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PROCESSOS EVOLUTIVOS SUBJACENTES AO GRADIENTE LATITUDINAL DE DIVERSIDADE DE PEIXES RECIFAIS

Dissertação submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do Grau de Mestre em Ecologia.

Orientador: Prof. Dr. Sergio Floeter

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"Processos evolutivos subjacentes ao gradiente latitudinal de diversidade de peixes recifais"

Por

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À vó Terezinha,
Cuja memória será eterna, trazendo conforto em seu colo e sutileza nas palavras

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“…*life is a copiously branching bush, continually pruned by the grim reaper of extinction, not a ladder of predictable progress*”

Stephen Jay Gould

RESUMO

O aumento na riqueza de espécies dos polos em direção aos trópicos é um dos padrões de distribuição da diversidade mais prevalentes na natureza. Apesar de já ter sido descrito para diversos táxons e muitas hipóteses terem sido propostas para explicá-lo, o gradiente latitudinal de diversidade (GLD) permanece pouco entendido com relação a seus processos geradores. Parte desta falta de entendimento ocorre, pois, durante muito tempo, fatores históricos e evolutivos foram negligenciados como parte da sua explicação. Os peixes recifais são modelos ideais para a análise de tais aspectos, pois apresentam grande diversidade distribuída entre ambientes tropicais e extratropicais, além de relações filogenéticas relativamente bem resolvidas. Então, com o objetivo de explorar a dinâmica evolutiva por trás do GLD de peixes recifais, o presente estudo avaliou as hipóteses de que (1) linhagens tropicais apresentam maiores taxas de diversificação do que linhagens extratropicais, (2) linhagens extratropicais são, em sua maioria, originárias de linhagens tropicais, e (3) a tolerância térmica é um atributo conservado na história evolutiva de peixes recifais. Utilizando filogenias de quatro famílias recifais, Chaetodontidae, Labridae, Pomacentridae e Sparidae, eu construí modelos evolutivos a partir de um método comparativo filogenético (GeoSSE). Este método permite estimar com máxima verossimilhança os parâmetros especiação, extinção e dispersão entre zonas geográficas a partir de filogenias calibradas no tempo. Para avaliar se espécies proximamente relacionadas tendem a compartilhar maior afinidade de nicho térmico do que o esperado ao acaso (sinal filogenético), eu usei um método de randomização de caracteres associada a uma matriz de custos de transição entre estados de caracter. As taxas de especiação foram mais elevadas e as taxas de extinção tenderam a ser menores em linhagens tropicais, embora essa diferença na extinção não tenha sido detectada em duas famílias. Combinando esses resultados, encontrei maiores taxas de diversificação líquida para linhagens tropicais em todas as famílias analisadas. Taxas de dispersão foram maiores para as linhagens com origens tropicais dispersando para ambientes extratropicais. Em três das quatro famílias analisadas (Chaetodontidae, Labridae e Sparidae) encontrei um forte sinal filogenético para o nicho térmico, sendo espécies proximamente relacionadas mais similares em termos de tolerância térmica. Ambientes tropicais são, portanto, importantes na geração e manutenção de espécies de peixes recifais, servindo ainda como fonte de linhagens para ambientes extratropicais. Os processos de especiação, extinção e dispersão de linhagens atuaram em sinergia para promover o GLD em peixes recifais. Estes resultados corroboram previsões clássicas sobre os processos evolutivos subjacentes ao gradiente latitudinal de diversidade enfatizando o essencial papel evolutivo dos ambientes tropicais marinhos. Além de desvendar o componente filogenético do GLD com peixes recifais, este trabalho ressalta a importância dos processos evolutivos na geração e manutenção dos padrões globais de diversidade biológica.

Palavras-chave: diversificação, especiação, extinção, dispersão, sinal filogenético

ABSTRACT

The increase in species richness from the poles toward the tropics is the most prevalent pattern of diversity distribution in nature. Although it has been described for many taxa and many hypotheses have been raised to explain it, the latitudinal diversity gradient (LDG) remains poorly understood with respect to its underlying processes. Part of this lack of understanding occurs because, for a long time, historical and evolutionary factors have been overlooked as part of the explanation. Reef fishes make ideal models for the analysis of these aspects, since they present great diversity distributed among tropical and extratropical environments and relatively well resolved phylogenetic relationships. The present study aimed to explore the evolutionary dynamics behind the LDG for reef fishes and evaluated the hypotheses that (1) tropical lineages have higher diversification rates than extratropical ones, (2) extratropical lineages are mainly originated from tropical ones, and (3) thermal tolerance is a conserved trait within the evolutionary history of reef fishes. Using phylogenies of four reef families, Chaetodontidae, Labridae, Pomacentridae and Sparidae, I built evolutionary models with a phylogenetic comparative method (GeoSSE). This method estimates the parameters speciation, extinction and dispersal between geographical areas by maximum likelihood from time calibrated phylogenies. To assess whether closely related species tend to share more thermal niche affinities than expected by chance (phylogenetic signal), I used a method of randomization of tip state information associated with a matrix of costs of character state transition. The speciation rates were higher and extinction rates tended to be lower in tropical lineages, although this difference in extinction has not been detected in two families. Combining these results, I found higher net diversification rates for tropical lineages in all families analyzed. Dispersal rates were higher for lineages with tropical origins dispersing into extratropical environments. In three of the four families analyzed (Chaetodontidae, Labridae and Sparidae) I found a strong phylogenetic signal for thermal niche, being closely related species more similar in terms of thermal tolerance. Tropical environments thus are important in generating and maintaining reef fish species, serving also as a source of evolutionary lineages to extratropical environments. The processes of speciation, extinction and dispersal have acted in synergy to promote the

LDG in reef fishes. These results corroborate classical predictions about the evolutionary processes underlying the latitudinal diversity gradient emphasizing the essential evolutionary role of tropical marine environments. In addition to unravel the phylogenetic component of LDG for reef fishes, this work highlights the importance of evolutionary processes in the generation and maintenance of global patterns in biodiversity.

Keywords: diversification, speciation, extinction, dispersal, phylogenetic signal

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INTRODUÇÃO GERAL

Padrões globais de diversidade biológica intrigam naturalistas e cientistas há séculos e a elucidação de seus processos subjacentes é um dos principais objetivos da Ecologia (Gaston, 2000). A influência de fatores determinísticos locais foi, durante muito tempo, um paradigma na explicação destes padrões, gerando conclusões incompletas com relação à distribuição da diversidade em maiores escalas (Ricklefs, 2006). Mais recentemente, entretanto, fatores históricos e evolutivos têm recebido maior atenção devido à grande influência que exercem na determinação da riqueza de espécies nas escalas regional e global (Cavender-Bares *et al.*, 2009). Segundo a ecologia evolutiva, padrões de diversidade biológica são muito influenciados pela dinâmica entre especiação, extinção e adaptação ao longo do processo evolutivo (Brooks & McLennan, 1991). Este processo evolutivo, por sua vez, é influenciado pelos atributos individuais dos organismos, que moldam seu desempenho nas diferentes condições ambientais em que ocorrem (Mayr, 2001). Sendo assim, a busca pela elucidação dos processos responsáveis pela geração e manutenção da riqueza de espécies deve combinar aspectos ecológicos locais, regionais e históricos para a melhor explicação dos padrões de diversidade.

O aumento no número de espécies em menores latitudes é um dos mais antigos e mais difundidos padrões ecológicos no mundo (Pianka, 1966; Rohde, 1992; Rosenzweig, 1995). Conhecido como gradiente latitudinal de diversidade (GLD), tal padrão geográfico na riqueza de espécies já havia sido reconhecido e descrito no século XIX por importantes naturalistas como Alexander von Humboldt, Alfred Russel Wallace e Charles Darwin (Hawkins, 2001; Willig *et al.*, 2003). Mais recentemente, o GLD foi formalmente quantificado em trabalhos científicos com diversos organismos como aves (Blackburn & Gaston, 1996, 1997), mamíferos (McCoy & Connor, 1980; Kaufman & Willig, 1998), peixes (Barbour & Brown, 1974), crustáceos (Dworschak, 2000), insetos (Cushman *et al.*, 1993), moluscos (Rex *et al.*, 1993), plantas (Gentry, 1988; Qian, 1998), corais (Harriott & Banks, 2002), protistas (Culver & Buzas, 2000) e bactérias (Fuhrman *et al.*, 2008). Em conjunto, estes estudos demonstram a consistência do padrão entre grupos taxonômicos e, apesar de algumas exceções terem sido documentadas (e.g. Janzen, 1981; Price *et al.*, 1998), o GLD apresenta ainda uma notável robustez entre diferentes habitats e entre escalas espaciais e temporais (Willig *et al.*, 2003; Hillebrand, 2004a). Entretanto, mesmo tendo sido reconhecida e estudada por tanto tempo, ainda há uma carência de consenso a respeito dos mecanismos que conduzem esta variação espacial na diversidade.

Diversos fatores que covariam com a latitude têm sido evocados como mecanismos causais subjacentes ao GLD, sendo difícil discriminar quaisquer deles como primordial. Aumento na disponibilidade de energia (Currie, 1991; Allen *et al.*, 2002), área (Rosenzweig, 1995) e intensidade de interações biológicas (Pianka, 1966) nos trópicos são exemplos de fatores propostos para explicar o aumento da diversidade em baixas latitudes. Porém, há um contínuo debate a respeito da importância relativa destas diferentes covariáveis e de suas possíveis interações (Currie, 1991; Rohde, 1997; Rosenzweig & Sandlin, 1997; Schemske *et al.*, 2009). Apesar de estas covariáveis apresentarem diferenças entre regiões tropicais e extratropicais, elas só podem afetar a riqueza de espécies influenciando as taxas e padrões de especiação, extinção e dispersão de linhagens (Mittelbach *et al.*, 2007; Dowle *et al.*, 2013). Portanto, explicações satisfatórias para a distribuição da diversidade entre ambientes tropicais e extratropicais devem necessariamente incluir a influência destes processos evolutivos. Sendo assim, Brown (2014) agrupou o conjunto de processos explicativos para o GLD entre dois componentes principais, sendo o primeiro ecológico e o segundo histórico. De acordo com suas conclusões, a maior energia cinética dos ambientes tropicais desencadeia respostas em diferentes escalas de organização, a partir das quais propriedades específicas emergem dos sistemas biológicos. Uma destas propriedades se relaciona ao componente filogenético das linhagens evolutivas pela relação de distribuição dos táxons entre ambientes tropicais e extratropicais em resposta à dinâmica de especiação e extinção.

Além da dinâmica entre especiação e extinção, o componente filogenético do GLD está sobre influência do processo de dispersão de linhagens entre diferentes zonas ecológicas (Ricklefs, 2006). Considerando estes fatores, existem quatro hipóteses principais para explicar a propriedade filogenética advinda do gradiente latitudinal de diversidade. A primeira, conhecida como ‘*evolutionary time hypothesis*’ (Fischer, 1960), considera que as linhagens tropicais tiveram mais tempo para diversificar, pois ambientes tropicais permaneceram relativamente mais estáveis ao longo do tempo geológico em comparação aos extratrópicos. A segunda, relacionada à primeira, é conhecida como ‘*tropical niche conservatism*’ (Wiens & Donoghue, 2004), e assume que espécies que compartilham ancestralidade comum tendem a compartilhar afinidades de nicho. Então, ela propõe que a maioria das linhagens teria se originado nos trópicos porque as áreas tropicais possuíam maior extensão geográfica no passado geológico recente e que as transições para zonas extratropicais seriam raras. Em conjunto, estas duas primeiras hipóteses preveem que linhagens tropicais seriam mais antigas enquanto as extratropicais seriam mais recentes e originárias das raras transições de linhagens vindas dos trópicos. A terceira hipótese, chamada de '*out of the tropics*' (Jablonski *et al.*, 2006), sugere que (I) a origem de linhagens (especiação) nos trópicos é maior; (II) as taxas de extinção são superiores ou iguais nos extratrópicos comparado aos trópicos; e (III) linhagens tropicais se dispersam para os extratrópicos com mais frequência do que o inverso, sem perder sua presença tropical. Finalmente, a '*evolutionary speed hypothesis*' (Rohde, 1992) propõe que as taxas de especiação seriam maiores em ambientes tropicais, principalmente devido ao aumento nas taxas de evolução molecular nos trópicos e à redução no tempo de geração de populações tropicais (revisado em Dowle *et al.*, 2013).

As hipóteses sobre a dinâmica evolutiva por trás do GLD não são mutuamente exclusivas, porém, o peso relativo de cada mecanismo pode ser variável entre períodos de tempo, regiões geográficas e escalas filogenéticas (Jansson *et al.*, 2013). Acessar o peso dos processos de especiação, extinção e dispersão foi, durante muito tempo, um fator limitante para o teste direto das hipóteses evolutivas relacionadas ao GLD pela falta de métodos específicos para tal. Entretanto, estudos recentes estão ajudando a desvendar o papel desses processos evolutivos entre ambientes tropicais e extratropicais associando o uso de métodos comparativos filogenéticos (e.g. Maddison *et al.*, 2007; Goldberg *et al.*, 2011) com filogenias calibradas no tempo (Pyron & Wiens, 2013; Pyron, 2014; Rolland *et al.*, 2014). Seus principais resultados sugerem que as taxas de especiação são maiores para linhagens tropicais em anfíbios e mamíferos (Pyron & Wiens, 2013; Rolland *et al.*, 2014), mas não em répteis da ordem Squamata (Pyron, 2014), enquanto as taxas de extinção foram mais elevadas para linhagens extratropicais em todos estes grupos. Os mesmos estudos também encontraram baixas taxas de dispersão dos trópicos para os extratrópicos em anfíbios e répteis Squamata, de acordo com o '*tropical niche conservatism*', enquanto que os mamíferos seguiram o modelo evolutivo '*out of the tropics*' com taxas mais elevadas de dispersão em direção a regiões extratropicais. Estes resultados reforçam a natureza idiossincrática dos processos evolutivos entre os grupos taxonômicos, no entanto, esses estudos foram concentrados em organismos terrestres. Para ambientes marinhos ainda não há consenso em relação à quais processos têm sido importantes para a geração do gradiente latitudinal de diversidade.

Embora muitos grupos marinhos exibam um claro GLD (Hillebrand, 2004b), ainda há uma lacuna na compreensão do componente filogenético e da história evolutiva subjacentes ao padrão, especialmente em sistemas tão diversos quanto os recifes de coral. Esses ambientes tendem ocorrer entre faixas latitudinais tropicais, já que são, em sua maioria, compostos por organismos dependentes de altas intensidades luminosas e temperaturas estáveis (Kleypas *et al.*, 1999). No entanto, condições periféricas extratropicais também podem permitir o estabelecimento de comunidades recifais complexas, como as florestas de *Kelp* e os recifes rochosos (Ebelin & Hixon, 1991). Ambientes recifais são reconhecidos como promotores de diversificação de linhagens, além de agirem como refúgios para os organismos associados em períodos de elevada extinção (Kiessling *et al.*, 2010; Cowman & Bellwood, 2011; Pellissier *et al.*, 2014). Dentre os elementos mais importantes destes ambientes estão os peixes recifais, que representam grande parte da riqueza e alocação de energia do sistema. Os peixes recifais não só exibem um gradiente latitudinal com mais espécies nos trópicos, como também um marcante gradiente longitudinal de diversidade com grande concentração espécies no arquipélago Indo-Australiano (Bellwood & Hughes, 2001; Mora *et al.*, 2003). Muitos esforços têm sido devotados a entender os fatores contemporâneos que influenciam esses padrões (e.g. Bellwood *et al.*, 2005; Tittensor *et al.*, 2010), sendo variáveis geométricas (área recifal e comprimento da costa) e biogeográficas reconhecidas como importantes preditoras da riqueza de espécies de peixes recifais (Parravicini *et al.*, 2013). Entretanto, nenhum estudo objetivou quantificar os papéis desempenhados pelos processos de especiação, extinção e dispersão na distribuição geográfica da riqueza de peixes recifais entre ambientes tropicais e extratropicais.

Apesar de desvendados alguns fatores responsáveis pela distribuição atual da riqueza de peixes recifais, ainda há uma necessidade de se explorar a dinâmica evolutiva por trás dos padrões de diversidade. Considerando que os trópicos apresentam maior estabilidade climática entre períodos geológicos com relação a ambientes extratropicais, as linhagens de ambientes recifais periféricos estariam sujeitas a maiores taxas de extinção e as comunidades seriam menos estáveis ao longo do tempo (Harmelin-Vivien, 2002). Sendo assim, ambientes recifais tropicais serviriam como fonte de acúmulo de linhagens (Cowman & Bellwood, 2013) que, paliativamente, colonizariam ambientes extratropicais ao longo da escala evolutiva. Este processo levaria a uma dinâmica de extinção de linhagens extratropicais e recolonização por linhagens evolutivas provindas dos trópicos. Com o objetivo de compreender esta dinâmica evolutiva, o presente estudo apresenta o teste de algumas predições relacionadas às hipóteses evolutivas do GLD utilizando métodos comparativos filogenéticos e peixes recifais como modelos de estudo.

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Capítulo Único

Evolutionary processes underlying reef fish latitudinal diversity gradient

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EVOLUTIONARY PROCESSES UNDERLYING REEF FISH LATITUDINAL DIVERSITY GRADIENT

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Abstract

Aim: To examine the dynamics among 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 assessed whether tropical reef fish lineages show higher diversification rates and whether the majority of extratropical reef fish lineages have originated from tropical areas. In addition, we tested whether thermal niche is a conserved trait within the evolutionary history of reef fishes.

Location: Shallow water tropical and extratropical reefs around the world.

Methods: Using fossil calibrated phylogenies for four reef associated fish families (Chaetodontidae, Labridae, Pomacentridae and Sparidae) we apply an evolutionary model (GeoSSE) that allows the estimation of speciation, extinction and dispersal rates associated with geographic range data. To test for phylogenetic signal on thermal niches, we used a method of randomization of tip state information associated with a matrix of costs of character state transition.

Results: We found that tropical lineages show higher rates of speciation and tended to have lower extinction rates, but two families share similar extinction rates among tropical and extratropical lineages. Combining these results we found higher net diversification rates for tropical lineages when compared to those in extratropical regions in all four families. Rates of dispersal were higher for lineages with tropical origins dispersing into the extratropics. In three of the four families analyzed (Chaetodontidae, Labridae, Sparidae) thermal niche was found to have a strong phylogenetic signal.

Main conclusions: Our results confirm predictions of the ‘out of the tropics’ model of evolution underlying the latitudinal diversity gradient for reef fish families extolling marine tropics as important evolutionary engines. Moreover, we show that reef fish lineages share deep thermal affinities which act in conjunction with evolutionary rates to generate and maintain the latitudinal differences in biodiversity.

Introduction

Global patterns of biological diversity have intrigued scientists and naturalists for a long time and uncovering its generating processes is one of the main aims in Ecology (Gaston, 2000). The increase in species richness from the poles toward the tropics is the most widespread ecological pattern in the world. Known as the latitudinal diversity gradient (LDG), this geographical pattern in species richness has been described for many taxonomical groups in different environments and scales (Hillebrand, 2004a). There is a wide range of hypotheses that attempt to explain the LDG, however it is difficult to distinguish any one of them as the primary mechanism underpinning this biodiversity pattern (Willig *et al.*, 2003). Although it has been described for many taxonomic groups with several hypotheses proposed to explain it, the LDG remains poorly understood with respect to its generating processes (Hillebrand, 2004a). Part of this lack of understanding occurs because, for a long time, historical and evolutionary factors have been overlooked as part of the explanation.

One of the main evolutionary properties that arise from the LDG is the uneven distribution of tropical and extratropical lineages in phylogenetic trees (Wiens & Donoghue, 2004). This phylogenetic component of lineage distribution depends on evolutionary mechanisms such as the dynamics of speciation and extinction (Mittelbach *et al.*, 2007), which seems to be ultimately affected by the higher kinetic energy in tropical environments (Brown, 2014). Besides this dynamics, the phylogenetic component of the LDG depends on the process of lineage dispersal between different ecological zones (Ricklefs, 2006). Thus, every evolutionary hypothesis 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. The first, known as ‘evolutionary time hypothesis’ (Fischer, 1960), considers that tropical lineages have had more time to diversify because tropical environments remained relatively more stable throughout geological times compared to the extratropics. The second hypothesis, known as ‘tropical niche conservatism’ (Wiens & Donoghue, 2004), assumes that species that share common ancestry tend to share similar niche affinities. It proposes that most lineages would have originated in the tropics because tropical areas had greater geographical extent in recent geological past and that the transition to extratropical zones would be rare. The third, named ‘out of the tropics’ (Jablonski *et al.*, 2006), suggests that (I) lineage origination (speciation) in the tropics is higher; (II) extinction rates are higher or equal in extratropics compared to the tropics; and (III) tropical lineages disperse to the extratropics more frequently than the reverse, without losing their tropical presence. 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).

The hypotheses concerning the evolutionary dynamics behind the LDG are not mutually exclusive, but the relative weight of each mechanism might be variable between time periods, geographic regions and phylogenetic scales (Jansson *et al.*, 2013). 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). The main results of these studies suggest that speciation rates are higher 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 have found support for the niche conservatism hypothesis in amphibians and squamate reptiles with limited dispersal from the tropics to the extratropics (Pyron & Wiens, 2013; Pyron, 2014), while mammals follow the ‘out of the tropics’ model of evolution with higher dispersal rates into extratropical areas (Rolland *et al.*, 2014). These results reinforce the idiosyncratic nature of evolutionary processes among taxonomical groups, yet these studies 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, 2004b), there is still a gap in our understanding of the underlying phylogenetic component and evolutionary history, especially in diverse systems like coral reefs. These environments tend to occupy tropical latitudinal bands, since they are mostly made up of organisms that depend of high light intensities and stable temperatures (Kleypas *et al.*, 1999). However, peripheral extratropical conditions may also allow the establishment of complex reef communities such as rocky reefs and kelp forests (Ebelin & Hixon, 1991; Fig. 1). Reef environments are also recognized as promoters of lineage diversification (Kiessling *et al.*, 2010), and to act as refugia for associated biodiversity in periods of elevated extinction (Cowman & Bellwood, 2011; Pellissier *et al.*, 2014). Among the most important elements of these environments are reef fishes, representing a major component of the system's richness and energy allocation. Reef fishes not only exhibit a marked latitudinal gradient with more species in the tropics but also a striking longitudinal diversity gradient with species richness peaking in the Indo-Australian Archipelago (Bellwood & Hughes, 2001; Mora *et al.*, 2003). Many efforts have been devoted to understand the contemporary factors that influences these patterns (e.g. Bellwood *et al.*, 2005; Tittensor *et al.*, 2010), with geometric (reef area and costal length) and biogeographic variables been identified as powerful predictors for reef fish species richness (Parravicini *et al.*, 2013). However, as yet, 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.

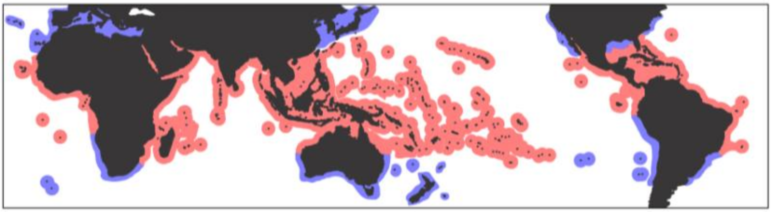

Figure 1. Map showing tropical (red) and extratropical (blue) reef locations around the world.

Here, we employed a phylogenetic comparative method (GeoSSE; Goldberg *et al.*, 2011) to test predictions about evolutionary processes underlying the reef fish latitudinal diversity gradient. We used time-calibrated phylogenies of four reef fish families that are known to have representatives in both tropical and extratropical environments to test for differences in speciation, extinction and dispersal 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 contemporary species richness patterns for this system (Mora *et al.*, 2003). Here, we accessed whether (I) tropical reef fish lineages show higher diversification rates than extratropical ones, and (II) if extratropical reef fish lineages are mainly originated from tropical ones.

Finally, we tested whether thermal niche is a conserved trait within reef fish evolutionary history.

Methods

Reef fish evolutionary relationships

We examined four perciform families with high phylogenetic resolution, known to be associated with both tropical and extratropical reef environments (Bellwood & Wainwright, 2002): the families Chaetodontidae, Labridae, Pomacentridae and Sparidae. For our phylogenetic comparative methods, we used the most recent constructed chronogram with Bayesian inferences using four mitochondrial genes and four nuclear genes for Chaetodontidae (see Cowman & Bellwood, 2011). This chronogram was calibrated using fossil data and included 95 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 – Version 3.1 (Paradis *et al.*, 2004) in R (R Core Team, 2014). This larger phylogeny including 303 species from 70 genera was then used in our comparative analysis.

For the Pomacentridae we employed the chronogram of Frédérich *et al.* (2013) for our phylogenetic comparative methods. This represents the most recent molecular and phylogenetic analysis of the family 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) in our comparative analysis. 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).

Geographic data

We assessed the geographic ranges of all nominal species in each family through four different sources: published data in books and papers (Allen, 1991; Allen *et al.*, 1998; Randall, 2005; Floeter *et al.*, 2008; Kuiter, 2010); Catalog of Fishes (Eschmeyer, 2014); IUCN's red list (IUCN, 2014); and FishBase (Froese & Pauly, 2014). The range data for each species was cross-checked among these four sources to avoid any probable large-scale geographic error. We then categorized each species according to the 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 20ºC (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 each family's phylogeny (Table S1).

Phylogenetic comparative methods

To test for differences in speciation, extinction and dispersal rates between tropical and extratropical regions, we used the model of "Geographic State Speciation and Extinction" (GeoSSE) (Goldberg *et al.*, 2011), implemented in the R package '*diversitree*' (FitzJohn, 2012). This is an explicit phylogenetic comparative method that uses a similar mathematical formulation as the BiSSE ("Binary State Speciation and Extinction") model (Maddison *et al.*, 2007). The BiSSE model uses an ultrametric phylogenetic tree with known character states for all terminal taxa to calculate the probabilities of character state changes along each branch of the tree. With these probabilities it is possible to estimate rates of speciation, extinction and character change associated with each of the two states for the whole phylogeny using a likelihood function. The GeoSSE model differs from BiSSE in that it allows species to be classified as widespread, being present in two regions simultaneously. This enables tests of evolutionary rates associated with geographical states rather than with discrete character states themselves.

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

We exposed the four family level chronograms to several models built using the parameters described above. First, we built unconstrained (full) models in which the seven parameters were allowed to vary freely. This was our basic model for comparison from which we built a set of nested sub-models. All possible combinations of sub-models were made with the constrained parameters: $\mathbf{s}_{\mathrm{Btw}}$ being equal to zero, $\mathbf{s}_{\mathrm{Trop}}$ being equal to $\mathbf{s}_{\mathrm{Ex}}$, $\mathbf{x}_{\mathrm{Trop}}$ being equal to $\mathbf{x}_{\mathrm{Ex}}$, and $\mathbf{d}_{\mathrm{Trop}}$ being equal to $\mathbf{d}_{\mathrm{Ex}}$. These combinations resulted in a set of sixteen models varying from the fully unconstrained model with seven parameters to the totally constrained model with only three parameters. We then compared this set of models using Akaike Information Criterion (AIC), choosing the best-fit model by the lowest delta AIC score (ΔAIC=0). We also performed likelihood ratio tests ($p<0.05$) to compare the support for the best-fit model against all others. 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 ran 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 speciation rates from extinction rates. For a better visualization of changes through time in geographic character states, we performed a simple marginal ancestral state reconstruction with GeoSSE's initial likelihood function.

Within the GeoSSE model it is possible to account for incomplete sampling by including the percentage of species from each geographical character state that are present in the trees. We performed the same modelling procedure as described above including the percentage of sampling species for each family's phylogeny (Table S1). This was done to test the robustness of the patterns found since the incorporation of this information reduces the power of the analysis (Goldberg *et al.*, 2011).

The GeoSSE model also 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. This happens when a possible accumulation of speciation events in the recent past would make extinction rates estimates lower in time constant models (Morlon *et al.*, 2010). We implemented the time variable model as in Rolland *et al.* (2014) for our four trees by assuming speciation rates to vary linearly as a function of time ($\boldsymbol{s}(t) = \boldsymbol{s}_0 + rt$), where $\mathbf{s}_0$ is the speciation rate at present, 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 time variation in speciation rates, the dispersal rate was constrained ($\mathbf{d}_{\mathrm{Trop}}=\mathbf{d}_{\mathrm{Ex}}$) and extinction rates were considered constant in the time variable model. The results of the time variable model were compared with the best-fit time constant model using AIC scores to investigate the robustness of the observed patterns.

To test if related species tend to have more similar geographical states than expected under a null distribution (phylogenetic signal), we used the method of ordered parsimony reconstructions and randomizations of the states across the tips in our four phylogenies (Maddison & Slatkin, 1991). This was implemented with the R function '*phylo.signal.disc*' (available: https://stat.ethz.ch/pipermail/r-sig-phylo/2011-March/001037.html) developed by Enrico Rezende. The method takes a matrix of costs of character state transition and compares the number of observed state transitions in the tree calculated by maximum-parsimony with a null-model generated by randomizations of tip state information. We set a matrix of costs that matches the GeoSSE notation, in which the widespread state is considered an intermediary state between tropical and extratropical states and the direct transition from tropical state to extratropical state is improbable and ran 999 randomizations.

Results

The families Chaetodontidae, Labridae and Pomacentridae are predominantly constituted by tropical species with some extratropical lineages, while the Sparidae has more extratropical than tropical species (Table S1). The set of best supported GeoSSE models showed that tropical lineages have higher speciation rates in all four analyzed families (Fig. 2; Table 1). However, the results for extinction and dispersal rates were variable among families.

Table 1. Comparison of best-fit models (ΔAIC $\leq$ 2) under GeoSSE for each family with respective degrees of freedom (d.f), log-likelihood (-Ln*L*), Akaike Information Criterion (AIC), Delta AIC (ΔAIC). Parameter estimates are: tropical speciation ($\mathbf{s}_{\mathrm{Trop}}$), extratropical speciation ($\mathbf{s}_{\mathrm{Ex}}$), between regions speciation ($\mathbf{s}_{\mathrm{Btw}}$), tropical extinction ($\mathbf{x}_{\mathrm{Trop}}$), extratropical extinction ($\mathbf{x}_{\mathrm{Ex}}$), dispersal from the tropics ($\mathbf{d}_{\mathrm{Trop}}$), dispersal from the extratropics ($\mathbf{d}_{\mathrm{Ex}}$).

Models	**d.f.**	**-Ln*L***	**AIC**	**ΔAIC**	$\mathbf{s}_{\mathrm{Trop}}$	$\mathbf{s}_{\mathrm{Ex}}$	$\mathbf{s}_{\mathrm{Btw}}$	$\mathbf{x}_{\mathrm{Trop}}$	$\mathbf{x}_{\mathrm{Ex}}$	$\mathbf{d}_{\mathrm{Trop}}$	$\mathbf{d}_{\mathrm{Ex}}$
Chaetodontidae											
$\mathbf{s}_{\mathrm{Btw}} = 0$	6	-333.1	678.3	0	2.0 e-01	2.6 e-02	-	5.8 e-02	3.2 e-01	2.8 e-01	2.8 e-08
$\mathbf{s}_{\mathrm{Btw}} = 0$, $\mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	5	-334.2	678.5	0.2	2.4 e-01	3.3 e-08	-	1.4 e-01	6.6 e-01	4.5 e-01	-
Full	7	-333.1	680.3	2.0	2.0 e-01	2.6 e-02	1.1 e-09	5.8 e-02	3.2 e-01	2.8 e-01	5.9 e-06
Labridae											
$\mathbf{s}_{\mathrm{Btw}} = 0$	6	-1279.7	2571.5	0	8.7 e-02	4.9 e-02	-	5.7 e-03	4.5 e-02	5.8 e-02	8.6 e-08
Full	7	-1279.7	2573.5	2.0	8.7 e-02	4.9 e-02	1.3 e-05	5.7 e-03	4.5 e-02	5.8 e-02	8.4 e-06
Pomacentridae											
$\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$, $\mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	5	-815.0	1640.6	0	8.1 e-02	1.4 e-02	1.1 e-02	4.8 e-07	-	1.2 e-02	-
$\mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	6	-819.1	1642.2	1.6	8.1 e-02	1.8 e-02	1.1 e-02	4.1 e-09	1.8 e-02	1.4 e-02	-
$\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$	6	-817.6	1642.4	1.8	8.2 e-02	1.2 e-02	1.0 e-02	1.8 e-07	-	1.2 e-02	2.0 e-05
Sparidae											
$\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$	6	-430.7	873.4	0	4.9 e-02	2.8 e-02	1.5 e-02	2.0 e-08	-	7.2 e-02	7.3 e-03
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}$, $\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$	5	-432.7	875.4	2.0	3.9 e-02	-	1.8 e-02	2.0 e-08	-	6.4 e-02	2.0 e-02
Full	7	-430.7	875.4	2.0	4.9 e-02	2.8 e-02	1.5 e-02	6.5 e-07	2.0 e-07	7.2 e-02	7.3 e-03

For the Chaetodontidae, the best-supported model considered the between-region speciation mode to be equal to zero, while other parameters were different between tropical and extratropical lineages (Table 1). Within this model, the extinction rate was higher for extratropical lineages compared to extinction rates of tropical lineages (Fig. 2A; Table 1). The dispersal rate was higher for lineages originated in the tropics dispersing into the extratropical region than the reverse (Fig. 2A; Table 1). Although this model received more support, the full parameter model and a model considering the between region speciation mode to be equal zero and equal dispersal rates also received support for Chaetodontidae (Table 1). However, both alternative models reported higher speciation rates and lower extinction rates in tropical lineages. The net diversification rate calculated for the best model was negative for extratropical lineages (-0.299 lineages Myr^{-1}) and positive for tropical lineages (0.142 lineages Myr^{-1}; Fig. 2A). The full set of GeoSSE models constructed for Chaetodontidae can be found in supplemental table S2.

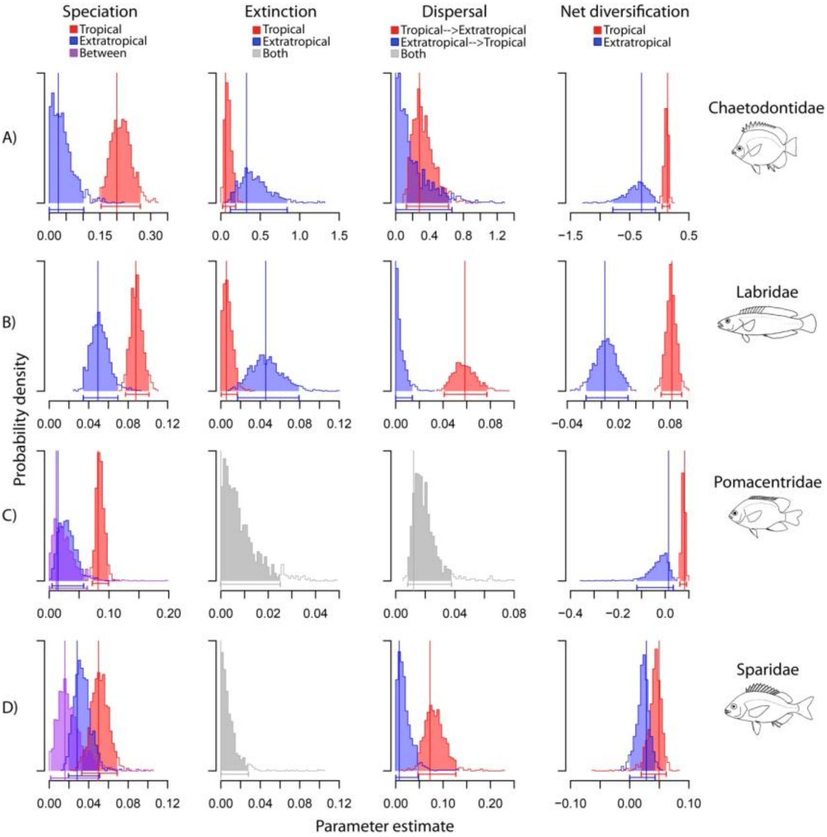

Figure 2. Rates of speciation, extinction, dispersal and net diversification (speciation minus extinction) for tropical (red) and extratropical (blue) lineages of four reef fish families, showing support for the 'Out of the Tropics' model of evolution. Probability density plots are based on 1000 Markov chain Monte Carlo samples of the best-fit model for each family under GeoSSE. Vertical lines represent parameter estimates based on Maximum Likelihood of the best-fit GeoSSE model for each family. For Pomacentridae and Sparidae the best-fit model considered the between regions speciation parameter (purple) to be >0, and extinction to be equal for both tropical and extratropical lineages (shown in grey). For Pomacentridae dispersal was also equal for lineages in both categories.

The best-fit model for the Labridae also considered the between-region speciation mode to be equal to zero (Table 1). The estimate for extinction rate in this model was higher for extratropical lineages compared to tropical ones (Fig. 2B; Table 1). Dispersal rate was found to be nearly zero for lineages that originated in the extratropics dispersing into the tropics, lower than the dispersal rate of lineages that originated in the tropics dispersing into extratropical regions (Fig. 2B; Table 1). The full model also received support in the Labridae analysis with very similar estimates for speciation, extinction and dispersal rates and a low estimated value for $\mathbf{s}_{\mathrm{Btw}}$ (Table 1). Based on the estimates for speciation and extinction rates we found positive values of net diversification for both tropical (0.082 lineages Myr^{-1}) and extratropical lineages (0.004 lineages Myr^{-1}), although tropical net diversification rate was more than twenty times higher (Fig. 2B). Supplemental table S3 shows the full set of GeoSSE models constructed for Labridae.

For the Pomacentridae the best-fit model considered both extinction and dispersal rates to be equal for tropical and extratropical lineages (Fig. 2C; Table 1). This model considers that the between-region speciation mode influenced the evolutionary history of the family with an estimated value for this parameter close to the estimated value for extratropical speciation (Fig. 2C; Table 1). The estimated value for extinction rate was low, causing the difference found for speciation rates to be the major influence in the observed difference among regions. We found a higher estimate for tropical net diversification rate (0.081 lineages Myr^{-1}) compared with extratropical diversification rate (0.014 lineages Myr^{-1}; Fig. 2C). Along with the best-fit model, three other models received support in the analysis of the Pomacentridae (Table S4): the model considering equal dispersal rates, the model with equal extinction rates, and the full model. Within these models, dispersal rates of lineages that originated in the tropics dispersing into the extratropics were higher and extinction in tropical lineages was lower (Table S4), a similar pattern found for the Chaetodontidae and Labridae.

Within the Sparidae, the best supported model considered equal extinction rates for tropical and extratropical lineages (Fig. 2D; Table 1). The estimated between-region speciation mode was lower than the extratropical and tropical speciation rates in this model. Dispersal rate was higher for lineages originated in the tropics dispersing into the extratropics than the opposite (Fig. 2D; Table 1). As in Pomacentridae, the estimated extinction rate for Sparidae was low, which resulted in a higher tropical net diversification rate (0.049 lineages Myr^{-1}) compared with the extratropical diversification rate (0.028 lineages Myr^{-1}; Fig. 2D). The model that considered both speciation and extinction rates to be equal and the full model also received support for sparids (Table 1). The dispersal rates in these models followed the same pattern of being higher for lineages with tropical origins. In the full model, the estimated value for extinction rates was higher for tropical lineages. Supplemental table S5 shows all GeoSSE models constructed for Sparidae.

When we accounted for incomplete sampling of the chronograms we found the same set of best-fit models for all families with little variation in the sequence of other supported models (Table S6). The differences between tropical and extratropical parameter estimates from the best-fit models accounting for incomplete sampling were also very similar to the observed in the analysis that did not considered missing species in all families (Fig. S1). This confirms the robustness of the patterns found in the main analysis.

When we considered time variation in evolutionary rates, the models received little support compared to the time constant models in all four families analyzed (Table S7). This indicates that the rates had little variation through time and shows that our estimates in the time constant models were not influenced by this variation.

The test of phylogenetic signal showed that the transitions between geographic states related to thermal tolerance are less common than expected by chance in the families Chaetodontidae (p=0.047), Labridae (p=0.001) and Sparidae (p=0.001; Fig. 3). This indicates that related species in these families tend to share similar thermal niches, which can be better visualized in the ancestral state reconstructions (Figs. S2−S5). Within the Pomacentridae we found that transitions between geographical states occur as expected by chance (p=0.3), which indicates no phylogenetic signal for thermal niches in this family.

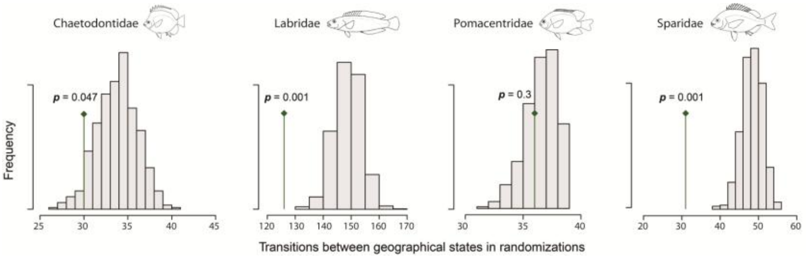

Figure 3. Phylogenetic signal of geographical categories related to thermal tolerance showing that related species tend to occupy more similar thermal niches than expected under a null distribution. Green sticks show the number of transitions observed in real data with respective significance level (*p*) compared to frequency distributions of 999 randomizations of species traits. Number of transitions was calculated by parsimony method.

Discussion

We found marked differences in tropical and extratropical evolutionary rates, with tropical lineages showing higher diversification compared to extratropical lineages in all reef fish families analyzed. This result was mainly driven by higher estimated values for tropical speciation rates and higher extratropical extinction rates. In addition to the higher tropical diversification rates, we report higher dispersal rates for lineages with tropical origins dispersing into the extratropics across all four families examined. This suggests that the majority of extratropical lineages have arisen from tropical ones. These results confirm the predictions of the ‘out of the tropics’ model of evolution (Jablonski *et al.*, 2006) for important reef fish families. In addition, we found evidence of a strong phylogenetic signal in thermal niche for three of the four families analyzed, suggesting it as a conserved trait within the evolutionary history of these reef fish groups. This is in agreement with one of the predictions of the tropical niche conservatism hypothesis, where species that share a common ancestry tend to share similar niche affinities (Wiens & Donoghue, 2004). Our results confirm the tropics as an important evolutionary engine for marine environments (Briggs, 2003), and highlights the complementarity of the predictions concerning the evolutionary dynamics behind the LDG for reef fishes.

The processes that generate and maintain biodiversity in marine environments seems to differ from those acting in terrestrial ones. While the allopatric speciation mode is believed to be the primary process of species formation in terrestrial systems, it is unlikely that this process has had the same relative importance in marine systems (Bowen *et al.*, 2013). Limited connectivity between oceanic regions imposed by biogeographic barriers might have promoted allopatric speciation in some lineages at large spatial scales (Cowman & Bellwood, 2013), but some barriers have not been effective for highly dispersive marine organisms such as reef fishes (Lessios & Robertson, 2006; Rocha & Bowen, 2008). Sympatric and parapatric speciation modes have been shown to be as important as classic allopatric or vicariant speciation in shaping longitudinal biodiversity patterns at smaller scales in tropical reefs (Bowen *et al.*, 2013). It is unclear how important marine barriers have been in promoting the LDG for fishes, but our results suggest that vicariance among these thermal zones (between-region speciation) has been rare or non-existent (Fig. 2). Our results of higher speciation rates for tropical reef fish lineages might thus be a consequence of higher opportunities for ecological specialization in tropical reef environments compared to extratropical ones, and lower rates of vicariance across latitudinal zones than longitudinal regions. This suggestion agrees with Brown (2014), who claimed that the temperature dependence of the LDG cannot be simplified to higher rates of speciation in tropical environments but it should also be related to the higher coevolutionary rates due to more and faster ecological interactions.

One of the hypothesis proposed to explain reef fish LDG is related to the influence of temperature in ecological interactions and consequently in coevolutionary rates. Harmelin-Vivien (2002) hypothesized that the long-term temperature stability in the tropics permitted more efficient use and transfer of energy in these environments, which resulted in a trophic LDG with more specialized species feeding on low quality diets (i.e. herbivores and sessile invertebrate feeders) in the tropics. Recently it has been shown that this trophic LDG could be explained by higher diversification of reef fish lineages that switched to consuming neglected low quality food items (Lobato *et al.*, 2014), suggesting a “density-dependent” diversification pattern in tropical reef fishes. Along with our findings, these works emphasize that reef fish LDG might be under the influence of both temperature dependent biotic interactions and speciation rates. Although we did not directly tested if higher rates of molecular evolution could be leading to higher speciation rates as proposed by the evolutionary speed hypothesis (Rohde, 1992), our results corroborate the prediction that speciation rates are higher in the tropics for reef fishes.

Most reef fishes depend on available tropical coral reef habitat (Bonin *et al.*, 2011), 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 families Chaetodontidae, Labridae and Pomacentridae are almost exclusively represented by reef associated species with the core of diversity occurring in tropical coral reefs (Bellwood & Wainwright, 2002). The areas in which coral reef habitats remained stable over geological times served as refugia from extinction during periods of drastic climatic fluctuations, such as the glacial cycles during the Pleistocene (Pellissier *et al.*, 2014). Even though habitat loss resulting from climatic oscillations and tectonic activity are 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 have also increased potential for speciation in some tropical regions (Pellissier *et al.*, 2014). Our results suggest that the effect of extinction is even more pronounced for extratropical lineages, with the lack of fragmented or stable extratropical refugia resulting in lower rates of speciation (Pellissier *et al.*, 2014). Our findings for Chaetodontidae and Labridae of higher extratropical extinction rates, and for Pomacentridae of equal (best-fit model) or higher extratropical extinction rates ($\mathbf{d}_{\mathrm{Trop}}=\mathbf{d}_{\mathrm{Ex}}$ and full models) suggest that peripheral extratropical reefs may have historically acted as reef fish biodiversity sinks. In particular for the Chaetodontidae a negative net diversification rate indicates the extratropics as a recipient of chaetodontid lineages through speciation in the tropics with little subsequent speciation to counteract the extratropical higher rate of extinction. As for the Sparidae, the result of equal extinction rates (best-fit model) or higher tropical extinction rate (full model) shows that climatic oscillations might have not adversely affected extratropical lineages compared to the other families examined here. This might be true considering that Sparidae contains fewer coral reef associated species than the other families analyzed and that it is mostly composed by extratropical lineages, which suggests a better adaptability to lower temperature, higher latitude environments.

Patterns of diversification have previously been examined for several reef fishes groups, with reef association linked to higher clade diversity (Alfaro *et al.*, 2007; Cowman & Bellwood, 2011) promoting morphological and ecological novelties within some lineages (Cowman *et al.*, 2009; Price *et al.*, 2011, 2013). Here, we show that reef fish diversification patterns also follow a clear geographical trend of higher net diversification rates for tropical lineages compared to extratropical ones. Our estimated values for tropical net diversification rates 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. The higher net diversification rates and the strong phylogenetic signal for thermal niche conservation support the link between latitudinal variation in marine diversity and environmental clines in sea surface temperature (Tittensor *et al.*, 2010). As for the Sparidae, our finding of a higher tropical net diversification rate is a surprising result considering that most of the contemporary species within this family are associated with extratropical environments. This suggests that the actual species richness distribution within this family might be under high influence of lineage dispersal process. Higher net diversification rates for tropical environments might be a widespread phenomenon in reef fish evolutionary history independently of the contemporary pattern of species richness distribution. By comparing our results to 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 vertebrate pattern in different phylogenetic scales and in both terrestrial and marine environments.

Complementing our results on lineage diversification, our findings for dispersal rates show clear tendencies of tropical reef fish lineages expanding their ranges to extratropical regions rather than the opposite pattern. The higher tropical dispersal rate found for Chaetodontidae confirms that, although extratropical lineages present negative diversification rates within this family, the maintenance of species in this environment is made possible by lineages dispersing from the tropics. Regarding the Sparidae, the higher dispersal rate shown for lineages with tropical origins associated with a possible higher tropical extinction rate (full model) seems to maintain the actual pattern of species richness distribution. Although net diversification rate for tropical sparid lineages is slightly higher, there is an even higher dispersal rate of lineages from the tropics that maintains more species in extratropical environments in this family. The dispersal of lineages originating in the extratropics into tropical zones seems to be unlikely in all families analyzed, since these values were close to zero. However, for Pomacentridae the dispersal rates were equal between tropical and extratropical lineages in the best-fit model. This might be associated with their different reproductive strategy since pomacentrids present a demersal spawning mode while the three other families show a pelagic egg release mode (Luiz *et al.*, 2013). Thus the low dispersal rate found for both tropical and extratropical pomacentrid lineages might be reflecting their low recolonization ability after climatic oscillations (Pellissier *et al.*, 2014) as they present shorter pelagic larval duration and lower swimming capacity in late pelagic stages (Luiz *et al.*, 2013). Overall, the main results for dispersal rates are in agreement with the 'out of the tropics' model of evolution (Jablonski *et al.*, 2006) that described the same pattern of lineage dispersal for marine invertebrates using paleontological data.

One of the predictions of the niche conservatism hypothesis is that the geographical distribution of lineages will be influenced, among other factors, by the ecological niche occupied by its ancestral lineages (Wiens & Donoghue, 2004). Our results confirmed this prediction for Chaetodontidae, Labridae and Sparidae, showing that there is a clear phylogenetic signal for thermal niches within these families. By looking at the phylogenetic ancestral state reconstructions (Figs. S2−S5) it becomes even clearer that thermal geographical states are deeply shared by some clades. Clear examples can be seen within the Labridae in the exclusively extratropical clade that includes the genus *Symphodus* and *Lapanella* and in the exclusively tropical clade including the genus *Cheilinus* and *Oxycheilinus* (Fig. S4). This phylogenetic signal was not observed for Pomacentridae, one of the two families that seem to have been influenced by speciation between regions (Fig. 1C, Table 1). This could lead to less conservation of thermal niche associated with more vicariance events between thermal zones within lineages. However, a sampling effect cannot be entirely discounted with only 1/3 of all recognized extratropical species represented in the tree (Table S1). The phylogenetic signal by itself is not enough to corroborate the niche conservatism hypothesis (Losos, 2008), however it adds an important piece of information on how thermal niche is distributed among reef fish lineages and its potential as a factor controlling latitudinal patterns of phylogenetic diversity.

Our ability to estimate accurate extinction rates from molecular phylogenies is still an important caveat in the absence of corroborating data from the fossil record (Rabosky, 2010). As recently shown, the power to precisely estimate extinction rates using the BiSSE model is lower compared to speciation and character change rates (Davis *et al.*, 2013). However, the pattern we report for extinction rates remains supported in the best-fit models even considering missing species (Fig. S1, Table S6) and time variation (Table S7) showing a general trend as predicted by the 'out of the tropics' model. It is important to note that the same study (Davis *et al.*, 2013) recommended caution when using small trees (less than 300 tips) with high tip state asymmetry (less than 10% tips in one state) because of reduced power to estimate speciation, extinction and character change rates in BiSSE. Although it is not certain if GeoSSE has the same limitations, our main focus here lies in the differences between tropical and extratropical rates rather than in the precision of the estimates. The differences in rate estimates we observe in the present study are consistent across families in the modelling procedure, independently of tree size and tip state asymmetry, and robust when accounting for incomplete sampling and time variation. This highlights that indeed differential rates of speciation, extinction and dispersal have played an important and consistent role in the LDG for reef associated fishes.

Although our results emphasize the climatic components influencing the diversity gradient for reef fishes, 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 actual 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 influenced the evolution of reef fishes by altering rates of speciation, extinction and dispersal is needed (Cowman, 2014). This will allow us to disentangle the historical, biogeographic and environmental factors and how they have interacted to shape global reef fish diversity patterns.

Conclusions

Our study suggests that the tropics enhance lineage origination and reduce lineage extinction in reef fishes while being a source of evolutionary lineages to extratropical environments. These results confirmed the main predictions of the 'out of the tropics' model of evolution for important marine groups. We have also shown that thermal niche is a conserved trait in the evolutionary history of reef fishes. Hence, our study proposes that speciation, extinction and dispersal complemented by strong thermal affinities shared by evolutionary lineages are key processes that have acted in synergy to generate and maintain higher tropical reef fish species richness. 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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Biosketch

Alexandre C. Siqueira is currently doing his masters being supervised by Sergio R. Floeter in the Marine Macroecology and Biogeography Lab (http://www.lbmm.ufsc.br/). His main interests are in evolutionary and ecological processes that determine contemporary patterns in species distributions.

Supporting Information

Appendix S1. *Supplemental tables*

Table S1 (Brief title). Proportion of species represented in phylogenies

Table S1. 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**		
State	**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 Phylo	0.89	0.71	0.56	0.62	0.44	0.67	0.57	0.56	0.33	0.83	0.59	0.79

Table S2 (Brief title). Complete set of models for Chaetodontidae

Table S2. Comparison between models constructed under GeoSSE for Chaetodontidae ordered by Delta AIC (ΔAIC), with respective degrees of freedom (d.f), log-likelihood (-Ln*L*) and Akaike Information Criterion (AIC). Parameter estimates are: tropical speciation ($\mathbf{s}_{\mathrm{Trop}}$), extratropical speciation ($\mathbf{s}_{\mathrm{Ex}}$), between regions speciation ($\mathbf{s}_{\mathrm{Btw}}$), tropical extinction ($\mathbf{x}_{\mathrm{Trop}}$), extratropical extinction ($\mathbf{x}_{\mathrm{Ex}}$), dispersal from the tropics ($\mathbf{d}_{\mathrm{Trop}}$), dispersal from the extratropics ($\mathbf{d}_{\mathrm{Ex}}$).

Models	**d.f.**	**-Ln*L***	**AIC**	**ΔAIC**	$\mathbf{s}_{\mathrm{Trop}}$	$\mathbf{s}_{\mathrm{Ex}}$	$\mathbf{s}_{\mathrm{Btw}}$	$\mathbf{x}_{\mathrm{Trop}}$	$\mathbf{x}_{\mathrm{Ex}}$	$\mathbf{d}_{\mathrm{Trop}}$	$\mathbf{d}_{\mathrm{Ex}}$
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} = 0; \mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	6	-333.16	678.3	0	2.00 e-01	2.65 e-02	-	5.84 e-02	3.26 e-01	2.80 e-01	2.87 e-08
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} = 0; \mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	5	-334.29	678.5	0.2	2.43 e-01	3.38 e-08	-	1.47 e-01	6.63 e-01	4.59 e-01	-
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} \neq 0; \mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	7	-333.16	680.3	2.0	2.00 e-01	2.65 e-02	1.18 e-09	5.87 e-02	3.27 e-01	2.81 e-01	5.94 e-06
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} \neq 0; \mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	6	-334.29	680.5	2.2	2.43 e-01	4.43 e-07	4.54 e-07	1.47 e-01	6.63 e-01	4.59 e-01	-
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} = 0; \mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	4	-337.68	683.3	5.0	0.20	-	-	0.13	0.96	0.60	-
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} = 0; \mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	4	-337.69	683.3	5.0	0.20	0.02	-	0.06	-	0.12	-
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} = 0; \mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	4	-338.02	684.0	5.7	0.18	-	-	0.22	-	0.11	2.14
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} = 0; \mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	5	-337.32	684.6	6.3	0.23	0.08	-	0.21	-	0.15	1.49
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} \neq 0; \mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	5	-337.64	685.2	6.9	0.13	-	0.18	0.23	-	0.14	3.00
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} \neq 0; \mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	5	-337.68	685.3	7.0	2.0 e-01	-	3.31 e-09	1.38 e-01	9.62 e-01	6.09 e-01	-
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} \neq 0; \mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	5	-337.69	685.3	7.0	2.02 e-01	2.31 e-02	2.15 e-07	6.32 e-02	-	1.20 e-01	-
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} = 0; \mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	5	-337.93	685.8	7.5	1.88 e-01	-	-	5.64 e-02	6.35 e-01	4.09 e-01	1.66 e-07
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} \neq 0; \mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	6	-337.32	686.6	8.3	2.33 e-01	8.80 e-02	5.96 e-08	2.10 e-01	-	1.56 e-01	1.49
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} \neq 0; \mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	6	-337.93	687.8	9.5	1.88 e-01	-	8.72 e-07	5.65 e-02	6.36 e-01	4.09 e-01	7.31 e-06
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} = 0; \mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	3	-349.61	705.2	26.9	0.14	-	-	0.03	-	0.09	-
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}; \mathbf{s}_{\mathrm{Btw}} \neq 0; \mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}; \mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	4	-349.61	707.2	28.9	1.50 e-01	-	3.35 e-08	3.41 e-02	-	9.34 e-02	-

Table S3 (Brief title). Complete set of models for Labridae

Table S3. Comparison between models constructed under GeoSSE for Labridae ordered by Delta AIC (ΔAIC), with respective degrees of freedom (d.f), log-likelihood (-Ln*L*) and Akaike Information Criterion (AIC). Parameter estimates are: tropical speciation ($\mathbf{s}_{\text{Trop}}$), extratropical speciation ($\mathbf{s}_{\text{Ex}}$), between regions speciation ($\mathbf{s}_{\text{Btw}}$), tropical extinction ($\mathbf{x}_{\text{Trop}}$), extratropical extinction ($\mathbf{x}_{\text{Ex}}$), dispersal from the tropics ($\mathbf{d}_{\text{Trop}}$), dispersal from the extratropics ($\mathbf{d}_{\text{Ex}}$).

Models	**d.f.**	**-Ln*L***	**AIC**	**ΔAIC**	$\mathbf{s}_{\text{Trop}}$	$\mathbf{s}_{\text{Ex}}$	$\mathbf{s}_{\text{Btw}}$	$\mathbf{x}_{\text{Trop}}$	$\mathbf{x}_{\text{Ex}}$	$\mathbf{d}_{\text{Trop}}$	$\mathbf{d}_{\text{Ex}}$
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	6	-1279.76	2571.5	0	8.77 e-02	4.94 e-02	-	5.73 e-03	4.55 e-02	5.84 e-02	8.65 e-08
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	7	-1279.77	2573.5	2.0	8.77 e-02	4.92 e-02	1.33 e-05	5.75 e-03	4.52 e-02	5.83 e-02	8.41 e-06
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	5	-1282.80	2575.6	4.1	9.09 e-02	3.78 e-02	-	1.21 e-02	-	4.26 e-02	4.14 e-07
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	5	-1283.76	2577.5	6.0	8.05 e-02	-	-	4.96 e-04	8.19 e-02	7.13 e-02	1.01 e-07
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	6	-1282.81	2577.6	6.1	9.09 e-02	3.78 e-02	1.02 e-07	1.21 e-02	-	4.27 e-02	5.32 e-06
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	6	-1283.76	2579.5	8.0	8.04 e-02	-	2.31 e-07	4.82 e-04	8.17 e-02	7.12 e-02	5.03 e-08
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	4	-1288.45	2584.9	13.3	9.02 e-02	4.58 e-02	-	1.32 e-02	-	3.47 e-02	-
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	5	-1288.45	2586.9	15.4	9.01 e-02	4.59 e-02	-	1.31 e-02	1.34 e-02	3.47 e-02	-
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	5	-1288.45	2586.9	15.4	9.02 e-02	4.58 e-02	1.56 e-07	1.32 e-02	-	3.47 e-02	-
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	6	-1288.45	2588.9	17.4	9.01 e-02	4.59 e-02	1.81 e-08	1.31 e-02	1.33 e-02	3.47 e-02	-
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	4	-1295.78	2599.5	28.0	7.63 e-02	-	-	4.88 e-03	3.56 e-02	3.73 e-02	-
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	5	-1295.78	2601.5	30.0	7.63 e-02	-	1.13 e-07	4.87 e-03	3.56 e-02	3.73 e-02	-
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	3	-1299.73	2605.4	33.9	7.55 e-02	-	-	1.25 e-02	1.25 e-02	3.36 e-02	-
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	4	-1299.06	2606.1	34.6	7.59 e-02	-	-	1.17 e-02	-	3.75 e-02	1.55 e-02
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	4	-1299.73	2607.4	35.9	7.54 e-02	-	4.04 e-06	1.25 e-02	-	3.35 e-02	-
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	5	-1299.06	2608.1	36.6	7.59 e-02	-	5.05 e-08	1.17 e-02	-	3.75 e-02	1.57 e-02

Table S4 (Brief title). Complete set of models for Pomacentridae

Table S4. Comparison between models constructed under GeoSSE for Pomacentridae ordered by Delta AIC (ΔAIC), with respective degrees of freedom (d.f), log-likelihood (-Ln*L*) and Akaike Information Criterion (AIC). Parameter estimates are: tropical speciation ($\mathbf{s}_{\text{Trop}}$), extratropical speciation ($\mathbf{s}_{\text{Ex}}$), between regions speciation ($\mathbf{s}_{\text{Btw}}$), tropical extinction ($\mathbf{x}_{\text{Trop}}$), extratropical extinction ($\mathbf{x}_{\text{Ex}}$), dispersal from the tropics ($\mathbf{d}_{\text{Trop}}$), dispersal from the extratropics ($\mathbf{d}_{\text{Ex}}$).

Models	**d.f.**	**-Ln*L***	**AIC**	**ΔAIC**	$\mathbf{s}_{\text{Trop}}$	$\mathbf{s}_{\text{Ex}}$	$\mathbf{s}_{\text{Btw}}$	$\mathbf{x}_{\text{Trop}}$	$\mathbf{x}_{\text{Ex}}$	$\mathbf{d}_{\text{Trop}}$	$\mathbf{d}_{\text{Ex}}$
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	5	-815.01	1640.6	0	8.18 e-02	1.45 e-02	1.17 e-02	4.88 e-07	-	1.20 e-02	-
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	6	-819.18	1642.2	1.6	8.18 e-02	1.87 e-02	1.19 e-02	4.16 e-09	1.81 e-02	1.43 e-02	-
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	6	-817.67	1642.4	1.8	8.21 e-02	1.26 e-02	1.04 e-02	1.82 e-07	-	1.23 e-02	2.07 e-05
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	7	-819.92	1644.0	3.4	8.21 e-02	1.65 e-02	1.07 e-02	4.08 e-08	2.24 e-02	1.54 e-02	1.51 e-07
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	5	-815.23	1645.8	5.2	8.17 e-02	3.60 e-02	-	2.17 e-06	5.41 e-02	1.82 e-02	-
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	4	-815.10	1646.9	6.3	8.65 e-02	1.63 e-02	-	8.41 e-03	-	1.28 e-02	-
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	6	-815.30	1647.3	5.7	8.21 e-02	3.23 e-02	-	1.06 e-06	6.20 e-02	2.05 e-02	2.16 e-06
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	4	-819.45	1647.9	6.7	7.91 e-02	-	-	2.37 e-07	1.02 e-01	2.24 e-02	-
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	5	-819.18	1648.3	7.2	7.85 e-02	-	9.55 e-03	6.85 e-09	9.81 e-02	2.20 e-02	-
$\mathbf{s}_{\text{Trop}} \neq \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	5	-817.92	1648.9	7.7	8.65 e-02	1.39 e-02	-	7.94 e-03	-	1.31 e-02	1.99 e-06
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	5	-819.49	1649.8	8.3	7.94 e-02	-	-	2.13 e-08	1.10 e-01	2.40 e-02	1.45 e-02
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} \neq \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	6	-824.88	1650.3	9.2	7.84 e-02	-	9.72 e-03	2.49 e-10	9.55 e-02	2.15 e-02	2.46 e-02
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	5	-819.94	1659.7	19.1	7.40 e-02	-	2.04 e-02	2.34 e-07	-	1.02 e-02	5.18 e-02
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} \neq 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	4	-827.81	1660.0	19.4	7.50 e-02	-	1.52 e-02	4.07 e-07	-	1.17 e-02	-
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} \neq \mathbf{d}_{\text{Ex}}$	4	-826.01	1663.6	23.0	8.04 e-02	-	-	1.17 e-02	-	1.08 e-02	7.28 e-02
$\mathbf{s}_{\text{Trop}} = \mathbf{s}_{\text{Ex}}$; $\mathbf{s}_{\text{Btw}} = 0$; $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$; $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	3	-829.29	1664.5	23.9	8.02 e-02	-	-	8.87 e-03	-	1.23 e-02	-

Table S5 (Brief title). Complete set of models for Sparidae

Table S5. Comparison between models constructed under GeoSSE for Sparidae ordered by Delta AIC (ΔAIC), with respective degrees of freedom (d.f), log-likelihood (-Ln*L*) and Akaike Information Criterion (AIC). Parameter estimates are: tropical speciation ($\mathbf{s}_{\mathrm{Trop}}$), extratropical speciation ($\mathbf{s}_{\mathrm{Ex}}$), between regions speciation ($\mathbf{s}_{\mathrm{Btw}}$), tropical extinction ($\mathbf{x}_{\mathrm{Trop}}$), extratropical extinction ($\mathbf{x}_{\mathrm{Ex}}$), dispersal from the tropics ($\mathbf{d}_{\mathrm{Trop}}$), dispersal from the extratropics ($\mathbf{d}_{\mathrm{Ex}}$).

Models	**d.f.**	**-Ln*L***	**AIC**	**ΔAIC**	$\mathbf{s}_{\mathrm{Trop}}$	$\mathbf{s}_{\mathrm{Ex}}$	$\mathbf{s}_{\mathrm{Btw}}$	$\mathbf{x}_{\mathrm{Trop}}$	$\mathbf{x}_{\mathrm{Ex}}$	$\mathbf{d}_{\mathrm{Trop}}$	$\mathbf{d}_{\mathrm{Ex}}$
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} \neq 0$; $\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	6	-430.74	873.4	0	4.98 e-02	2.82 e-02	1.59 e-02	2.06 e-08	-	7.24 e-02	7.30 e-03
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} \neq 0$; $\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	5	-432.74	875.4	2.0	3.90 e-02	-	1.86 e-02	2.00 e-08	-	6.47 e-02	2.04 e-02
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} \neq 0$; $\mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	7	-430.74	875.4	2.0	4.98 e-02	2.82 e-02	1.59 e-02	6.50 e-07	2.03 e-07	7.24 e-02	7.36 e-03
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} \neq 0$; $\mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	6	-432.74	877.4	4.0	3.90 e-02	-	1.85 e-02	1.46 e-06	1.71 e-06	6.47 e-02	2.04 e-02
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} \neq 0$; $\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	4	-435.19	878.3	4.9	3.96 e-02	-	1.95 e-02	1.40 e-07	-	3.84 e-02	-
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} \neq 0$; $\mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	5	-434.89	879.7	6.3	4.02 e-02	-	1.96 e-02	9.05 e-03	6.59 e-09	4.30 e-02	-
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} \neq 0$; $\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	5	-435.19	880.3	6.9	3.91 e-02	3.99 e-02	1.95 e-02	4.48 e-08	-	3.84 e-02	-
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} = 0$; $\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	5	-435.61	881.2	7.8	5.7 e-02	3.32 e-02	-	1.19 e-02	-	8.07 e-02	7.99 e-03
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} = 0$; $\mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	5	-435.64	881.2	7.8	4.80 e-02	-	-	1.97 e-07	3.36 e-02	1.10 e-01	4.52 e-03
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} \neq 0$; $\mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	6	-434.76	881.5	8.1	4.52 e-02	3.75 e-02	1.93 e-02	1.42 e-02	2.16 e-07	4.54 e-02	-
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} = 0$; $\mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	6	-435.41	882.8	9.4	5.31 e-02	3.99 e-02	-	4.48 e-03	2.51 e-02	9.96 e-02	4.93 e-03
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} = 0$; $\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} \neq \mathbf{d}_{\mathrm{Ex}}$	4	-437.68	883.3	9.9	4.63 e-02	-	-	1.27 e-02	-	7.28 e-02	2.21 e-02
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} = 0$; $\mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	5	-436.97	883.9	10.5	6.10 e-02	3.59 e-02	-	3.41 e-02	1.62 e-06	4.85 e-02	-
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} = 0$; $\mathbf{x}_{\mathrm{Trop}} \neq \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	4	-438.51	885.0	11.6	4.63 e-02	-	-	2.53 e-02	4.26 e-03	4.68 e-02	-
$\mathbf{s}_{\mathrm{Trop}} = \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} = 0$; $\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	3	-440.03	886.0	12.6	4.71 e-02	-	-	1.36 e-02	-	4.37 e-02	-
$\mathbf{s}_{\mathrm{Trop}} \neq \mathbf{s}_{\mathrm{Ex}}$; $\mathbf{s}_{\mathrm{Btw}} = 0$; $\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$; $\mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	4	-440.02	888.0	14.6	4.65 e-02	4.76 e-02	-	1.36 e-02	-	4.37 e-02	-

Table S6 (Brief title). Models considering missing species

Table S6. Comparison of best-fit models (ΔAIC ≤ 2) under GeoSSE for each family considering the missing species with respective degrees of freedom (d.f), log-likelihood (-Ln*L*), Akaike Information Criterion (AIC) and Delta AIC (ΔAIC). Parameter estimates are: tropical speciation ($\mathbf{s}_{\text{Trop}}$), extratropical speciation ($\mathbf{s}_{\text{Ex}}$), between regions speciation ($\mathbf{s}_{\text{Btw}}$), tropical extinction ($\mathbf{x}_{\text{Trop}}$), extratropical extinction ($\mathbf{x}_{\text{Ex}}$), dispersal from the tropics ($\mathbf{d}_{\text{Trop}}$), dispersal from the extratropics ($\mathbf{d}_{\text{Ex}}$).

Models	**d.f.**	**-Ln*L***	**AIC**	**Δ AIC**	$\mathbf{s}_{\text{Trop}}$	$\mathbf{s}_{\text{Ex}}$	$\mathbf{s}_{\text{Btw}}$	$\mathbf{x}_{\text{Trop}}$	$\mathbf{x}_{\text{Ex}}$	$\mathbf{d}_{\text{Trop}}$	$\mathbf{d}_{\text{Ex}}$
Chaetodontidae											
$\mathbf{s}_{\text{Btw}} = 0$	6	-332.96	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
$\mathbf{s}_{\text{Btw}} = 0$, $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	5	-334.05	678.1	0.2	3.2 e-01	3.4 e-06	-	2.2 e-01	6.6 e-01	3.9 e-01	-
Full	7	-332.96	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
Labridae											
$\mathbf{s}_{\text{Btw}} = 0$	6	-1279.60	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
$\mathbf{s}_{\text{Btw}} = 0$, $\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$	5	-1281.35	2572.7	1.5	0.12	0.048	-	0.0096	-	0.040	0.010
Pomacentridae											
$\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$, $\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	5	-813.79	1637.5	0	1.0 e-01	2.9 e-02	1.7 e-02	5.8 e-09	-	1.5 e-02	-
$\mathbf{d}_{\text{Trop}} = \mathbf{d}_{\text{Ex}}$	6	-813.66	1639.3	1.8	1.0 e-01	3.7 e-02	1.8 e-02	4.9 e-07	1.7 e-02	1.7 e-02	-
$\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$	6	-813.78	1639.5	2.0	1.0 e-01	2.9 e-02	1.7 e-02	2.8 e-07	-	1.5 e-02	2.0 e-05
Sparidae											
$\mathbf{x}_{\text{Trop}} = \mathbf{x}_{\text{Ex}}$	6	-429.36	870.7	0	6.2 e-02	3.3 e-02	1.6 e-02	8.2 e-07	-	6.7 e-02	7.1 e-03
Full	7	-429.36	872.7	2.0	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

Table S7 (Brief title). Comparison with time variable models

Table S7. Comparison of the best-fit constant and time-variable model under GeoSSE for each family with respective degrees of freedom (d.f), log-likelihood (-Ln*L*), Akaike Information Criterion (AIC) and Delta AIC (ΔAIC). Parameter estimates are: tropical speciation ($\mathbf{s}_{\mathrm{Trop}}$), rate of change in tropical speciation through time ($\mathbf{r}_{\mathrm{Trop}}$), extratropical speciation ($\mathbf{s}_{\mathrm{Ex}}$), rate of change in tropical speciation through time ($\mathbf{r}_{\mathrm{Ex}}$), between regions speciation ($\mathbf{s}_{\mathrm{Btw}}$), rate of change in between region speciation through time ($\mathbf{r}_{\mathrm{Btw}}$), tropical extinction ($\mathbf{x}_{\mathrm{Trop}}$), extratropical extinction ($\mathbf{x}_{\mathrm{Ex}}$), dispersal from the tropics ($\mathbf{d}_{\mathrm{Trop}}$), dispersal from the extratropics ($\mathbf{d}_{\mathrm{Ex}}$).

Models	**d.f.**	**-Ln*L***	**AIC**	**ΔAIC**	$\mathbf{s}_{\mathrm{Trop}}$	$\mathbf{r}_{\mathrm{Trop}}$	$\mathbf{s}_{\mathrm{Ex}}$	$\mathbf{r}_{\mathrm{Ex}}$	$\mathbf{s}_{\mathrm{Btw}}$	$\mathbf{r}_{\mathrm{Btw}}$	$\mathbf{x}_{\mathrm{Trop}}$	$\mathbf{x}_{\mathrm{Ex}}$	$\mathbf{d}_{\mathrm{Trop}}$	$\mathbf{d}_{\mathrm{Ex}}$
Chaetodontidae														
$\mathbf{s}_{\mathrm{Btw}} = 0$	6	-333.1	678.3	0	2.0 e-01		2.6 e-02		-		5.8 e-02	3.2 e-01	2.8 e-01	2.8 e-08
Time variable	9	-333.9	685.8	7.5	2.2 e-01	-4.8 e-03	1.8 e-02	4.5 e-03	2.6 e-06	-8.1 e-08	6.2 e-02	2.6 e-01	2.3 e-01	-
Labridae														
$\mathbf{s}_{\mathrm{Btw}} = 0$	6	-1279.7	2571.5	0	8.7 e-02		4.9 e-02		-		5.7 e-03	4.5 e-02	5.8 e-02	8.6 e-08
Time variable	9	-1286.5	2591.0	9.5	7.8 e-02	1.3 e-03	3.5 e-02	1.3 e-03	4.1 e-05	4.3 e-07	8.9 e-03	2.6 e-02	3.5 e-02	-
Pomacentridae														
$\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$, $\mathbf{d}_{\mathrm{Trop}} = \mathbf{d}_{\mathrm{Ex}}$	5	-815.0	1640.6	0	8.1 e-02		1.4 e-02		1.1 e-02		4.8 e-07	-	1.2 e-02	-
Time variable	9	-812.5	1643.0	2.4	7.0 e-02	1.0 e-03	7.2 e-04	3.4 e-03	1.4 e-02	-2.7 e-04	6.8 e-06	8.5 e-02	2.1 e-02	-
Sparidae														
$\mathbf{x}_{\mathrm{Trop}} = \mathbf{x}_{\mathrm{Ex}}$	6	-430.7	873.4	0	4.9 e-02		2.8 e-02		1.5 e-02		2.0 e-08	-	7.2 e-02	7.3 e-03
Time variable	9	-431.5	881.1	7.7	2.9 e-02	-4.8 e-04	2.5 e-03	3.9 e-04	2.4 e-07	2.9 e-02	8.3 e-02	3.7 e-02	1.4 e-01	-

Appendix S2. *Supplemental figures*

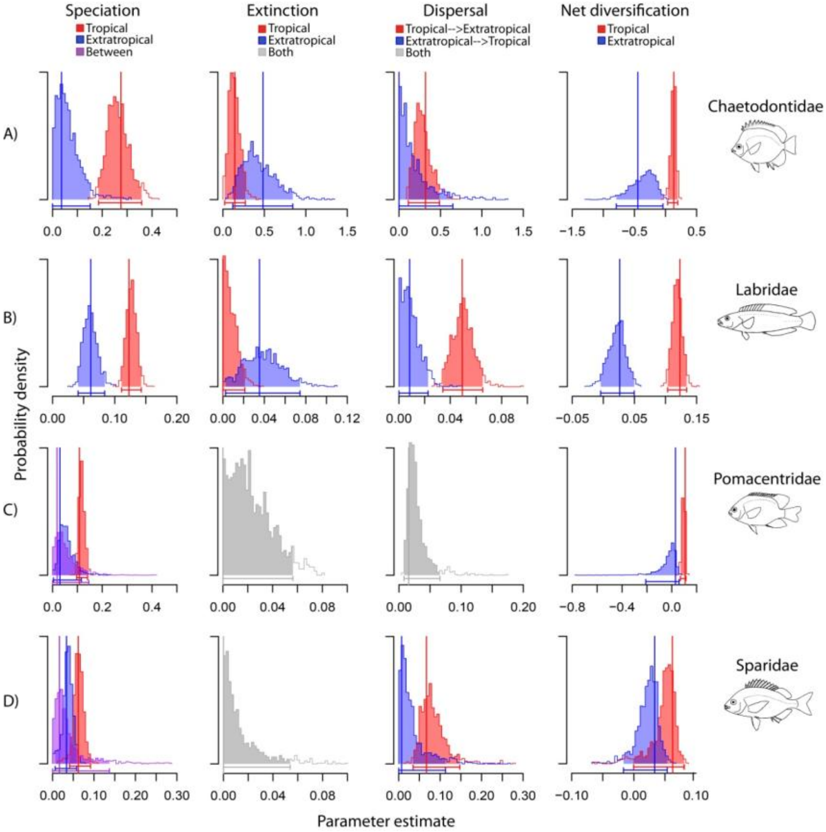

Figure S1 (Brief title). Result plots under GeoSSE considering missing species

Figure S1. Rates of speciation, extinction, dispersal and net diversification (speciation minus extinction) for tropical (red) and extratropical (blue) lineages of four reef fish families. Probability density plots are based on 1000 Markov chain Monte Carlo samples of the best-fit model for each family under GeoSSE considering missing species. Vertical lines represent parameter estimates based on Maximum Likelihood of the best-fit GeoSSE model considering missing species in each family. For Pomacentridae and Sparidae the best-fit model considered the between regions speciation parameter (purple) to be >0, and extinction to be equal for both tropical and extratropical lineages (shown in grey). For Pomacentridae dispersal was also equal for lineages in both categories.

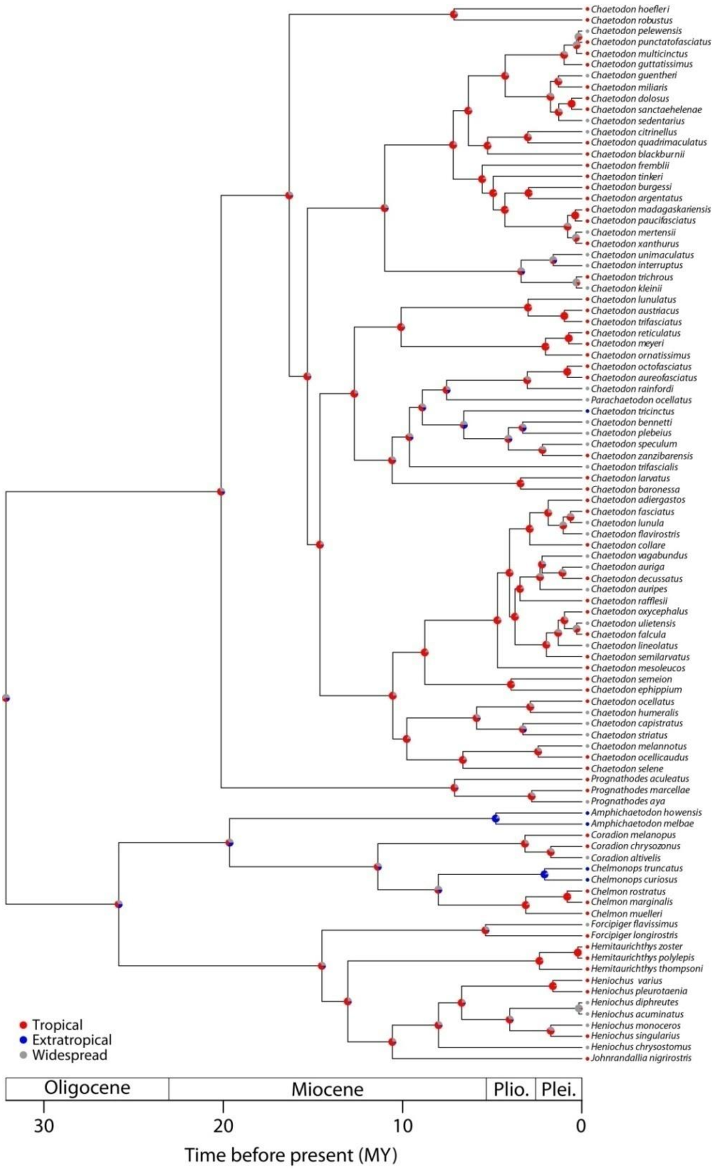

Figure S2 (Brief title). Ancestral state reconstruction for Chaetodontidae

Figure S2. Ancestral state reconstruction for Chaetodontidae under GeoSSE model considering three character states: tropical (red), extratropical (blue), widespread (grey). Tip circles represent actual species states and pie charts represent the probability of ancestral character states.

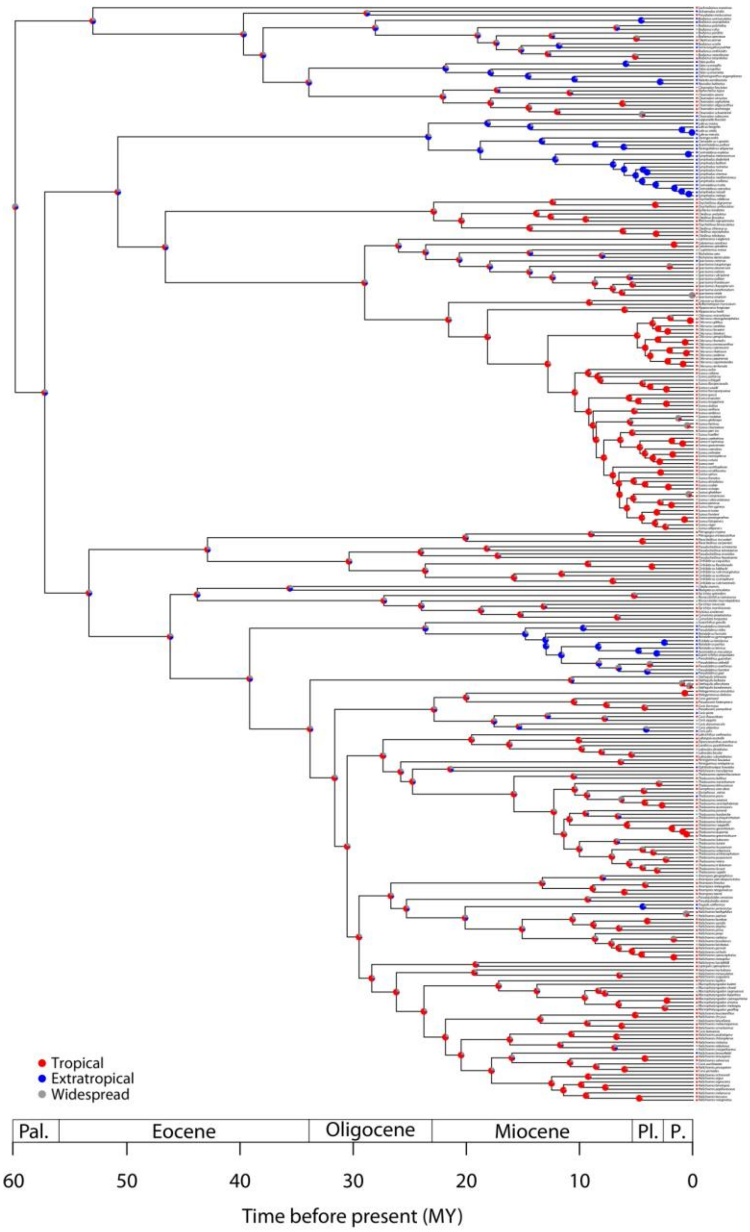

Figure S3 (Brief title). Ancestral state reconstruction for Labridae

Figure S3. Ancestral state reconstruction for Labridae under GeoSSE model considering three character states: tropical (red), extratropical (blue), widespread (grey). Tip circles represent actual species states and pie charts represent the probability of ancestral character states.

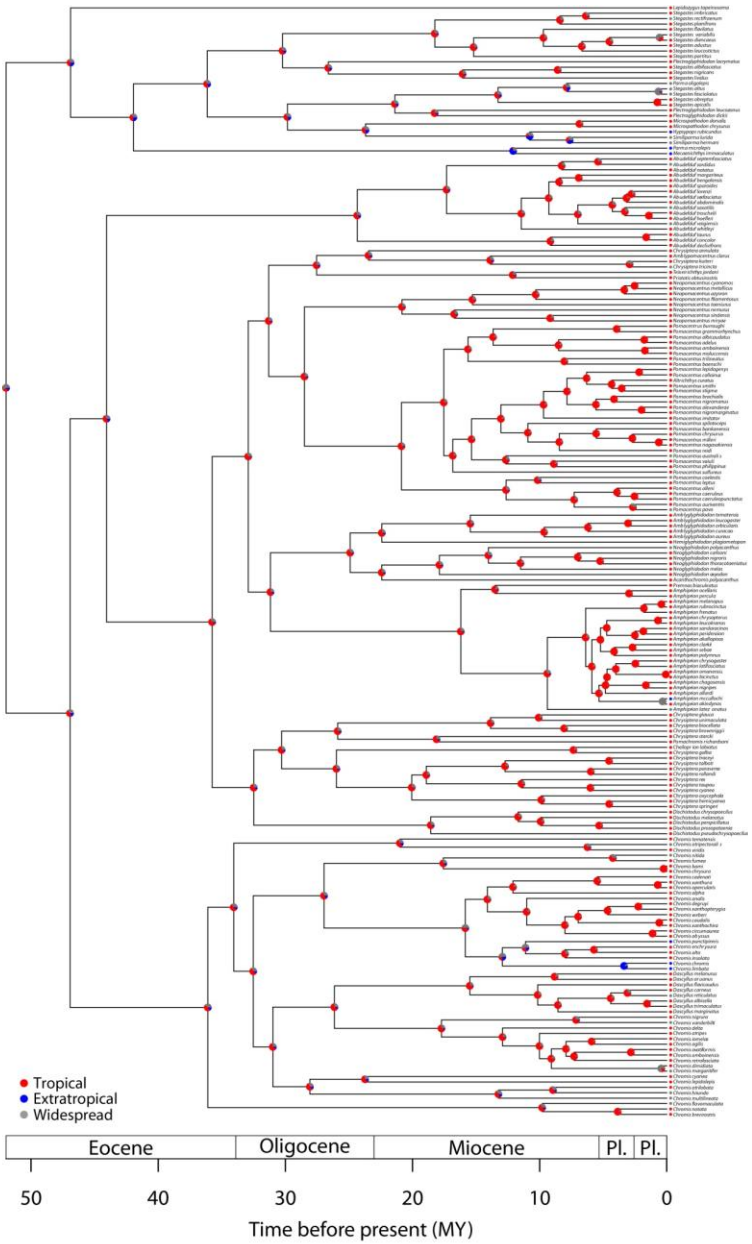

Figure S4 (Brief title). Ancestral state reconstruction for Pomacentridae

Figure S4. Ancestral state reconstruction for Pomacentridae under GeoSSE model considering three character states: tropical (red), extratropical (blue), widespread (grey). Tip circles represent actual species states and pie charts represent the probability of ancestral character states.

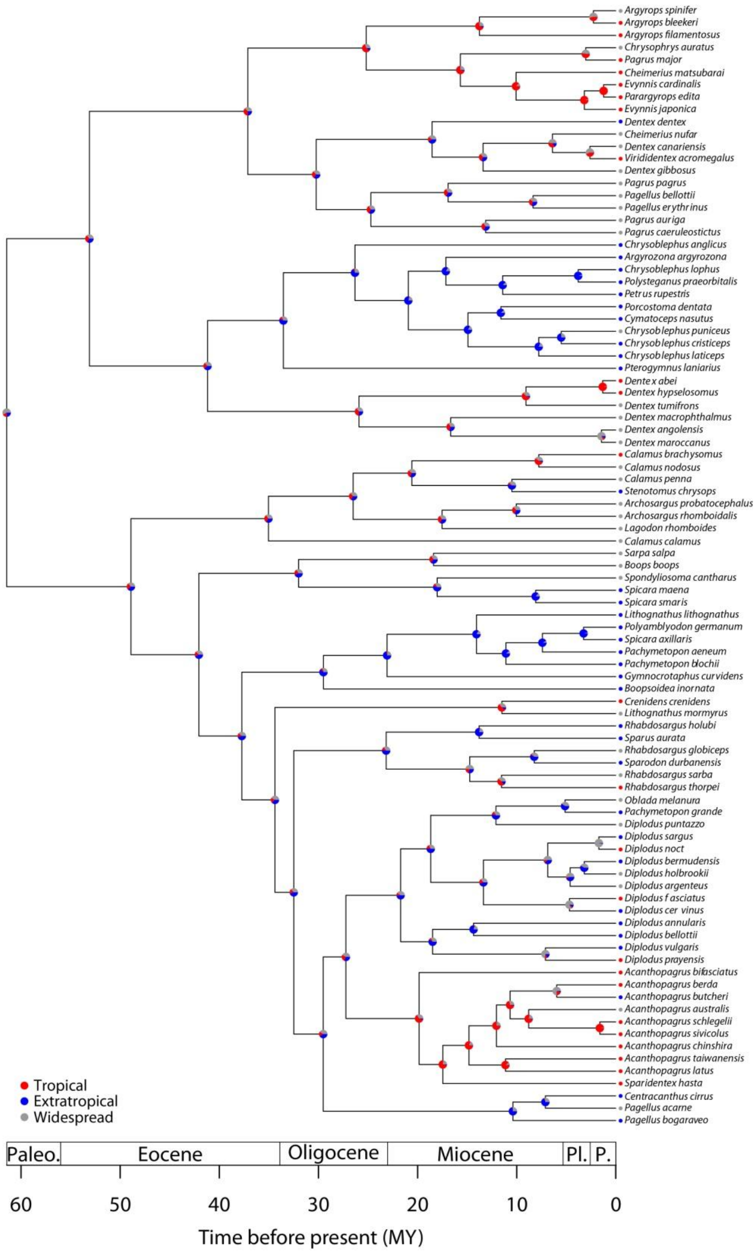

Figure S5 (Brief title). Ancestral state reconstruction for Sparidae

Figure S5. Ancestral state reconstruction for Sparidae under GeoSSE model considering three character states: tropical (red), extratropical (blue), widespread (grey). Tip circles represent actual species states and pie charts represent the probability of ancestral character states.