 2003) driven by the development of complex

mating behaviours and phenotype throughout sexual selection. But a number of other factors could also be involved. Both clades also have a complex longitudinal biogeographical history (Cowman & Bellwood, 2013). Both clades have pan-tropical distributions (Bernardi *et al.*, 2004; Choat *et al.*, 2012), and in the case of *Thalassoma*, speciation and rapid range overlap have already been identified (Quenouille *et al.*, 2011). Other functional traits such as diet have also been shown to play an important role in differences in diversification rate (Lobato *et al.*, 2014). Further research is needed to tease apart the geographical and ecological components of speciation in these clades.

Although some caution has been raised recently about the SSE methods (Davis *et al.*, 2013; Rabosky & Goldberg, 2015), the differences in rate estimates we observe in the present study are consistent across families in the modelling procedure and robust when accounting for time variation. Moreover, our simulation results show that the Type I error rates from the GeoSSE model might be well below those found for the BiSSE model (Rabosky & Goldberg, 2015), which reinforces the robustness of the differences found among geographical regions. With the Monte Carlo method, we also assessed the power of our analysis to detect real differences between models, which has been considered a major issue in phylogenetic comparative methods (Boettiger *et al.*, 2012). The results from this model selection framework showed that both the 'out of the tropics' and the 'evolutionary speed' models fit our data equally and the direction of parameters estimated by these models are consistent with each evolutionary hypothesis. This highlights that differential rates of speciation have played a major and consistent role in the latitudinal differences in biodiversity for reef-associated fishes, although we cannot discard extinction and dispersal as possible drivers of this pattern.

Our results emphasize a climatic component influencing the biodiversity pattern for reef fishes, however, we do not rule out the influence of other processes that are also known to have generated and maintained reef fish diversity through time. Processes such as tectonic activity, changes in sea level, oceanographic conditions and geomorphological configuration are also recognized as important drivers of extant patterns of reef fish diversity (Renema *et al.*, 2008; Bellwood *et al.*, 2012). While these processes have been associated with the marked longitudinal diversity gradient presented by reef fishes and other reef-associated organisms, their influence on the LDG has yet to be fully determined. A better understanding of how these processes have influenced the evolution of reef fishes by altering rates of speciation, extinction and dispersal is needed. This will allow us to disentangle the historical, biogeographical and environmental factors and how they have interacted to shape global patterns of reef fish diversity.

CONCLUSIONS

Our study suggests that the tropics enhance lineage origination and may have reduced lineage extinction rates in reef

fishes while being a source of evolutionary lineages for extra-tropical environments. We also highlight two tropical lineages in the family Labridae which have undergone sequential diversification potentially associated with extreme sexual dichromatism. Alternatively, higher diversification in these clades might have been driven by longitudinal biogeography across the marine tropics. Hence, our study proposes that speciation, extinction and dispersal are key processes that generate and maintain the higher species richness of reef fish in the tropics. To our knowledge, this is the first time that these processes have been examined across multiple reef fish groups to reveal the mechanisms that promote latitudinal differences in biodiversity. We suggest that further studies should explore how these macroevolutionary dynamics influence other patterns in marine 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:

Appendix S1. Supporting tables.

Table S1. Models built according to evolutionary hypotheses.

Table S2. Comparison of time constant and time variable models.

Table S3. Comparison of character-dependent and character-independent models.

Table S4. Type I error rates of geographic state speciation and extinction model parameters for reef fish families.

Appendix S2. Supporting figures.

Figure S1. Ancestral state reconstruction for Chaetodontidae.

Figure S2. Ancestral state reconstruction for Labridae.

Figure S3. Ancestral state reconstruction for Pomacentridae.

Figure S4. Ancestral state reconstruction for Sparidae.

Figure S5. Distributions of δ -values for model comparison.

BIOSKETCH

A. C. Siqueira obtained his MSc at the Universidade Federal de Santa Catarina, being supervised by S. R. Floeter in the Marine Macroecology and Biogeography Lab. His main research interests lie in the historical, evolutionary and ecological processes that determine present-day patterns in species distributions.

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