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1 **Evolutionary processes underlying reef fish latitudinal differences in biodiversity**

2

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27

28 **ABSTRACT**

29

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

35 **Location:** Shallow water tropical and extratropical reefs globally.

36 **Methods:** Using fossil calibrated phylogenies for four reef associated fish families  
37 (Chaetodontidae, Labridae, Pomacentridae and Sparidae) we apply evolutionary models  
38 (GeoSSE and HiSSE) that allow the estimation of speciation, extinction and dispersal rates  
39 associated with geographic ranges and exploring potential biases from unsampled characters.

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

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

52

## 53 INTRODUCTION

54 Although being the most widespread macroecological pattern in the world, the latitudinal  
55 diversity gradient (LDG) remains poorly understood with respect to its generating processes  
56 (Hillebrand, 2004). This limited understanding stems from a lack of focus on the historical and  
57 evolutionary factors driving this pervasive biodiversity pattern. The uneven distribution of  
58 tropical and extratropical lineages in phylogenetic trees is an evolutionary property that arises  
59 from the LDG depending on the dynamics between speciation and extinction (Mittelbach *et al.*,  
60 2007). Besides this, the phylogenetic component of the LDG depends on the process of lineage  
61 dispersal between different ecological zones (Ricklefs, 2006). Thus, every evolutionary  
62 hypothesis concerning the LDG must take into account at least one of these three fundamental  
63 processes that alter species richness: speciation, extinction and dispersal (Dowle *et al.*, 2013).

64 Considering these processes, there are four main hypotheses to explain the phylogenetic  
65 properties arising from the LDG. (1) The '*evolutionary time*' hypothesis (Fischer, 1960),  
66 considers that tropical lineages have had more time to diversify because tropical environments  
67 remained more stable throughout geological time. According to this hypothesis, evolutionary  
68 rates would be equal among geographic regions, however, tropical lineages would be older than  
69 extratropical ones, leading to more extant species in the tropics. (2) The '*tropical niche*  
70 *conservatism*' hypothesis (Wiens & Donoghue, 2004), assumes that species that share common  
71 ancestry tend to share niche affinities. It proposes that most lineages would have originated in  
72 the tropics because tropical areas had greater geographical extent in recent geological past and  
73 that the transition to extratropical zones would be rare. In terms of evolutionary rates, speciation  
74 and extinction were supposed to be equal among geographic regions and dispersal would be  
75 more frequent from extratropical zones to the tropics. (3) The '*out of the tropics*' (Jablonski *et*  
76 *al.*, 2006) is an explicit hypothesis about differences in all evolutionary rates. It suggests that

77 lineage origination is higher in the tropics, extinction rates are higher or equal in extratropics  
78 compared to the tropics, and that tropical lineages disperse to the extratropics more frequently  
79 than the reverse. (4) Finally, the ‘*evolutionary speed*’ hypothesis (Rohde, 1992) proposes that  
80 speciation rates would be higher in tropical environments, mainly due to increased rates of  
81 molecular evolution in the tropics (reviewed in Dowle *et al.*, 2013). Thus, this hypothesis  
82 considers that extinction and dispersal rates would not vary among geographic regions.

83         Recent studies are helping to disentangle these evolutionary processes by using time-  
84 calibrated phylogenies to make explicit tests of speciation, extinction and dispersal rates  
85 between tropical and extratropical lineages (Pyron & Wiens, 2013; Pyron, 2014; Rolland *et al.*,  
86 2014). Their main results suggest higher speciation rates for tropical lineages in amphibians  
87 and mammals (Pyron & Wiens, 2013; Rolland *et al.*, 2014), but not in squamate reptiles (Pyron,  
88 2014), while higher extinction rates have been reported for extratropical lineages in all groups.  
89 As for dispersal rates, these studies showed more lineage dispersal from the extratropics to the  
90 tropics in amphibians and squamate reptiles, while mammals follow the opposite pattern. These  
91 results reinforce the idiosyncratic nature of evolutionary processes among taxonomical groups,  
92 yet they have focused on terrestrial organisms. It is still unclear which processes have been  
93 important in marine systems for generating latitudinal patterns of biodiversity.

94         Although many marine groups exhibit a strong LDG (Hillebrand, 2004), there remains a  
95 gap in our knowledge of the underlying phylogenetic component, especially in diverse systems  
96 like coral reefs. These environments tend to occupy tropical latitudinal bands, but peripheral  
97 extratropical conditions may also permit the establishment of complex, non-coral dominated  
98 reef communities (Ebeling & Hixon, 1991; Fig. 1). It is the transition from tropical coral  
99 dominated reef to extratropical rocky reef and kelp forest systems that forms the latitudinal  
100 diversity gradient for reef-associated organisms. Coral reef environments are recognized as

101 important promoters of lineage diversification, in particular for associated fishes, where they  
102 have acted as refugia for biodiversity in periods of elevated extinction (Cowman & Bellwood,  
103 2011; Pellissier *et al.*, 2014). Reef fishes not only exhibit a marked latitudinal gradient with  
104 more species in the tropics but also a striking longitudinal gradient with species richness  
105 peaking in the Indo-Australian Archipelago (Mora *et al.*, 2003). Many efforts have been  
106 devoted to understand the contemporary factors that influences these patterns (e.g. Bellwood *et*  
107 *al.*, 2005; Tittensor *et al.*, 2010), with geometric (reef area and costal length) and biogeographic  
108 variables identified as powerful predictors for reef fish species richness (Parravicini *et al.*,  
109 2013). However, as yet, no study has attempted to quantify the roles played by processes of  
110 speciation, extinction and dispersal in large-scale patterns of reef fish richness among tropical  
111 and extratropical regions.

112 Here, we employed phylogenetic comparative methods to test predictions of the  
113 evolutionary hypotheses concerning reef fish latitudinal differences in biodiversity. We used  
114 time-calibrated phylogenies of four families that are known to have representatives in both  
115 tropical and extratropical reefs to test for differences in speciation, extinction and dispersal rates  
116 among lineages. Although these three processes have not been tested for reef fishes in the  
117 context of the LDG, they are recognized as important drivers of contemporary species richness  
118 patterns for this system (Mora *et al.*, 2003). Specifically, we assessed which evolutionary  
119 hypothesis (*'evolutionary time'*, *'tropical niche conservatism'*, *'out of the topics'* or  
120 *'evolutionary speed'*) drives the formation and maintenance of higher reef fish diversity in the  
121 tropics.

122

## 123 **METHODS**

### 124 **Reef fish evolutionary relationships**

125 We examined four percomorph families with high phylogenetic resolution, known to be  
126 associated with both tropical and extratropical reef environments (Bellwood & Wainwright,  
127 2002): Chaetodontidae, Labridae, Pomacentridae and Sparidae. The Chaetodontidae, Labridae  
128 and Pomacentridae are among the most species rich families in reef environments and have a  
129 good phylogenetic resolution. However, they are predominantly associated with tropical coral  
130 reefs. To capture a good representativeness both in terms of species richness and variation in  
131 occupation of tropical vs. extratropical environments we also included the family Sparidae,  
132 which is characteristic of extratropical reefs (Bellwood & Wainwright, 2002). For our  
133 phylogenetic comparative methods, we used recent published chronograms for each family.

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

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

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

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

149

## 150 **Geographic data**

151 We assessed the geographic ranges of all nominal species in each family through four  
152 different sources: published data in books and papers (e.g. Allen, 1991; Randall, 2005; Kuitert,  
153 2010); Catalog of Fishes (Eschmeyer, 2014); IUCN's red list (IUCN, 2014); and FishBase  
154 (Froese & Pauly, 2014). The range data for each species was cross-checked between these four  
155 sources to avoid any probable large-scale geographic error. We then categorized each species  
156 according to the presence or absence in tropical and extratropical regions, leading to three  
157 discrete geographical states: tropical, extratropical and widespread. This categorization was  
158 made considering the isocryme of 20°C (Fig. 1) - mean sea surface temperature for the coldest  
159 month - as a latitudinal distribution limit for tropical marine fauna (Briggs, 1974). We also  
160 calculated the proportion of species in each of the three geographical states that were present in  
161 each family's phylogeny (Table 1).

162

## 163 **Phylogenetic Comparative methods**

164 To test for differences in speciation, extinction and dispersal rates between tropical and  
165 extratropical regions, we used the model of "Geographic State Speciation and Extinction"  
166 (GeoSSE; Goldberg *et al.*, 2011), implemented in the R package '*diversitree*' (FitzJohn, 2012).  
167 This is a phylogenetic comparative method that uses a similar mathematical formulation as the  
168 BiSSE ("Binary State Speciation and Extinction") model, but enables tests of evolutionary rates  
169 associated with geographical states rather than with discrete character states. Recent concerns  
170 have been raised about the BiSSE and related methods (Rabosky & Goldberg, 2015), regarding  
171 the possibility of phylogenetic pseudoreplication and high Type I error rates associated with  
172 speciation estimates. To mitigate these potential biases we employed three approaches: (1) We



173 replicate the GeoSSE models across families of varying size and tip state ratio (Table 1). (2)  
174 We built models using the “Hidden State Speciation and Extinction” (HiSSE) framework  
175 (Beaulieu & O’Meara, 2016), a new approach which considers that unmeasured characters  
176 (*‘hidden traits’*) related to the ones in the model might be influencing diversification estimates.  
177 (3) We run simulation models to explicitly assess the Type I error rates associated with GeoSSE  
178 model in our data. By assessing models across multiple reef fish families we can identify robust  
179 patterns, and with the implementation of HiSSE we can explore the potential effects of  
180 unsampled character traits to deal with the problem of phylogenetic pseudoreplication.  
181 Simulation tests help to assure that our results are not examples of mistaken inferences by the  
182 models (Rabosky & Goldberg, 2015).

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

193 We used the four chronograms to test several models that were built according to the  
194 predictions of each evolutionary hypothesis proposed to explain the LDG. First, we built  
195 unconstrained (full) models in which the seven parameters were allowed to vary freely,  
196 representing the notation of the ‘*out of the tropics*’ model of evolution that predicts differences

197 in all rates. We also built models by constraining all rates to be equal among regions,  
198 representing the ‘*evolutionary time*’ hypothesis that predicts no difference in evolutionary rates.  
199 To represent the ‘*evolutionary speed*’ hypothesis, we built models in which only speciation  
200 rates varied geographically, constraining extinction and dispersal rates to be equal among  
201 regions. Finally, we constrained speciation and extinction to fit the ‘*niche conservatism*’, that  
202 predicts higher dispersal rates from the extratropics to the tropical regions. As it is not possible  
203 to constrain the direction of parameter values when fitting our models, consistency with an  
204 evolutionary hypothesis depends on a superior fit and finding the correct parameter direction.  
205 From the four evolutionary models, we built four other sub-models by constraining the  $s_{\text{Btw}}$   
206 parameter to be equal to zero to assess the effect of between-region speciation mode in each  
207 family. These combinations resulted in a set of eight models varying from the fully  
208 unconstrained (‘*out of the tropics*’) model with seven parameters to the totally constrained  
209 (‘*evolutionary time*’) model with only three parameters (Table S1 - Appendix S1 in Supporting  
210 Information).

211 For the modeling process, we implemented a searching procedure throughout the  
212 parameter space with 50 different combinations of initial parameters to assure we reached the  
213 maximum likelihood (global optimum). After that, we used one of these convergent results as  
214 starting values to run our models. We then compared our set of models using Akaike  
215 Information Criterion (AIC), choosing the best-fit model by the lowest delta AIC score  
216 ( $\Delta\text{AIC}=0$ ). To assess the power in model selection for our original data, we also used a Monte  
217 Carlo approach described by Boettiger *et al.* (2012). We simulated 100 phylogenies with  
218 parameters estimated under GeoSSE for each model (‘*out of the tropics*’, ‘*evolutionary speed*’,  
219 ‘*evolutionary time*’ and ‘*niche conservatism*’), which resulted in four sets of 100 simulated  
220 phylogenies. Then, we assessed the distribution of likelihood ratio statistic ( $\delta$ ) values for each

221 set of simulated phylogenies by re-estimating and comparing model fit for the most complex  
222 model (*'out of the tropics'*) against each respective simpler models (*'evolutionary speed'*,  
223 *'evolutionary time'* and *'niche conservatism'*).

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

236 We compared the regular time-constant GeoSSE model to a recently modified version of  
237 this model that allows the incorporation of time dependency in evolutionary rates with a  
238 function developed by Rolland *et al.* (2014). This function was created to avoid a potential bias  
239 of time variance in the estimation of evolutionary rates. We implemented the time-variable  
240 model as in Rolland *et al.* (2014) for our four trees by assuming speciation rates to vary linearly  
241 as a function of time ( $s(t) = s_0 + rt$ ), where  $s_0$  is the speciation rate at present,  $r$  is the component  
242 associated with the variation in speciation rate through time and  $t$  is the interval of time from  
243 the present to the past. As we were interested in the effect of time variation in speciation rates,  
244 dispersal and extinction rates were considered constant in the time-variable model. The results

245 of the best-fit time-constant model were compared with the correspondent time-variable model  
246 using AIC scores to investigate the robustness of the observed patterns.

247 As the HiSSE method only deals with binary character states, we reclassified the  
248 widespread species as tropical or extratropical according to the predominant geographical range  
249 for each species. Since our GeoSSE models showed a higher diversification rate for tropical  
250 lineages (see results), we built, for each family, a character dependent model (BiSSE  
251 equivalent), and a character independent model in which we associated a “hidden” character  
252 state with the tropical state using the HiSSE notation. All models also included the percentage  
253 of species from each measured character state that were present in the phylogenies to deal with  
254 incomplete sampling. These models were compared using AIC scores to assess if the higher  
255 tropical diversification rates were indeed associated with the geographical character or if it is  
256 likely that other unmeasured character could account for the differences observed. We  
257 implemented these analyses in the R package ‘*hisse*’ (Beaulieu & O’Meara, 2016).

258 We assessed the Type I error rates associated with the GeoSSE model for our four families  
259 by building models with simulated neutral traits. By using the package ‘*diversitree*’, we  
260 simulated 100 phylogenies with initial parameters estimated from our totally constrained model  
261 (‘*evolutionary time*’) of the empirical GeoSSE model and with respective number of tips for  
262 each family. For each of these neutral trees, we estimated parameters from an unconstrained  
263 GeoSSE likelihood function and accessed the posterior distribution of estimated parameters  
264 using MCMC for 1000 generations. These distributions of likelihood ratios for each parameter  
265 were compared to check if there were differences among regions and the Type I error rates were  
266 calculated based on the proportion of neutral trees in which the estimated parameters differed  
267 among geographical regions. As suggested by Rabosky & Goldberg (2015), we employed the  
268 results from the simulations to adjust the critical value of significance by dividing the threshold

269 of 0.05 by the growth rate of spurious results (Type I error rates/0.05) for each parameter in the  
270 four families with the empirical dataset. For those parameters in which the Type I error rates  
271 were below the threshold of 0.05, we kept this value as the critical significance level.

272

## 273 RESULTS

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

279 For Chaetodontidae, the best supported model was the '*out of the tropics*' model that  
280 prohibits between-region speciation (Table 2). Within this model, extinction rate was higher for  
281 extratropical lineages (Fig. 2A; Table 2). Dispersal rate was higher for tropical lineages  
282 expanding ranges into extratropical regions rather than the reverse (Fig. 2A; Table 2).  
283 Considering that speciation rate was higher in the tropics, we found that net diversification rate  
284 was negative for extratropical lineages ( $-0.446$  lineages  $\text{Myr}^{-1}$ ) and positive for tropical lineages  
285 ( $0.132$  lineages  $\text{Myr}^{-1}$ ; Fig. 2A).

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

293 For Pomacentridae the best-fit model was the ‘*evolutionary speed*’ model permitting  
294 between-region speciation (Fig. 2C; Table 2). The estimated value for the between-region  
295 speciation was similar to that estimated for extratropical speciation. Extinction rate was low for  
296 both tropical and extratropical lineages, causing the difference found for speciation rates to be  
297 the major influence in the observed difference in diversification rate among regions. We found  
298 a higher tropical net diversification rate (0.108 lineages Myr<sup>-1</sup>) compared with the extratropics  
299 (0.029 lineages Myr<sup>-1</sup>; Fig. 2C).

300 Within the Sparidae, the best supported model was also the ‘*out of the tropics*’ model, but  
301 permitting between-region speciation (Fig. 2D; Table 2). The estimated between-region  
302 speciation was lower than extratropical and tropical speciation rates in this model. Dispersal  
303 rate was higher for tropical lineages expanding ranges into the extratropics rather than in the  
304 opposite direction (Fig. 2D; Table 2). As in the Pomacentridae, the estimated extinction rate for  
305 Sparidae was low for both regions, which resulted in a higher tropical net diversification rate  
306 (0.062 lineages Myr<sup>-1</sup>) compared with the extratropics (0.033 lineages Myr<sup>-1</sup>; Fig. 2D).

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

314 When we considered time variation in evolutionary rates, the models received little  
315 support compared to time-constant models in Pomacentridae and Sparidae (Table S2),  
316 indicating little variation in rates through time. For Chaetodontidae and Labridae, the time-

317 variable model received support against the time-constant model, indicating that evolutionary  
318 rates varied through time in these families. However, the differences among tropical and  
319 extratropical rates showed the same pattern as in the time-constant models (Table S2), which  
320 highlights the robustness of the predicted differences among regions in the these models.

321 The comparison of character dependent (BiSSE equivalent) and character independent  
322 (HiSSE) models showed that for the Chaetodontidae, Pomacentridae and Sparidae, the presence  
323 of unmeasured characters could not account for rate differences, since the character dependent  
324 model received more support (Table S3). The pattern of higher tropical diversification rates  
325 was maintained in the character dependent model for these families, which is consistent with  
326 GeoSSE results. However, for Labridae, the character independent model received more  
327 support (Table S3), indicating that some unmeasured character might be driving the pattern of  
328 higher tropical diversification. When we plotted the net diversification along the labrid  
329 phylogeny, we detected higher rates associated with the tropical clade that includes the genus  
330 *Thalassoma* + *Gomphosus* and the tropical clade including the genus *Scarus* + *Chlorurus* (Fig.  
331 3). These results does not invalidate the GeoSSE results as extratropical lineages were still  
332 associated with lower net diversification rates, however, they show that most tropical lineages  
333 had intermediate diversification rates, while two tropical clades displayed exceptionally higher  
334 net diversification (Fig. 3; Table S3).

335 The simulation results showed that the Type I error rates of the GeoSSE model are  
336 moderate to low. For speciation rates, the maximum error rates were 0.1 in Chaetodontidae,  
337 while for net diversification we detected an error rate of 0.11 in the Labridae (Table S4). For  
338 all other parameters, the GeoSSE model performed well in all families and we found Type I  
339 error rates around 0.06 and 0.09 with some remaining below the 0.05 threshold. By using these

340 values to adjust the critical significance value for the empirical dataset, we found no differences  
341 in results of parameter comparisons among geographical regions (Fig. 2).

342

## 343 **DISCUSSION**

344 We found marked differences in tropical and extratropical evolutionary rates with tropical  
345 lineages showing higher diversification, mainly driven by more speciation in the tropics. In  
346 addition, we report a tendency of higher dispersal rates for tropical lineages expanding ranges  
347 into the extratropics. This suggests that the majority of extratropical lineages have arisen from  
348 tropical ones. These results support the predictions of the ‘*out of the tropics*’ model of evolution  
349 (Jablonski *et al.*, 2006), although we also found support for the ‘*evolutionary speed*’ hypothesis  
350 (Rohde, 1992). Our results confirm the tropics as an important evolutionary engine for marine  
351 environments (Briggs, 2003), and highlight the complementarity of the predictions concerning  
352 the evolutionary dynamics behind latitudinal differences in biodiversity for reef fishes.  
353 Moreover, we find that two tropical Labridae lineages exhibit exceptionally higher  
354 diversification than that expected by latitudinal differences alone.

355 Most reef fishes depend on available coral reef habitats, so geological climatic changes  
356 that affected these environments might have also had a negative influence in their persistence  
357 (Cowman & Bellwood, 2011; Pellissier *et al.*, 2014). The areas in which coral reef habitats  
358 remained stable over geological times served as refugia from extinction during periods of  
359 drastic climatic fluctuations, such as the Pleistocene glacial cycles (Pellissier *et al.*, 2014). Even  
360 though habitat loss resulting from climatic oscillations and tectonic activity are likely to have  
361 caused extinctions in tropical fish and other reef associated lineages in the past (Renema *et al.*,  
362 2008), fracturing and isolation of refugia may have also increased potential for speciation in  
363 some tropical regions (Pellissier *et al.*, 2014). Our results show that this effect might be less



364 pronounced for extratropical lineages, with the lack of fragmented or stable extratropical  
365 refugia resulting in lower rates of speciation. Peripheral extratropical reefs may have  
366 historically acted as reef fish biodiversity sinks. In particular for Chaetodontidae, the estimated  
367 negative net diversification indicates that the extratropics might be a recipient of lineages  
368 through speciation and dispersal from the tropics with little subsequent speciation to counteract  
369 the extratropical higher rate of extinction.

370 Patterns of diversification have previously been examined for several reef fish groups,  
371 with reef association linked to higher clade diversity (Alfaro *et al.*, 2007; Cowman & Bellwood,  
372 2011). Here, we show that reef fish diversification patterns also follow a clear geographical  
373 trend of higher diversification rates for tropical lineages compared to extratropical ones. Our  
374 estimated values for tropical net diversification in Chaetodontidae, Labridae and Pomacentridae  
375 are very similar to whole family estimates calculated by Cowman & Bellwood (2011),  
376 reflecting the predominance of tropical species within these families. As for Sparidae, our  
377 finding of a higher tropical lineage diversification is a surprising result considering that most  
378 of the contemporary species within this family are associated with extratropical environments.  
379 This suggests that the actual species richness distribution within this family might be greatly  
380 influenced by lineage dispersal. By comparing our results to other works that used a similar  
381 approach but different taxa (Pyron & Wiens, 2013; Pyron, 2014; Rolland *et al.*, 2014), it is  
382 possible to infer that higher tropical net diversification might be a general pattern for vertebrates  
383 across different phylogenetic scales and in both terrestrial and marine environments.

384 In addition to the geographical results, we show that exceptionally high rates of lineage  
385 diversification are associated with two predominantly tropical clades in the family Labridae.  
386 Similar rate shifts in the Labridae have been reported previously (Alfaro *et al.*, 2009), associated  
387 with the tribe Julidines and a clade containing *Scarus* + *Chlorurus*. Here, we show that the rate

388 shifts previously reported to be associated with the Julidines might represent a trickle-down  
389 effect driven by the sub-clade including *Thalassoma* + *Gomphosus* (Fig. 3). In the case of  
390 *Scarus* + *Chlorurus*, the previously identified shift in diversification rate was associated with  
391 their pronounced dichromatism and other social and behavioral characters related to sexual  
392 selection (Alfaro *et al.*, 2009; Kazancioglu *et al.*, 2009). It is possible that this same trait might  
393 also explain an elevated diversification rate in the clade *Thalassoma* + *Gomphosus*, since  
394 species within this group also display extreme sexual dichromatism (Kuitert, 2010). If true, then  
395 these two tropical clades might have undergone a sequential pattern of diversification  
396 (Streelman & Danley, 2003) driven by the development of complex mating behaviors and  
397 phenotype throughout sexual selection. But, a number of other factors could also be involved.  
398 Both clades also have a complex longitudinal biogeographic history (Cowman & Bellwood,  
399 2013). Both clades have pantropical distributions (Choat *et al.*, 2012; Bernardi *et al.*, 2004),  
400 and in the case of *Thalassoma*, speciation and rapid range overlap have already been identified  
401 (Quenouille *et al.*, 2011). Other functional traits such as diet have also been shown to play an  
402 important role in diversification rate differences (Lobato *et al.*, 2014). Further research is  
403 needed to tease apart the geographic and ecological components of speciation in these clades.

404         Although some caution has been raised recently about the SSE methods (Davis *et al.*,  
405 2013; Rabosky & Goldberg, 2015), the differences in rate estimates we observe in the present  
406 study are consistent across families in the modeling procedure and robust when accounting for  
407 time variation. Moreover, our simulation results show that the Type I error rates from the  
408 GeoSSE model might be well below those found for the BiSSE model (Rabosky & Goldberg,  
409 2015), which reinforces the robustness of the differences found among geographical regions.  
410 With the Monte Carlo method, we also assessed the power of our analysis to detect real  
411 differences between models, which has been considered a major issue in phylogenetic

412 comparative methods (Boettiger *et al.*, 2012). The results from this model selection framework  
413 showed that both the ‘*out of the tropics*’ and the ‘*evolutionary speed*’ models equally fit our  
414 data and the direction of parameters estimated by these models were consistent with each  
415 evolutionary hypothesis. This highlights that differential rates of speciation have played a major  
416 and consistent role in the latitudinal differences in biodiversity for reef associated fishes,  
417 although we cannot discard extinction and dispersal as possible drivers of this pattern.

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

430

## 431 **CONCLUSIONS**

432 Our study suggests that the tropics enhance lineage origination and may have reduced  
433 lineage extinction rates in reef fishes while being a fountain of evolutionary lineages to  
434 extratropical environments. We also highlight two tropical lineages in the family Labridae  
435 which have undergone sequential diversification potentially associated with extreme sexual

436 dichromatism. Alternatively, higher diversification in these clades might have been driven by  
437 longitudinal biogeography across the marine tropics. Hence, our study proposes that speciation,  
438 extinction and dispersal are key processes that generate and maintain higher tropical reef fish  
439 species richness. To our knowledge, this is the first time that these processes have been  
440 examined across multiple reef fish groups to reveal the mechanisms that promote latitudinal  
441 differences in biodiversity. We suggest that further studies should explore how these  
442 macroevolutionary dynamics influence other patterns in marine biodiversity.

443

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570

## 571 BIOSKETCH

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

576

577



578 **TABLES**

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

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

582

583

584 **Table 2.** Comparison between models constructed under GeoSSE for each family ordered by Delta AIC  
585 ( $\Delta$ AIC), with respective degrees of freedom (d.f.), log-likelihood (lnL) and Akaike Information Criterion  
586 (AIC). Parameter estimates are: tropical speciation ( $s_{Trop}$ ), extratropical speciation ( $s_{Ex}$ ), between regions  
587 speciation ( $s_{Btw}$ ), tropical extinction ( $x_{Trop}$ ), extratropical extinction ( $x_{Ex}$ ), dispersal from the tropics  
588 ( $d_{Trop}$ ), dispersal from the extratropics ( $d_{Ex}$ ).

589

Models	d.f.	lnL	AIC	$\Delta$ AIC	$s_{Trop}$	$s_{Ex}$	$s_{Btw}$	$x_{Trop}$	$x_{Ex}$	$d_{Trop}$	$d_{Ex}$
<b>Chaetodontidae</b>											
<i>Out of the tropics</i> ( $s_{Btw}=0$ )	6	-332.9	677.9	0	2.7 e-01	3.6 e-02	-	1.4 e-01	4.8 e-01	3.2 e-01	3.9 e-08
<i>Out of the tropics</i>	7	-332.9	679.9	2.0	2.7 e-01	3.5 e-02	2.4 e-10	1.4 e-01	4.8 e-01	3.2 e-01	2.3 e-08
<i>Evolutionary speed</i> ( $s_{Btw}=0$ )	4	-336.0	680.1	2.2	2.8 e-01	3.5 e-02	-	1.5 e-01	-	1.5 e-01	-
<i>Evolutionary speed</i>	5	-336.0	682.1	4.2	2.8 e-01	3.5 e-02	1.5 e-08	1.5 e-01	-	1.5 e-01	-
<i>Niche conservatism</i>	5	-336.3	682.7	4.8	1.2 e-01	-	5.3 e-01	2.9 e-01	-	1.7 e-01	3.0
<i>Niche conservatism</i> ( $s_{Btw}=0$ )	4	-337.4	682.9	5.0	2.4 e-01	-	-	2.9 e-01	-	1.0 e-01	1.6
<i>Evolutionary time</i> ( $s_{Btw}=0$ )	3	-347.1	700.3	22.4	1.9 e-01	-	-	7.0 e-02	-	9.5 e-02	-
<i>Evolutionary time</i>	4	-347.1	702.3	24.4	1.9 e-01	-	8.4 e-09	7.0 e-02	-	9.5 e-02	-
<b>Labridae</b>											
<i>Out of the tropics</i> ( $s_{Btw}=0$ )	6	-1279.6	2571.2	0	1.2 e-01	6.1 e-02	-	5.6 e-07	3.5 e-02	4.9 e-02	8.2 e-03
<i>Out of the tropics</i>	7	-1279.6	2573.4	2.2	1.2 e-01	5.9 e-02	3.3 e-06	3.8 e-07	4.2 e-02	5.2 e-02	4.5 e-06
<i>Evolutionary speed</i> ( $s_{Btw}=0$ )	4	-1284.7	2577.4	6.2	1.3 e-01	2.3 e-02	-	7.1 e-03	-	3.3 e-02	-
<i>Evolutionary speed</i>	5	-1284.7	2579.4	8.2	1.3 e-01	5.3 e-02	6.3 e-09	7.1 e-03	-	3.3 e-02	-
<i>Evolutionary time</i> ( $s_{Btw}=0$ )	3	-1306.5	2619.0	48.2	1.0 e-01	-	-	9.2 e-03	-	3.0 e-02	-
<i>Niche conservatism</i> ( $s_{Btw}=0$ )	4	-1305.7	2619.4	48.6	1.0 e-01	-	-	8.1 e-03	-	3.3 e-02	7.4 e-07
<i>Evolutionary time</i>	4	-1306.5	2621.0	50.2	1.0 e-01	-	8.1 e-07	9.1 e-03	-	3.0 e-02	-
<i>Niche conservatism</i>	5	-1305.7	2621.4	50.6	1.0 e-01	-	1.2 e-06	8.2 e-03	-	3.3 e-02	6.2 e-06
<b>Pomacentridae</b>											
<i>Evolutionary speed</i>	5	-813.7	1637.5	0	1.0 e-01	2.9 e-02	1.7 e-02	5.8 e-09	-	1.5 e-02	-
<i>Evolutionary speed</i> ( $s_{Btw}=0$ )	4	-815.7	1639.5	2	1.1 e-01	3.7 e-02	-	8.9 e-03	-	1.5 e-02	-
<i>Out of the tropics</i>	7	-813.6	1641.2	3.7	1.0 e-01	3.6 e-02	1.7 e-02	5.2 e-10	2.0 e-02	1.8 e-02	1.0 e-02
<i>Out of the tropics</i> ( $s_{Btw}=0$ )	6	-815.0	1642.1	4.6	1.0 e-01	5.5 e-02	-	3.6 e-07	4.9 e-02	2.1 e-02	7.9 e-03
<i>Niche conservatism</i> ( $s_{Btw}=0$ )	4	-821.1	1650.2	12.7	1.0 e-01	-	-	9.4 e-03	-	1.1 e-02	6.6 e-02
<i>Niche conservatism</i>	5	-820.1	1650.3	12.8	1.0 e-01	-	1.7 e-02	3.9 e-03	-	1.1 e-02	7.7 e-02
<i>Evolutionary time</i> ( $s_{Btw}=0$ )	3	-822.3	1650.7	13.2	1.0 e-01	-	-	4.8 e-03	-	1.3 e-02	-
<i>Evolutionary time</i>	4	-821.6	1651.3	13.8	1.0 e-01	-	1.0 e-02	1.8 e-03	-	1.3 e-02	-
<b>Sparidae</b>											
<i>Out of the tropics</i>	7	-429.3	872.7	0	6.2 e-02	3.3 e-02	1.6 e-02	2.3 e-07	2.4 e-07	6.7 e-02	7.1 e-03
<i>Evolutionary speed</i>	5	-433.5	877.0	4.3	1.6 e-02	2.8 e-07	2.2 e-01	2.8 e-03	-	1.2 e-01	-
<i>Out of the tropics</i> ( $s_{Btw}=0$ )	6	-432.5	877.1	4.4	6.6 e-02	4.2 e-02	-	4.5 e-03	1.4 e-02	7.6 e-02	5.4 e-03
<i>Evolutionary time</i> ( $s_{Btw}=0$ )	4	-435.3	878.6	5.9	8.4 e-03	-	2.2 e-01	4.1 e-03	-	1.2 e-01	-
<i>Niche conservatism</i> ( $s_{Btw}=0$ )	4	-435.4	878.8	6.1	5.4 e-02	-	-	8.1 e-03	-	6.0 e-02	1.9 e-02
<i>Evolutionary time</i>	3	-436.8	879.7	7.0	5.5 e-02	-	-	1.0 e-02	-	4.0 e-02	-
<i>Niche conservatism</i>	5	-435.2	880.4	7.7	8.8 e-03	-	2.1 e-01	3.6 e-03	-	1.3 e-01	1.1 e-01
<i>Evolutionary speed</i> ( $s_{Btw}=0$ )	4	-436.6	881.3	8.6	6.0 e-02	5.2 e-02	-	9.8 e-03	-	3.9 e-02	-

590

591

592 **FIGURE LEGENDS**

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

596

597 **Figure 2.** Rates of speciation, extinction and net diversification (speciation minus extinction) for tropical  
598 (red) and extratropical (blue) lineages of four reef fish families. Dispersal rates are also shown with  
599 tropical lineages expanding ranges into extratropical environments (green) and extratropical lineages  
600 expanding ranges into the tropics (yellow). Probability density plots are based on 1000 Markov Chain  
601 Monte Carlo samples of the best-fit model for each family under GeoSSE. Vertical lines represent  
602 parameter estimates based on Maximum Likelihood of the best-fit GeoSSE model for each family.  
603 Credibility intervals were adjusted by the Type I error rates calculated for each parameter using the  
604 results from GeoSSE simulations in each family. For Pomacentridae and Sparidae the best-fit model  
605 permitted the between regions speciation parameter (purple) to be  $> 0$ . For Pomacentridae, dispersal and  
606 extinction were found to be equal for both tropical and extratropical lineages (shown in grey).

607

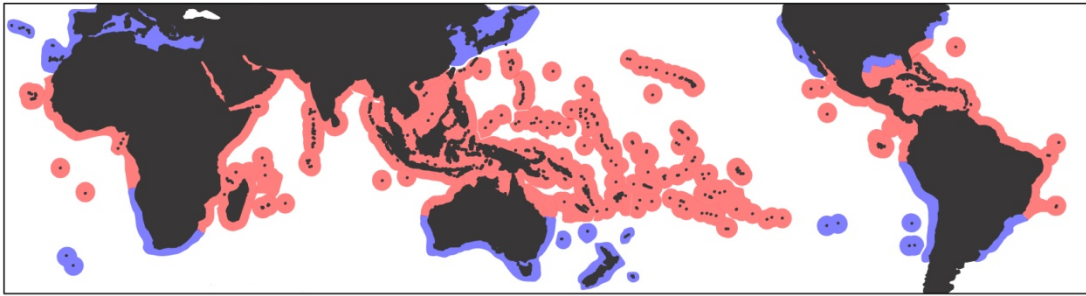
608 **Figure 3.** Labridae phylogeny built under HiSSE notation, showing tropical lineages (black branches)  
609 and extratropical lineages (white branches), with respective net diversification rates (color gradient from  
610 blue – lower diversification – to red – higher diversification). Four clades are highlighted, being two  
611 tropical clades with high net diversification rates (*Scarus* + *Chlorurus* and *Thalassoma* + *Gomphosus*),  
612 and two extratropical clades with low net diversification rates (Labrines and Odacines). The graph shows  
613 the frequency of net diversification rates on the tips of the phylogeny, highlighting that there are few  
614 lineages with high rates and more lineages with lower to intermediate rates.

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616

617 **FIGURES**

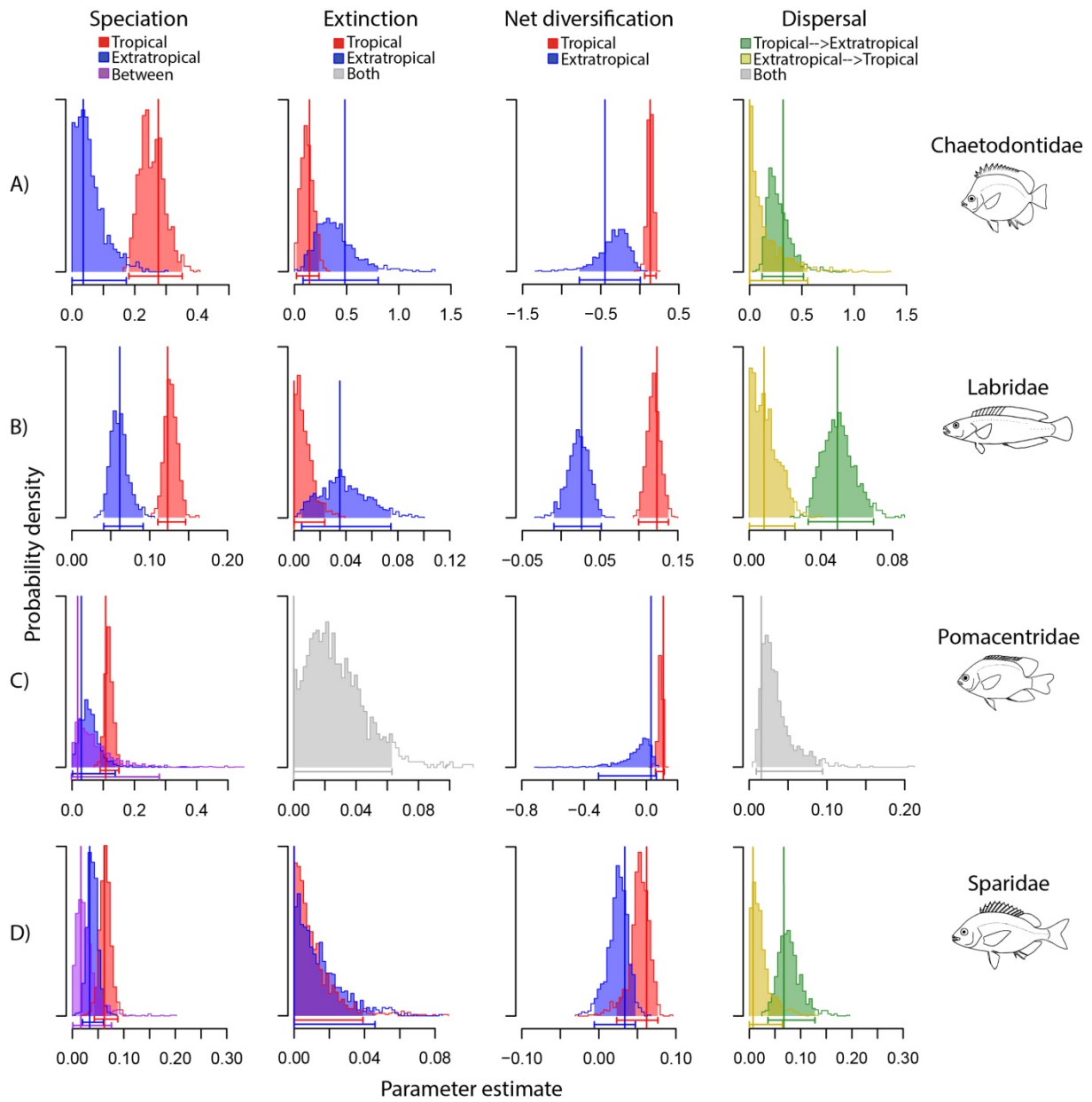
618 **Figure 1.**



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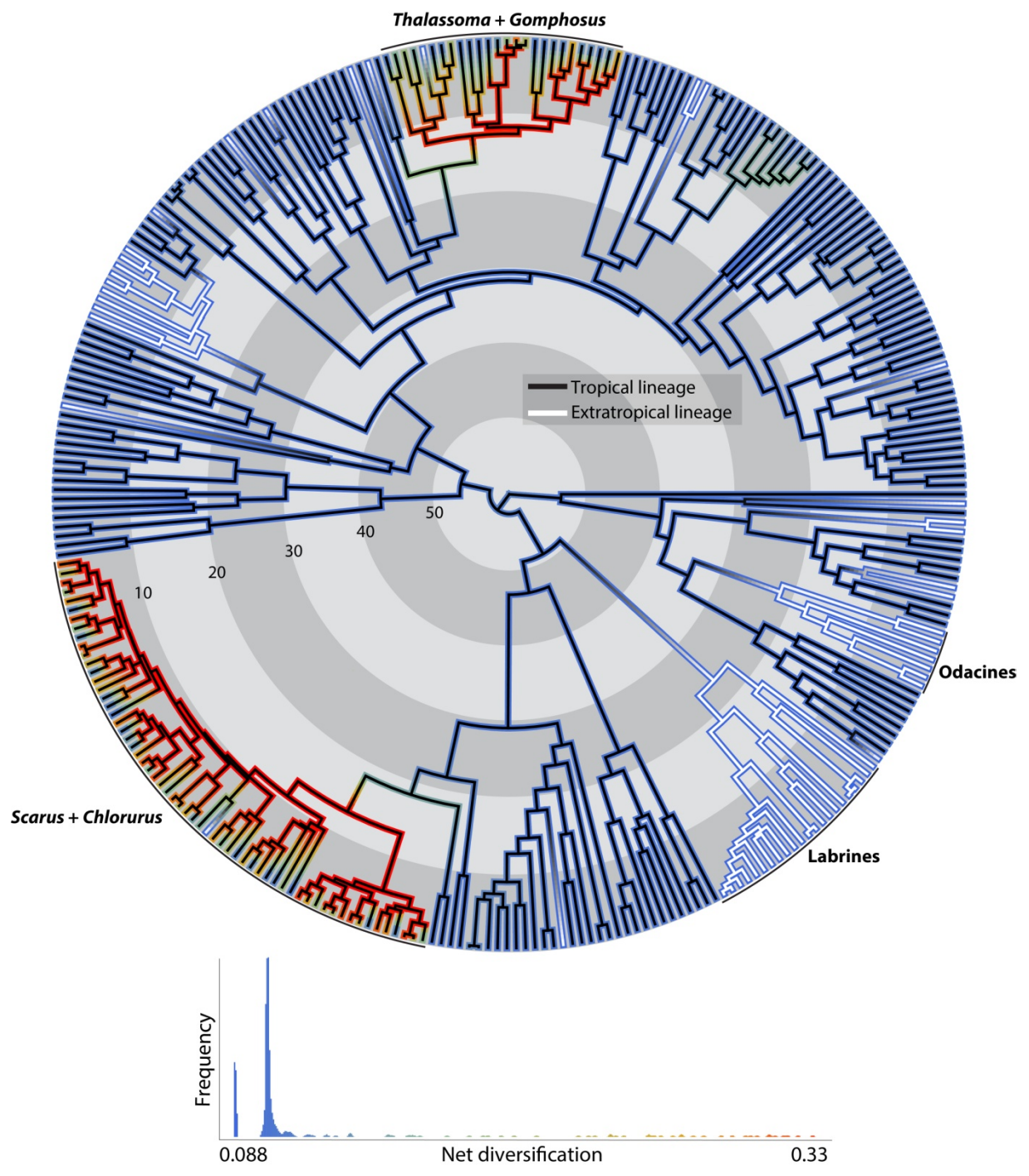
621 **Figure 2.**



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623

624 **Figure 3.**



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