UNIVERSIDADE FEDERAL DE SANTA CATARINA
Centro de Ciências Biológicas
Programa de Pós-graduação em Ecologia

FÁBIO LUIZ LOBATO

TAXAS DE DIVERSIFICAÇÃO EM PEIXES RECIFAIS: A INFLUÊNCIA DA QUALIDADE DO ALIMENTO

Florianópolis/ SC
2010

FÁBIO LUIZ LOBATO

TAXAS DE DIVERSIFICAÇÃO EM PEIXES RECIFAIS: A INFLUÊNCIA DA QUALIDADE DO ALIMENTO

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, Departamento de Ecologia e Zoologia do Centro de Ciências Biológicas da Universidade Federal de Santa Catarina, como requisito parcial para a obtenção do título de mestre em Ecologia

Orientador: Sergio R. Floeter

Florianópolis/ SC
2010

Catalogação na fonte pela Biblioteca Universitária
da
Universidade Federal de Santa Catarina

L796t Lobato, Fábio Luiz
Taxas de diversificação em peixes recifais [dissertação] : influência da qualidade do alimento / Fábio Luiz Lobato ; orientador, Sergio Ricardo Floeter. - Florianópolis, SC, 2010.
78 p.: grafs., tabs.

Dissertação (mestrado) - Universidade Federal de Santa Catarina, Centro de Ciências Biológicas. Programa de Pós-Graduação em Ecologia.

Inclui referências

1. Ecologia. 2. Diversificação - Taxas. 3. Densidade. 4. Peixe - Alimentação. I. Floeter, Sergio Ricardo. II. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Ecologia. III. Título.

CDU 574.4

“Nada em biologia faz sentido,
senão sob a luz da evolução”
(Theodosius Dobzhansky)

AGRADECIMENTOS

Este trabalho, não diferente de outros trabalhos científicos, é resultado de anos de estudo e aprimoramento técnico. Quando iniciei no campo da biologia evolutiva aplicada a ecologia ainda na graduação, pouco ou nada sabia sobre as bases teóricas e metodológicas requeridas por tal. Para chegar à conclusão desde mestrado muito teve de ser galgado e nenhum passo teria sido dado se não fosse a colaboração preciosa de varias pessoas.

Meus pais, Fábio e Fátima, são certamente os maiores merecedores de meus agradecimentos, não só pelo que fizeram durante toda minha vida, mas principalmente por toda atenção que despenderam a mim nos últimos anos não permitindo que eu me abalasse, ou desistisse de meus objetivos diante das dificuldades. Pelas mesmas razões agradeço a meus dois irmãos mais velhos, Alexandre e Fernanda, que sempre tiveram um papel fundamental em minha vida.

Grande parte de meu desenvolvimento científico nos últimos anos passa pela figura de meu orientador, Sergio. Um profissional dedicado a oportunizar importantes experiências acadêmicas aos seus alunos e cujas orientações os levam a níveis de excelência cada vez mais elevados em seus trabalhos.

Agradecimentos especiais aos professores Alberto e Marcio, membros dessa banca, que despenderam fundamental atenção ao me receberem em seus laboratórios para discussões teóricas e auxilio em questões técnicas como preparação de dados e manipulação de softwares.

Aos amigos e colegas de trabalho, Diego e Ana, sinceros agradecimentos pelo excelente auxílio nas discussões e revisões de texto.

Finalmente e não menos importantes, agradecimentos emocionados a todas as coisas especiais da minha vida sem as quais não seria possível eu viver: os queridos amigos, as paixões, o Grêmio e o *rock 'n' roll*.

RESUMO

O impacto da atividade humana sobre as comunidades biológicas não só promove a extinção de espécies, mas também, interfere fortemente em processos ecológicos e evolutivos sobre os quais nós ainda não conhecemos o suficiente. Para ser capaz de criar estratégias de conservação eficazes em termos de grande escala espacial e temporal é preciso entender mais sobre os processos que determinam a diversificação das espécies e suas distribuições. A diversidade varia muito entre grupos taxonômicos e sobre a superfície da Terra, mais evidente como uma diminuição na diversidade de seu pico nos trópicos para latitudes mais altas. O número de espécies em uma região e as espécies viventes de uma linhagem evolutiva reflete o equilíbrio entre especiação e extinção agindo por longos períodos. Os fatores ambientais das regiões e os atributos das espécies em uma linhagem são apontados como responsáveis por influenciar taxas de diversificação de linhagens e produzir tanto as diferenças entre regiões como entre as linhagens. Os recentes avanços em reconstruir filogenias a partir de dados moleculares têm permitido a biólogos desenvolver vários métodos para investigar taxas de diversificação das linhagens ao longo da história e testar hipóteses que explicam as diferenças de diversidade entre as regiões e taxons. Neste trabalho foram reconstruídas filogenias moleculares de quatro importantes clados de peixes recifais (Acanthuroidei, Chaetodontidae, Labridae e Pomacentridae) para estimar o tempo de radiação de seus subclados e testar se riqueza de espécies maior que a esperada e/ou mudanças nas taxas de diversificação estão relacionados com a utilização diferenciada de recursos alimentares. Nossa hipótese de que clades que utilizam recursos alimentares relativamente de baixa qualidade são mais jovens e derivados em relação a outros clados foi confirmada. Quatro dos seis clados que apresentaram riqueza de espécies maior que a esperada e taxas de diversificação acima das taxas globais de seus taxons superiores (família, subordem, etc), foram clados que utilizam recursos alimentares de baixa qualidade. A explanação dos resultados juntamente com informações da história biogeográfica do Pacifico Indo-Oeste sugere que taxas de diversificação de linhagens de peixes recifais podem ser reguladas, dentre outros fatores, por modelos de oportunidade ecológica onde o uso de dietas de baixa qualidade pode ter implicado em queda mais lenta das taxas de diversificação em relação às taxas de linhagens de alta qualidade na dieta, provavelmente devido à ocupação primária dos recursos de alta qualidade. Tomados em

conjunto as evidências, o estudo sugere que a utilização dos recursos de baixa qualidade é provavelmente mais relacionada com a menor velocidade de queda das taxas de diversificação em ambientes ricos em espécies do que acelerar as taxas de diversificação. Nossos resultados também concordam com a hipótese de Harmelin-Vivien (2002) que justifica o estabelecimento do gradiente latitudinal de diversidade de peixes recifais pela melhor utilização dos recursos alimentares nos trópicos. A presente dissertação mostra a grande importância em se melhorar análises filogenéticas e métodos de investigação das radiações; é indispensável olhar também para a história evolutiva para se compreender as estruturas de comunidades biológicas, e consequentemente melhorar a precisão nas previsões.

ABSTRACT

The current impact of human activity over biological communities is not only promoting species extinction but also, strongly interfering in ecological and evolutionary processes of which, we still do not know enough about. To be able to design optimal conservation strategies in terms of broad spatial and temporal scales we need to understand more about processes ruling species diversification and distribution. Diversity varies widely among taxonomic groups and over Earth surface, most evidently as a decrease in diversity from its peak in the tropics towards higher latitudes. The number of species in a region and the alive species in a evolutionary lineage reflects the balance between speciation and extinction acting over long periods. Environmental factors of regions and species attributes in a lineage are thought to influence diversification rates of lineages and produce both differences among regions and lineages. The current advance in reconstructing phylogenies from molecular data have allowed biologist to develop several methods to investigate lineages diversification rates through history and test hypothesis that explain diversity differences among regions and taxa. Here, molecular phylogenies of four major reef fish clades (Acanthuroidei, Chaetodontidae, Labridae and Pomacentridae) were reconstruct to estimate the radiation timing of their subclades and test whether higher than expected species richness and/or shifts in diversification rates are related to differential use of food resources. Our hypothesis that clades that use relatively low-quality food resources are younger and more derived than other clades was confirmed. Four out of the six clades that presented higher than expected species richness and diversification rates above mean background rates of their higher taxon (family, suborder, etc), were clades that use low-quality food resources. The explanation of our results together with biogeographic information of Indo-West Pacific geologic history suggest that diversification rates of reef fish lineages may have been regulated, among other factors, by ecological opportunity models where the use of low-quality diets could imply in slower decline of diversification rates relative to those of high-quality diet feeder lineages, likely due to the first occupation of high-quality resources. Taken together the evidences, the study suggest that the use of low-quality resources is likely more related to slower decrease of diversification rates in speciose environments than accelerating diversification rates. Our results also agree with Harmelin-Vivien (2002)

hypothesis to explain latitudinal gradients in reef fish diversity through a better use of the food resources at the tropics. As main conclusion the present dissertation shows the great importance in to improve phylogenetic analysis and methods to investigate lineages radiation. Only looking at the long-term history we will be able to understand the structures of biological communities, hence improve our prediction accuracy.

LISTA DE FIGURAS

Material suplementar

LISTA DE TABELAS

SUMÁRIO

INTRODUÇÃO

Biodiversidade pode ser entendida como a variação entre espécies e outros elementos biológicos, incluindo alelos e complexos gênicos, populações, guildas, comunidades, ecossistemas, biomas e regiões biogeográficas. Pode ser expressa como a variação em uma dada localidade, ou a variação entre elementos através de unidades geográficas. Esta variação pode incluir o número de diferentes tipos de espécies ou elementos, suas freqüências relativas, o grau de variação entre esses elementos, ou variação em processos chaves como dispersão, fluxo gênico, relações interespecíficas e sucessão ecológica. (Lomolino et al., 2005).

Dentro deste conceito amplo, a perda de espécies significa a diminuição da biodiversidade desde escalas genéticas e locais a biogeográficas e globais, pois que à extinção de uma espécie sempre está associado perda de processos ecológicos e evolutivos (e.g. migração, dispersão, fluxo gênico, relações interespecíficas, guildas tróficas, etc.).

Assim sendo, podemos entender como o objetivo da conservação biológica preservar, não só as espécies, mas a distribuição dessas – a geografia da natureza. Assim fazendo, preservaríamos a diversidade de populações de cada espécie e os processos ecológicos e evolutivos associados, conservando a biodiversidade em larga escala espacial e temporal.

Para tanto, uma vez que é impossível preservar integralmente toda a configuração biogeográfica global, faz-se necessário o entendimento de quais são e como funcionam tais processos que regulam a diversificação e distribuição das espécies de maneira que se possa aperfeiçoar previsões e estratégias de conservação.

A investigação da história das linhagens tem sido cada vez mais aprimorada nos últimos anos principalmente devido ao aperfeiçoamento das técnicas de reconstrução filogenética a partir de dados moleculares (Felsenstein, 1973; Felsenstein, 1985; Felsenstein, 1988) e do melhor entendimento da história da superfície terrestre (Siddall et al., 2003; Briggs, 1987). Tal investigação é extremamente fundamental para o entendimento dos processos responsáveis pela geração, manutenção e distribuição da riqueza de espécies (Ricklefs & Schluter, 1997; Wiens & Donoughue, 2004; Ree et al., 2005; Ricklefs, 2007a).

Hotspots de biodiversidade (áreas ricas em espécies endêmicas), por exemplo, é foco de várias hipóteses ecológicas e evolutivas (Jokiel & Martinelli, 1992; Briggs, 2000; Briggs, 2003; Karlson et al., 2004;) que têm orientado o planejamento de atuais estratégias de conservação (Roberts et al., 2002; Briggs, 2005). Tais hipóteses têm sido testadas atualmente com sucesso através de análises filogenéticas combinadas a dados de distribuição de espécies e eventos tectônicos e climáticos (Williams & Duda, 2008; Carnaval et al., 2009; Halas & Winterbottom, 2009).

Estudos envolvendo modos de especiação também têm tido grandes avanços utilizando ferramentas de reconstrução filogenética (Barraclough & Volgler, 2000). Especialmente aquelas com base em dados moleculares, pois que permitem obter maiores resoluções na identificação de espécies irmãs, bem como estimar grau de divergência genética e idade dos ramos. Tais informações combinadas a dados de distribuição e capacidade de dispersão das espécies e histórico geográfico das regiões, têm revelado muito sobre a ocorrência e importância de especiações alopátricas, simpátricas e parapátricas na geração e distribuição da biodiversidade (Barraclough & Volgler, 2000; Dieckmann & Doebeli, 1999; Fry, 2003; Puebla, 2009, Sobel et al., 2009) e fomentado intensas discussões relevantes a ecologia e conservação (Gravilets, 2003; Doebeli et al., 2005; Gravilets, 2005).

O aumento da disponibilidade de dados filogenéticos, poder de processamento de dados e ferramentas de informática também têm possibilitado diversos estudos que aplicam métodos filogenéticos a Ecologia de Comunidades (Webb et al., 2002; Cavenders-Bares et al., 2009). Em particular, tais estudos têm ajudado a revelar a multiplicidade dos processos, principalmente evolutivos, na formação das comunidades biológicas (Gillespie, 2004; Fine et al., 2006; Vamosi et al., 2008).

Especialmente interessante para este trabalho, análises filogenéticas recentemente têm ajudado substancialmente a responder perguntas que permanecem em discussão desde os primórdios da biologia evolutiva – por que algumas regiões apresentam maior biodiversidade que outras e por que algumas linhagens são mais especiosas em relação a outras (Ricklefs, 2007b)? Há muita variação na riqueza de espécies ao longo da superfície terrestre e marinha, mais evidentemente como uma diminuição gradual na diversidade de regiões tropicais para latitudes mais elevadas (Hillebrand, 2004). O número de espécies em uma região reflete o balanço entre especiação e extinção durante longos períodos (Mittelbach et al., 2007) de modo que biólogos vêm adotando diferentes abordagens para avaliar como a variação nas taxas de especiação e de extinção influencia os padrões globais de distribuição da riqueza de espécies (Davies et al., 2004; Cardillo et al., 2005; Allen & Gillooly, 2006). A riqueza de espécies também varia bastante entre grupos taxonômicos. Características que incluem diferentes maneiras de utilização de recursos, relacionamento ecológico, mecanismos de reprodução e dispersão bem como a força da seleção sexual são utilizadas para explicar variações em taxas de especiação e extinção e conseguintemente, variações no número de espécies de cada táxon (Barraclough et al., 1998; Cardillo, 1999; Dnoghue, 2005; Paradis; 2005).

Assim, quantificar especiação e extinção pode nos ajudar a compreender as causas da variação na diversidade entre regiões e entre táxons. Ricklefs (2007b) em sua revisão define como o ponto central desse esforço – a diversificação do clado – ou seja, o balanço entre especiação e extinção que origina um grupo de espécies viventes a partir de um ancestral comum e em um determinado tempo. O autor revisa vários métodos para estimar taxas de diversificação (especiação–extinção) a partir da reconstrução das relações filogenéticas entre as espécies de um clado.

Estimar taxas de especiação e extinção depende primeiramente do modelo de diversificação randômica adotado. O mais simples e mais utilizado é “processo especiação-extinção randômica” (Hey, 1992; Nee et al., 1992; Magallon & Sanderson, 2001; Nee, 2006) que se assemelha ao modelo nascimento-morte (*birth-death model*) utilizado para estudar flutuações estocásticas e risco de extinção em populações (Lande 1993; Engen et al., 2002). Nesse modelo cada ramo resultante da divisão de um nó no desenrolar de uma árvore pode se exaurir ou de se dividir novamente em dois novos ramos. A probabilidade de cada alternativa ocorrer é instantânea o que faz com que a probabilidade de um dado clado se extinguir ou continuar esteja condicionada a um intervalo de tempo. Logo, a distribuição de probabilidade do tamanho de um clado sobre o tempo muda de maneira previsível (de acordo com parâmetros estipulados). Já num processo de ramificação simples, onde extinção não é considerada (Processo *Yule* ou *Pure Birth Model*) o número (médio) de espécies esperadas em um clado cresce exponencialmente com o tempo. Se nenhuma extinção ocorre o logaritmo do numero de espécies cresce linearmente com o tempo e a taxa de especiação. Aqui o tamanho do clado, em qualquer tempo, tem uma distribuição de probabilidade geométrica.

Os modelos acima citados são uteis para criar modelos nulos de diversificação e testar a influência de condições ambientais ou característica de espécies na taxa de diversificação comparando o número de espécies em clados que se diferem nestes atributos. Tais comparações vão depender além do modelo de diversificação randômico escolhido das idades dos clados, que na ausência de registro fóssil podem ser estimadas a partir de árvores filogenéticas tempo-calibradas. Há diferentes maneiras de fazer tal comparação; algumas das quais serão abordadas neste presente trabalho; todas bem discutidas no trabalho de Ricklefs (2007b).

O presente trabalho tem por objetivo se utilizar de reconstruções filogenéticas para investigar a influencia de características de espécies e ambientes nas diferenças de riqueza de espécies entre táxons e regiões respectivamente.

Does the use of relatively low-quality food resources leads to rapid diversification in reef fishes?

Does the use of relatively low-quality food resources leads to rapid diversification in reef fishes?

Lobato, F.L.[a]*; Floeter, S.R.[a]; Barneche, D.[a]; Liedke, A.M.R.[a]; Lindner, A.[a]; Pie, M.[b]

[a] Departamento de Ecologia e Zoologia. Universidade Federal de Santa Catarina. Edifício Fritz Müller, Florianópolis, SC, 88010-970, Brazil,
[b] Setor de Ciências Biológicas. Universidade Federal do Paraná. Curitiba, PR, 81531-980, Brazil.

*Corresponding author: lobato.bio@gmail.com Phone: 55 48 3721-5521 Fax: 55 48 3721-5156

(Seguindo formato para publicação em *Molecular Phylogenetics and Evolution*)

Abstract

To explain wide disparity in species richness of different evolutionary lineages is one of the oldest issues in evolutionary biology and competitive interactions has been argued to be an important factor to determine this. Here we reconstruct molecular phylogenies of four major reef fish clades (Acanthuroidei, Chaetodontidae, Labridae and Pomacentridae) to estimate the radiation timing of their subclades and test whether higher than expected species richness is related to differential use of food resources. With exception of Pomacentridae, the remaining three clades seem to agree with the idea that the use of low-quality food resources is a derived condition which has evolved one or more times independently in the clade history. However, it is a relatively old condition present in clades history since the early Eocene, far from the origin of modern reef fish genera in the Miocene. The results with Acanthuroidei, Chaetodontidae and Pomacentridae confirmed the hypothesis based on density-dependent diversification principles that, clades of species using low-quality diets originated inside periods of high diversity levels in reef communities would present higher than expected number of extant species. Our study suggest that the diversification of reef fish lineages may be ruled by models of ecological opportunity in which competitive interaction would have an important role. Over a large spacial, phylogenetic and ecological scale, clade diversity might be directly proportional to how much competition is repealed, finding unoccupied resources to speciation.

Keywords. Density-dependent; Diversification rate; Reef fishes; Ecological opportunity; Low-quality diets; Acanturoidei; Chaetodontidade; Labridae; Pomacentridae.

1. Introduction

1.1. Diversification and ecological opportunity

To explain wide disparity in species richness of different evolutionary lineages has been focus of evolutionary biology since Darwin and still remains as one of the greatest challenges among current biologist (Ricklefs 2009, Rabosky, 2009). The main goal of recent investigations is to test hypothesis of processes ruling clades diversification rates, i.e. how environmental and biological factors are interfering in the balance between speciation and extinction through time to produce disparate number of extant species among clades ( ).

Recent studies are focused in testing the existence of diversification rates dependent on niche availability in biological communities (Phillimore and Price, 2008; Rabosky and Lovette, 2008; White et al., 2010). The concept of density-dependent diversification rate suggests that speciation occurs most likely when resources are abundant and potential competitors are scarce. As a radiation progresses, ecological niche-space become increasingly saturated, resulting in fewer opportunities for speciation (Phillimore & Price, 2008; Rabosky & Lovette, 2008). Studies with fossil have identified explosive radiations after mass extinction periods followed by an abrupt decline in species-level diversification rates through time (Sepkoski, 1998). Also, studies with molecular phylogenies of extant taxa have shown evidences of early rapid diversification followed by the same temporal decline (Ricklefs, 2003; Ruber and Zardoya, 2005; Phillimore and Price, 2008). Although density-dependent diversification predicts the observed data, it remains unclear if other processes might be producing the pattern (Rabosky and Lovette, 2008).

1.2. Reef fishes

Reef fishes form an ideal group to investigate evolutionary process in the marine domain (Allen Allen, 2000; Halas and Winterbottom, 2009; Rezende et al., 2009). They are one of the most speciose vertebrate assemblages, distributed across tropical and temperate seas according to global patterns of latitudinal and longitudinal diversity gradients (Briggs, 2000; Harmelin-Vivien, 2002, Briggs, 2003; Floeter et al., 2004; Allen, 2007). They present remarkable diversification in the use of micro-habitats and food resources, being involved with complex ecological relationship networks in their communities (Wainwright and Bellwood, 2002). The spawning mode may be pelagic or demersal, but virtually all reef fishes present a pelagic larval stage in which they can disperse via ocean currents (Cowen, 2002; Rocha and Bowen, 2007; Cowen and Sponaugle, 2009). According to Bellwood and Wainwright (2002), 75% of reef fish species belong to the order Perciformes, including the 10 main families defined in Bellwood (1998) as the 'consensus families' representing the bulk of reef fishes: Acanthuridae, Apogonidae, Blenniidae, Carangidae, Chaetodontidae, Holocentridae, Labridae, Mullidae, Pomacentridae and Scaridae. Currently, molecular phylogenies has shown Scaridae as a monophyletic group evolved inside Labrid radiation (Westneat and Alfaro, 2005; Kazancıoglu et al., 2009), and the subfamily status within Labridae (Scarinae) would be more appropriate. The same happens to Odacidae, an Australian temperate family of reef fishes (Clements et al., 2000; Westneat and Alfaro, 2005). In this study we worked with the families Chaetodontidae, Labridae, Pomacentridae and Acanthuridae, this last one together with other related families of the suborder Acanthuroidei. We also considered both Scaridae and Odacidae to be Labrid subfamilies.

The first occurrence of modern reef fish lineages are pointed to the early Tertiary (50 Ma), where the oldest fossil record of these characteristic reef fish families (except Chaetodontidae) are reported (Bellwood, 1996; Bellwood, 1999), although biogeographic evidences suggest a possible late Cretaceous (70 Ma) or even early Cretaceous (100 Ma) origin for the group (Bellwood and Wainwright, 2002).

1.2.1. Labridae

The family Labridae, or wrasses, are a diverse group of over 600 species in 82 genera with great diversification of body shape, size (from few grams to 100 kg), coloration, and habitat preference (Kuiter, 2010). They inhabit tropical and temperate waters worldwide, and are most common in shallow water habitats such as coral and rocky reefs and associated areas as flat sand bottoms and seagrass beds (Kuiter, 2010). Feeding habits of most species encompass a great variety of hard-shelled invertebrates, but some lineages evolved to use other types of resources such as algae in Scarinae (Parrotfishes), plankton, coral mucus, ectoparasites and fishes.

Westneat and Alfaro (2005) proposed the first high-level molecular phylogeny for the family. They explored the biogeography of the group and pointed evidences for the origin of the group during the Gondwanan break-up. Recently, Cowman et al. (2009) aggregated some species to Westneat & Alfaro's tree and produced a chronogram to investigate the chronology of origination of trophic novelty and determine whether trophically specialized groups are a relatively recent phenomenon. They observed origins for the family in the late Cretaceous to earliest Tertiary and a rapidly radiation after the K/T boundary at 65 Ma. Also, they pointed that the group radiated generally to use hard shelled food item with new trophic modes rising at different times. However, they did not explore the possible changes in diversification rates due to trophic evolution.

Very recently, Alfaro et al. (2010), downloaded GenBank (Benson et al., 2005) sequence data for 131 labrid species from three previously published studies with Labridae (Westneat & Alfaro, 2005), Odacinae (Clements et al., 2004), and Scarinae (Smith et al., 2008), for two mitochondrial and two nuclear genes, to construct a time-calibrated phylogeny. They tested whether diversification rates shifted at two scales where major pharyngeal jaw innovations have evolved: across all of Labridae and within the subclade of parrotfishes (Scarinae). Major modifications to the pharyngeal jaw apparatus are considered as a recurring evolutionary key innovation that has promoted adaptive radiation in many speciose clades of Percomorpha (Liem, 1973; Liem, 1981). They found rapid initial radiation within two relative recent lineages, Julidinae and Scarinae, however, not necessarily correlated with pharyngeal jaw modifications.

1.2.2. Pomacentridae

The family Pomacentridae (damselfishes) numbering over 380 species in 29 genera is one of the four-most speciose families of reef fishes (Allen, 1991; Nelson, 1994; Robertson, 1998), and, at local scale, are often the most abundant fishes on tropical and temperate reefs around the world (Bellwood, 1996; Myers, 1991). Despite this great diversity and abundance, damselfishes exhibit a low degree of trophic diversity compared to their close related family Labridae (Wainright and Bellwood, 2002; Wainright et al., 2004). This relatively restricted ecological diversity is associated with what seems to be low morphological variation (Emery, 1973). Some species, as the ones from the genus *Chromis* are exclusively zooplanktivorous, while others complement their diet through herbivory with higher (herbivorous) or lower (omnivorous) strength. According Cooper and Westneat (2009) similar biomechanical character states have evolved convergently many times during the radiation of the damselfishes entailing widespread convergence on herbivory, omnivory and planktivory among multiple damselfish clades.

Molecular phylogenetics for this group was already presented in Tang (2001) using partial mitochondrial ribosomal and tRNA-Phe genes to infer relationships among 23 species representing 14 genera. Jang-Liaw et al. (2002) focused on partial 12S sequences to present a hypothesis of relationship for 48 pomacentrid species representing 18 genera. The taxonomic sample of Quenouille et al. (2004) includes other species to those previous studies in a total 103 species of 18 genera, and a protein-coding gene were also partially sequenced. Cooper et al. (2009) published the best resolved molecular phylogeny of Pomacentridae with 104 species of all 29 genera, sequencing six partial genes from mitochondrial and nuclear origin. All these phylogenies focused essentially in the systematic of the family not exploring the implications of trophic evolution in the diversification history of pomacentrids.

1.2.3. Chaetodontidae

The family Chaetodontidae (butterflyfishes and bannerfishes) includes over 120 species with spectacular coloration, high levels of ecological and morphological diversity, generally found throughout shallow and tropical reefs around the world, mainly in the Indo-west Pacific region (Fessler and Westneat, 2007). They can be classified as predators on a range of prey taxa, including sponges, algae, zoanthids, coral, polychaetes, and other invertebrates, but in all cases the fishes directly bite the substrate to capture the prey (Wainright & Bellwood, 2002). At the most speciose genus, *Chaetodon* (83 species), several species are obligate or facultative coral feeders, a remarkable feature of this family extremely associated with coral reefs in its history (Kuiter and Debelius, 2003).

The first high-level molecular phylogeny of chaetodontids was proposed by Fessler and Westneat (2007) to assess the validity of *Chaetodon* subgenera, and examine the relative rates of molecular evolution, dates of divergence of major groups, and biogeographic history of butterflyfishes. Using five partial gene sequences (12s,16s, RAG2, 4c4 and ND3) from 71 chaetodontids, they found evidence that the widespread consuming coral polyps by butterflyfishes (Pratchett, 2005) may have originated during the period of closure of the Tethys Sea and final formation of separate Atlantic and Pacific basins between 12 and 18 Ma. Recently, Bellwood et al. (2009) provided a new molecular phylogeny based on three partial gene sequences (ETS2, S7II and cytb) from 56 species (many species overlapping with Fessler and Westneat's taxon sampling) getting evidences for inferences similar to those of Fessler and Westneat (2007). They observed higher species richness than expected under global diversification rates of chaetodontids in some *Chaetodon*'s subclades, which might be evidence for changes in diversification rate in the origin of genus.

1.2.4. Acanthuroidei

The Acanthuroidei is a monophyletic suborder that includes the families Acanthuridae (surgeonfishes) with 81 species, Siganidae (rabbitfishes) with 25 species, the motypic Zanclidae (*Zanclus cornutus*), the monotypic Luvaridae (*Luvarus imperialis*), Ephippidae (spadefishes) with 15 species and Scatophagidae (scats) with four species (Winterbottom and McLennan, 1993; Tang *et al.*, 1999). Most species are marine and many are common reef fishes of tropical and subtropical seas worldwide. Like chaetodontids, acanthuroids mostly feed by biting attached prey, although zooplanktivory has also evolved within the group. Most surgeonfishes and rabbitfishes feed on attached algae and/or detritus (Jones, 1968; Bryan, 1975; Woodland, 1990; Purcell and Bellwood, 1993), taking their food from the benthos, and a wide variety of morphological and physiological modifications of the jaws, pharyngeal apparatus, and intestines, underlie a considerable radiation within this general feeding pattern (Jones, 1968; Purcell and Bellwood, 1993).

Tang et al. (1999) proposed the first and unique molecular phylogeny for the group based only on partial sequences of two mitochondrial genes (12s and 16s) and morphological data from 14 acanthuroid species. They only discussed taxonomic issues around the group.

1.3. Low-quality food resources and ecological opportunity in reef fishes

In the reef fish trophic context, algae and sessile invertebrates as sponges, cnidarians and ascidians are considered relatively low-quality food resources because they present low caloric value (Bruggemann et al., 1994; Bowen et al., 1995; Ferreira et al., 1998; Horn, 1998), structural and chemically defenses against grazing (Hay, 1991; Paul; 1992; Epifânio et al., 1999; Burns and Ilan, 2003; Burns et al., 2003), and are less easily digestible compared to motile invertebrates (polychaetes, molluscs, crustaceans, equinoderms) and fishes (Horn, 1989; Choat, 1991; Meylan,1991; Choat and Clements, 1998), which are known to be the preferred food items of fishes (Harmelin-Vivien, 1981; Parrish *et al.,* 1985; Harmelin-Vivien, 1989; Gerking, 1994). Thus, to be able to use low-quality diets would imply specific morphological, physiological, and behavioral adaptations that would have had an energetic cost during reef fish evolution (Choat and Clements, 1998; Choat and Clements, 2002). In his study whit teleosts Kotrschal (1987) shows that the accessibility to sessil preys is lower among basal teleost lineages than to derived lineages. Indeed, most herbivorous occur in highly derived fish families, such as the Pomacentridae, Blenniidae, Acanthuridae, Siganidae, Monacanthidae and the labrid subfamily Scarinae. These groups are among the youngest reef fish families and have rapidly evolved during the early Tertiary, 50 to 30 Ma (Choat and Bellwood, 1991). In the family level, Harmelin-Vivien (2002), based on morphological phylogenies of Chaetodontidae (Blum, 1989), Acanthuridae (Winterbottom and McLennan, 1993) and Scarinae (Bellwood, 1994), point a negative correlation between evolutionary derived positions and caloric level of food habits.

In her review, Harmelin-Vivien (2002) theorize an evolutionary process in which stable moderately high temperature and high stability of the environment, both between seasons and over geological times, have operated at molecular, organism and community levels to lead to a better use of low-quality food resources among tropical reef fish communities, in relatively derived lineages. At the molecular level high temperatures would care to increased rate of mutations, and long-term stability through seasonal and geological time would be responsible to keep the genetic polymorphisms. At the organism level high temperatures leads to high metabolism in ectothermics. It allows low-quality diet feeders to keep high foraging rates to compensate for low nutritional value in their diets. Finally, at the community level long-term stability through seasonal and geologic time would imply lower extinction rates at the tropics which would lead to a saturation of high-quality resources available for new species. In such case, to be able to use food resources neglected by other species would become an advantage since high rates competitive interactions may reinforce the selection pressures (those assumptions are referenced in Harmelin-Vivien, 2002). In her assumptions, high levels of species richness on tropical reef communities would have an important role, by competitive pressures, to the rise of recently derived lineages which find abundant, diverse and neglected resources using relatively low-quality diets.

We may take these assumptions together with the dynamic of radiations based on density-dependent diversification principles to infer another prediction. If species within most reef fish lineages preferably occupy high-quality resources, and species-level speciation rate decreases while niches get filled, lineages in which species are able to use low-quality food resources would be experimenting less competitive interactions in specioses environments, and would diversify with higher rates.

1.4. Hypothesis and expected results.

In this study, we reconstruct molecular phylogenies of four major reef fish clades (Acanthuroidei, Chaetodontidae, Labridae and Pomacentridae) to estimate the radiation timing of their subclades and test whether: (1) low-quality diet rises at derived lineages, in historical periods expected to correspond to high levels of reef communities species richness; and (2) there is a relation between groups with low-quality diets and higher than expected species richness in the crown group.

It must be given attention to the fact that all four groups in this study have predominant distribution and probable origin at the Indo-West Pacific region ( ). According to the study of Renema et al. (2008) with eight groups of marine organisms including reef fishes, the high level of species richness found in major modern genera of IWP have been established among 2–23 Ma in the Pliocene+Miocene and they attributed such burst of diversification to the collision of Australia with

Pacific arcs and the southeast Asian margin at 20–25 Ma. Williams & Duda (2008) studying gasthropod genera phylogenies have shown clades with significantly increased rates of diversification with origins at the same period (20–25 Ma). They argue that the same tectonic event leaded to an increase of the coral-reef carbonate platforms in central IWP resulting and more opportunities for speciation.

Following the evolutionary process suggested in Harmelin-Vivien (2002) we expect to find the rise of low-quality diets within derived subclades originated during the Miocene, the period of origin of most reef fish modern genera. Note, we are not testing Harmelin-Vivien's (2002) hypothesis, only, one of the topics of it. Competitive interaction is only one of the factors in the evolutionary process proposed, but it is has an important role, as in many other proposed evolutionary processes, which must be evaluated as its implication.

According to the principles of density-dependence diversification reef fish lineages of the IWP should present relatively constant diversification rates until the boom of speciation of the Miocene. Later, as niches get filled, species-level speciation rate of lineages should decline and that would be more deeply as specie's food resources are preferred among species arising. Thus, we expect to find higher than expected species richness in subclades of species with low-quality diets originated during the Miocene, since such food resources are supposed to be neglected among major reef fish lineages.

2. Materials and Methods

2.1. Taxon sampling and sequence alignment

The taxon sampling and molecular data in this study was get from previous phylogenetic studies with the four groups. DNA sequences were downloaded from Genbank following all ascension numbers displayed in (1) Tang et al. (1999) for Acanthuroidei, (2) Fessler & Westneat (2007) for Chaetodontidae, (3) Westneat & Alfaro (2005) for Labridae and (4) Cooper et al. (2009) for Pomacentridae. The taxa sampled consist in (1) 14 acanthuroids, (2) 71 chaetodontids, (3) 84 labrids and (4) 104 pomacentrids.

For most species in the four groups of this study the taxonomy of species are well resolved morphologically and recent molecular phylogenies of families and genera have confirmed most of this classification. There are some exceptions as the genus *Halichoeres* in the family Labridae, for example, which is a polyphyletic genus in the phylogeny selected in this study. However, all different lineages containing *Halichoeres* species fall into the subclade we are interested to investigate (the tribe Julidines in this case), which allow trustable measure of subclades species richness. Both phylogenies of Chaetodontidae and Pomacentridae include all genera. Therefore, we assumed it is known where all species, in each family, are located according the set of subclades. In the subordem Acanthuroidei all families are represented in the phylogeny and only two genera are not represented in the family Ephippidae, which corresponds to 5% of all acanthuroid species. The missing genera in the labrid phylogeny correspond to 12% of labrid species and are mostly monotypic genera. (see Table 1 to check details about missing taxa).

Sequences for outgroup species were also downloaded as follows in each of the respective articles. Sequences downloaded for each species corresponds to fragments of (1) two mitochondrial genes (12s, 16s) for acanthuroids, (2) three mitochondrial (12s, 16s, ND3) and two nuclear (Tmo4C4, RAG2) genes for chaetodontids, (3) two mitochondrial (12s and 16s) and two nuclear (Tmo4C4, RAG2) genes for labrids, and (4) three mitochondrial (12s, 16s, ND3) and three nuclear (RAG1, RAG2, bmp4) genes for pomacentrids.

ClustaX 2.0 (Thompson et al., 1997) was used to produce initial alignment for all gene sequences. Later, we manually refined the alignments excluding ambiguous and loop regions, and visually editing for alignment of gaps in instances of insertion or deletion using MacClade 4.0 (Maddison and Maddison, 2000). After sequence edition the whole dataset consists in 1,341 bp for Acanthuroidei; 3,106 bp for Chaetodontidae; 2,736 bp for Labridae; and 4,129 bp for Pomacentridae.

2.2. Phylogenetic analysis

We performed BI (Bayesian Inference) to calculate posterior probabilities of clades using MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Huelsenbeck et al., 2001). Data was partitioned by gene in Chaetodontidae and Pomacentridae; for Acanthuroidei the two genes were set as a single partition and for Labridae the mitochondrial genes were set as single partition while the nuclear genes as independent partitions. These combinations of genes to set the partitions are the ones which presented the bests bayesian factors in previous runs (see Table 1 at the supplementary material available online). We assigned GTR+G model (Nst = 6) in separate to each partition since this model seems to fit adequately in previous studies with reef fishes (Bellwood et al, 2004; Taylor and Hellberg, 2005; Miller and Cribb, 2006; Clements et al., 2003; Thacker and Roje, 2009, Yamanoue et al., 2009), and like in Fessler and Westneat (2007) the model choice seems to have little effect on topology and support values in our analysis.

To construct each tree, two MCMC (Markov Chain Monte Carlo) simulations were run simultaneously for 10 million generations, with trees sampled and saved every 1000 generations (15,000 trees saved per run). Default settings were used for all other parameters, which include branch length of Exp 10, alpha parameter of the gamma distribution of rate heterogeneity as uniform (0.0–200), base frequencies of Dirichlet (1,1,1,1), substitution rates of Dirichlet (1,1,1,1,1,1) and tree topology parameters as uniform over all possible topologies.

All trees prior to stationarity and convergence of the runs were discarded. Stationarity was assigned starting at the plateau of stable log likelihood scores and convergence was assumed when the value for the standard deviation of split frequencies remained below 0.01. We, then, compute a majority rule consensus tree (50%) and posterior probabilities of clades with the post-burn trees.

All runs were conducted on the CBSU Web Computing Interface (accessed online at http://cbsuapps.tc.cornell.edu/mrbayes.aspx), and results analyzed at Tracer 1.5 (Rambaut and Drummond, 2007).

2.3. Dates estimation and fossil calibration

Divergence times of lineages in all four groups of study were performed in BEAST 1.5.4 (Drummond and Rambaut, 2007). Because of the uncertainty in the topologies due to gaps or missing data in the molecular sequences it is important to evaluate the variability associated with the estimation of parameters (Cowman et al., 2009). Thus, BEAST implements BI and MCMC analysis to simultaneously estimate branch lengths, topology, substitution model parameters and dates based on fossil calibrations. BEAST does not assume autocorrelated substitution rates across lineages. Rates are estimated independently from an uncorrelated exponential distribution (UCED) or lognormal distribution (UCLD). This is also important once previous studies have been shown not to demonstrate autocorrelation of rates and times (Drummond et al., 2006; Alfaro et al., 2007; Brown et al., 2008).

We specified a Yule (pure birth) prior on rates of cladogenesis. The partitions described above were assumed to have evolved under a GTR model with gamma-distributed rate heterogeneity. We assigned hard lower bounds and 95% soft upper bounds to the prior distributions of all fossil calibrations points using lognormal distributions as described in the Table 2. For all calibration points the hard lower bounds were based on the age of the oldest fossil record of the clade (Table 2), following the respective references (Table 2).

Since the vast majority of reported chaetodontids fossils are demonstrably erroneous (Bannikov, 2004), to the Chaetodontidae tree we followed Bellwood et al. (2010) to assign an 95% soft upper bound of 65 Ma at the outgroup node. This age represents the transition of fish faunas at the K⁄ T boundary (following Bellwood and Wainwright, 2002; Bellwood et al., 2004; Fessler and Westneat, 2007) beyond which there is no fossil record of modern reef fish families. For the same reason, we set the 95% soft upper bound of 65 Ma at the root of Pomacentridae; at the origin of Scatophagidae+Ephippidae and at the origin of Acanthuridae in the Acanthuroid tree; at the origin of the Hypsigenyinae and at the origin of Hypsigenyine’s sister group in the labrid tree. The root of Labridae received the same soft upper bounds but with ln(mean) closer to 65 Ma than 50 Ma. Only in the Scarine node (Family Labridae) the 95% soft upper bound was placed at 55 Ma from which dates the oldest fossil record of Labridae (Bannikov and Sorbini, 1995).

For each of the four groups of study we used CBSU Web Computing Interface (accessed online at http://cbsuapps.tc.cornell.edu/beast.aspx) to run three independent analysis of 10 million generations, sampling trees every 500 generations. Resulting log files were examined using Tracer 1.4 (Rambaut and Drummond, 2007) to ensure trees convergence. After excluded the first 10% burnin, tree files were then combined using LogCombiner (Drummond and Rambaut, 2007). With the resulting file, we compute a maximum clade credibility tree using TreeAnnotator (Drummond and Rambaut, 2007) to display mean node ages and highest posterior density (HPD) intervals at 95% (upper and lower) for each node.

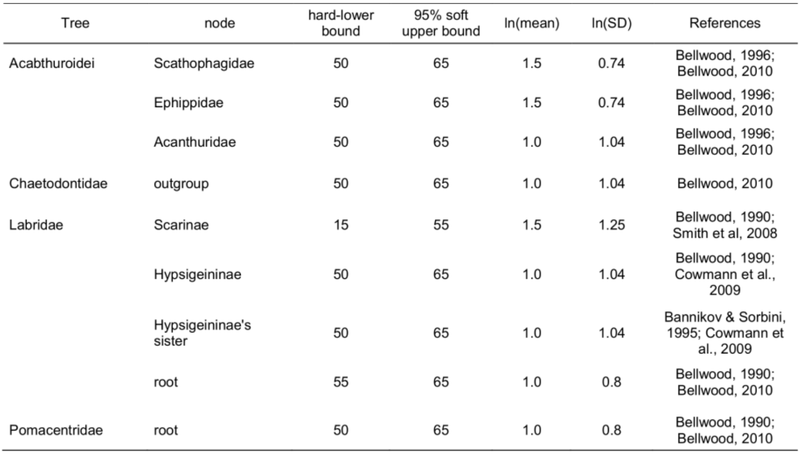
Table 1. Taxa sampled and missing species. "% not represented" = percentage of species not represented by the presence of their respective genus in the taxa sampled. LDF = Low-quality diet feeder species.

Tree	clades	Nº sampled	Nº missing	Total	% not represented	% LQF within not represented	Total % LQF
Acanthuroidei	Ephippidae	2	13	15	47	0	0
	Scatophagidae	2	2	4	0	0	0
	Siganidae	1	27	28	0	0	100
	Luvaridae	1	0	1	0	0	0
	Zanclidae	1	0	1	0	0	0
	Naso	1	18	19	0	0	0
	Acanthuridae (-*Naso*)	6	56	62	0	0	98
	Total	14	116	130	5	0	70
Chaetodontidae	Bannerfishes	17	9	26	0	0	0
	Progathodes	2	9	11	0	0	0
	Chaetodon	52	39	91	0	0	99
	Total	71	57	128	0	0	71
Labridae	Scarinae	6	90	96	10	100	100
	Odacinae	2	10	12	58	86	92
	Labrichthyinae	7	19	25	48	0	36
	other labrids	69	414	484	9	0	0,2
	Total	84	533	617	12	22	17
Pomacentridae	*Lepidozygus*	1	0	1	0	0	0
	Stegastinae	19	48	67	0	0	100
	Chrominae	21	88	109	0	0	0
	Abudefdufinae	9	11	20	0	0	0
	Pomacentrinae	54	130	184	0	0	60
	Total	104	277	381	0	0	48

2.4. Character optimization

First, species trophic modes were defined according the following criteria of classification:

Table 2. Log-Normal distribution priors and references for the calibration points.



Tree	node	hard-lower bound	95% soft upper bound	ln(mean)	ln(SD)	References
Acabthuroidei	Scathophagidae	50	65	1.5	0.74	Bellwood, 1996; Bellwood, 2010
	Ephippidae	50	65	1.5	0.74	Bellwood, 1996; Bellwood, 2010
	Acanthuridae	50	65	1.0	1.04	Bellwood, 1996; Bellwood, 2010
Chaetodontidae	outgroup	50	65	1.0	1.04	Bellwood, 2010
Labridae	Scarinae	15	55	1.5	1.25	Bellwood, 1990; Smith et al, 2008
	Hypsigeininae	50	65	1.0	1.04	Bellwood, 1990; Cowmann et al., 2009
	Hypsigeininae's sister	50	65	1.0	1.04	Bannikov & Sorbini, 1995; Cowmann et al., 2009
	root	55	65	1.0	0.8	Bellwood, 1990; Bellwood, 2010
Pomacentridae	root	50	65	1.0	0.8	Bellwood, 1990; Bellwood, 2010

Acanthuroidei – (1) herbivorous (more than 50% algae over the total ingested); (2) Omnivorous (less than 50% algae over the total ingested); (3) mobile invertebrates feeders; (4) zooplanktivorous.

Chaetodontidae – (1) obligate coralivorous (diet includes > 90% coral), (2) facultative coralivorous (diet includes corals, sponges, ascidians, algae and tinny mobile invertebrates), (3) zooplanktivorous and tinny mobile invertebrates feeders.

Labridae – (1) herbivorous, (2) coral mucus feeders, (3) hard-shelled invertebrates (molluscians, crustasceans, equinoderms) feeders, (4) zooplaktivorous, (5) ecto-parasites feeders, (6) piscivorous.

Pomacentridae – (1) herbivorous (more than 50% algae over the total ingested), (2) omnivorous (less than 50% algae over the total ingested), (3) zooplanktivorous (more than 90% zooplankton over the total ingested).

Such classifications are based, but not equal, to those used in Bellwood et al. (2010) for chaetodontids, Cowman et al. (2009) for labrids and Cooper (2006) for pomacentrids. To define the limit between herbivory and omnivory for Acanthuroidei and Pomacentridae might be tricky, since is not common to find a 100% herbivorous in such clades. It is also known that lots of omnivorous present plasticity in the use of food sources varying the proportion of consume between high and low-quality diets according season, region or community structure (Horn, 1983). Therefore, for Acanthuridae and Pomacentridae we set as herbivorous those species we know to have a general pattern of diet based on algae, and as omnivorous those which have in zooplanktivory and/or mobile invertebrate predation the main trophic mode. We search for species trophic mode using the proper data-bases available in the bibliography (e.g. Allen, 1991; Kuiter, 2002a; Kuiter, 2002b, Kuiter and Debelius, 2003; Randall, 2004; Froese and Pauly, 2010, Kuiter, 2010). Trophic mode of species not included in taxa sampled were also investigated to define whether all the species in the subclade represented by a given taxon shares the same type of character, or only a percentage of it (see Table 1 for details). To define the species of possible monophyletic subclades represented by a given taxon sampled, we consulted the Catalog of Fishes database (Eschmeyer, 2010). Afterward, we classified trophic modes observed in low-quality food feeders (herbivorous, obligate and facultative coralivorous and coral mucus feeders) and high-quality food feeders (the remaining categories).

These traits were then optimized on the resulting phylograms from BI analysis using Mesquite 2.6 (Maddison and Maddison, 2007). Trophic character under both criteria of classification (food items and food quality) was optimized with MP (Maximum Parsimony) analysis to identify the independent evolution of feeding traits.

2.5. Diversification statistics

All diversification statistics were performed in R 2.7.2 (Ihaka and Gentleman, 1996) using APE (Paradis, 2010), GEIGER (Harmon et al., 2008) and LASER (Rabosky, 2006) packages. First, to look for general pattern of declining species-level diversification rate we apply the CR test of Pybus and Harvey (2000) to estimate the γ statistic of each of the four BEAST chronograms. Under a Yule process, γ values of completely sampled phylogenies have been shown to fit a standard normal distribution with mean = 0 (Pybus and Harvey 2000). Significantly negative gamma values (< -1.645 for one-tailed test, i.e. internal nodes distributed more towards the root than expected under a pure birth process) indicate a decrease in rates of cladogenesis over time. The undersampling in our analysis tends to generate underestimated number of nodes toward the present, and the CR test may accuse for false slowdown in diversification rate (Pybus and Harvey 2000). To correct such bias, we performed the MCCR (Markov Chain Constant Rates) test (Pybus and Harvey 2000) in which full topologies are simulated under the Yule process and then randomly subsampled to generate a corrected null distribution. The observed γ values were compared to the 95% confidence interval of a null distribution based on 10,000 topologies simulated for each of the four groups.

Global diversification rate (r**G**) for each of the four groups in this study was estimated using the method of Magallon and Sanderson (2001). This estimation considers extinction rates (э), thus, we estimated r**G** under different values of э (0.0, 0.5, 0.9 and 0.99). To look for subclades with higher than expected species richness we used the method of moments estimator of Magallon and Sanderson (2001) to calculate the 95% confidence interval of expected species richness for a lineage with origin at time (t) and evolving under a given r**G** and э, and then to compare with the observed species richness. Subclades were defined at highest monophyletic clades in which species shares the same type of trophic mode (quality criterion). The species richness of such lineages was measured based on valid names displayed at Catalog of Fishes (Eschmeyer, 2010) and crown ages were obtained from BEAST chronograms. For lineages with a single species sampled we used stem ages.

It is important to use methods with different approaches to correct for possible equivocal interpretation of the results given the limitations of each method. The method of moments estimator of Magallon and Sanderson (2001) considers basically a relation between species richness and age. Thus, we used the RC (Relative Cladogenesis) statistic of Nee et al. (1992) and the method described in Rabosky (2006b); Rabosky et al. (2007) to look for significant shifts in diversification rates.

The RC test identify lineages with significantly faster or slower rates of cladogenesis using a chronogram to calculates the probability that an internal node with n descendent tips to get partitioned into two subclades of size *r* and *s*, using a broken-stick distribution as the null expectation (Nee et al. 1992).

To apply Rabosky's (2006) method, we first reduced the trees at the level of the subclades we were interested, by pruning all but one species per subclade from the chronograms. Then, we assigned species richness to each terminal branch as a phenotype vector (Rabosky, 2006b). This method uses a birth–death estimator based on phylogenetic and taxonomic data to estimate diversification rate and compute the respective likelyhood. It contrasts the likelihood of the data under a model with equal diversification rates for all lineages (constant model) to the likelihood under a model where an ancestral diversification rate r1 shifts to a new rate r2 along some branch in the tree (flexible model) (Sanderson 1994; Sanderson and Wojciechowski 1996). For the flexible model, the tree is sequentially split at each branch and r is optimized to the resulting pair of subtrees. The node resulting in the maximum combined likelihood for the bipartite tree is the ML estimate of the shift point. Analyses were conducted under extinction fractions of э = 0.0, 0.5, 0.9 and 0.99. To contrast the model we used likelihood ratio test statistic (LRT X^2 distribured with 2 *d.f.*). Our hypothesis predict that the flexible model would be more likely than the constant model especially when assigning higher diversification rates at the origin of clades containing low-quality diet feeders. However, it does not mean necessarily that the diversification rates has increased at such node, but also, that the clade has retained an ancestral but elevated rate, while another clade or clades exhibited a decline in diversification. To check this, we used a constrained version of the two-rate model ('rate-decrease model'), where the highest diversification rate must occur in the tree bipartition containing the root node, therefore, no rate increase is allowed on the path from the root to the clade assigned by the shifting point (Rabosky et al. 2007). This method was previously used in Kazancioglu et al. (2009) in their study with Scarinae.

3. Results

3.1. Bayesian Inferences

Bayesian inferences produced the four topologies as well as the general patterns of Bayesian posterior probabilities very close to those of the original articles (Acanthuroidei: –lnL = 8,757.58; Chaetodontidae: –lnL = 32,088.41; Labridae: –lnL = 55,703.05; Pomacentridae: –lnL = 62,724.69). However, the basal relationships of Acanthuroidei are not completely resolved, probably because of the absence of nuclear gene sequences in the dataset. The original tree of Tang et al. (1999) also includes morphological information and do not present such uncertainty. To correct this in our chronogram, we used commands of BEAST to force monophyly of the families pointed by Tang et al. (1999). At the other trees some disagreements are found only where the original tree also pointed doubtful relationship at level of the tips, and do not influence in the set of high-level lineages. Although, there is a special case in Pomacentridae. As also obtained in Cooper et al. (2009), the phylogenetic position of the monotypic genus *Lepidozygus* is equivocal. For all trees stationarity and convergence were reached before 10% of generations. Valid estimations were indicated by good effective sample size. All phylograms with posterior probabilities might be checked at the supplementary material available online (figures 1, 2, 3 and 4).

3.2. Dates estimation and character optimization

The mean evolutionary rate was 1.24E-3 substitutions per site per million years for Acanthuroidei (95% HPD: 8.2E-4 – 1.6E-3), 5.51E-3 for Chaetodontidae (95% HPD: 3.9E-3 – 7.2E-3), 3.89E-3 for Labridae (95% HPD: 3.4E-4 – 4.3E-3) and 2,66E-3 for Pomacentridae (95% HPD: 2E-4 – 3.2E-3). The Yule process birth rate was 1.19E-2 for Acanthuroidei (HPD: 6.1E-3 – 1.8E-2), 8.4E-2 for Chaetodontidae (HPD: 5.6E-2 – 0.1), 4.7E-2 for Labridae (HPD: 3.6E-2 – 5.8E-2) and 5.1E-2 for Pomacentridae (HPD: 3.9E-3 – 6.5E-2). The data agree with an unclock-like behavior showing coefficients of variation of 0.54 for Acanthuroidei (HPD: 0.3 – 0.7), 0.37 for Chaetodontidae (HPD: 0.2 – 0.4), 0.48 for Labridae (HPD: 0.4 – 0.5) and 0.47 for Pomacentridae (HPD: 0.4 – 0.5). The data also reject hypothesis of rates autocorrelated across lineages with mean covariance of -0.11 for Acanthuroidei (HPD: -0.4 – 0.1), -1.3E-2 for Chaetodontidae (HPD: -0.1 – 0.1), 7.3E-2 for Labridae (HPD: -0.07 – 0.2) and 8.7E-2 for Pomacentridae (HPD: -0.04 – 0.2). The BEAST chronograms with mean node heights and bars representing 95% HPD of each node might be checked at supplementary material online (figures 5, 6, 7 and 8).

Chaetodontids chronogram (Figure 2) seems to agree very well with the one from Bellwood et al. (2010) (which have used other dataset to construct the tree), and with the ultrametric tree of Fessler & Westneat (2007) (from which we got our dataset). The latter has used NPRS (Nonparametric rate smooth) methods of Sanderson (Sanderson, 2004), while the first also have constructed a BEAST chronogram. Our labrid chronogram (Figure 3) is very similar to that of Cowmann et al. (2009), which also used BEAST to produce a chronogram based on the same sequences displayed in Westneat & Alfaro (2005) with the addition of some species. Cooper (2006) thesis brings a NPRS ultrametric tree based on the same sequences displayed in Cooper et al.

(2009) and his Pomacentridae chronogram also looks a lot like ours (Figure 4).

The 95% HPD interval was high for all basal relationships of Acanthuroidei. It is expected since, as exposed above, the absence of nuclear gene sequences may lead to unclear resolution at the base of the tree. Such bias might generate some uncertainty about the estimation of acanthuroids root at 120 Ma (95% HPD: 162-84), which is far from the origin of main reef fish families. However, Alfaro et al (2007) investigating the radiation timing of Tetraodontiformes found a similar pattern, with the order rooted about 100 Ma and reef families about 50 Ma. Scatophagidae and Ephippidae, used for the calibration, both have origin estimated at 55 Ma (95% HPD: 60–50 Ma) and the family Acanthuridae (the third calibration point) at 61 Ma (95% HPD: 86–50 Ma) (Figure 1). Character optimization indicates that the low-quality food habit has evolved two different times at Siganidae (stem age = 92 Ma, 95% HPD: 130–64 Ma) and Acanthuridae (-*Naso*) at 52 Ma (95% HPD: 76–34 Ma) (Figure 1). The Oldest Fossil record of Siganidae (possible crown age), as in the Family Acanthuridae, dates from the same Monte Bolca deposits of 50 Ma (Bellwood 1996, Tyler & Bannikov, 1997), which suggest that the two origins of low-quality food habit in Acanthuroidei may had occurred at the same time within the period of main reef fish families origin. The origin of the most speciose clade [75% of all Acanthuridae (-*Naso*)] formed by the genera *Acanthurus* + *Ctenochaetus* at 20 Ma (95% HPD: 31–10 Ma) coincides with the Oligo-Miocene period of tectonic activity on the IWP (Figure 1).

The origin of chaetodontids outgroup (taxonomically related reef fish families) was estimated at 55 Ma (95% HPD: 65–50 Ma) as we set in our prior. As expected, the family Chaetodontidae seems to be a relative young reef fish family originated at 33 Ma (95% HPD: 45–21 Ma) (Figure 2). The low-quality food habit would have evolved in the family about 20 Ma (95% HPD: 28–13) at clade "*Chaetodon*" during the Miocene. Character optimization suggests that firstly chaetodons started using low-quality food resources with more plasticity, feeding on a variety of sessil invertebrates (asciadians, sponges and corals), algae, and high-quality food items as tinny mobile invertebrates in lower proportion (right tree at Figure 2). The specialization into obligate coralivory appears at similar period 18 Ma (95% HPD: 24–12 Ma), in the sister clade of Chaetodon 2 formed by Chaetodon 3 + Chaetodon 4 (Figure 2).

The origin of Pomacentridae estimated at 52 Ma (95% HPD: 61–50 Ma) is very close to the age of the oldest fossil of the family used to set a hard lower bound prior (Figure 4). Low-quality diet appears soon at the first split in Stegastinae + *Lepidozigus*. Character optimization according food items classification indicates that earlier pomacentrid lineages were probably herbivorous and derived lineages converged four times to omnivory and 2 times to zooplanktivory (right tree at Figure 4). There are three other clades of species with low-quality diets: Pomacentrinae 1 (31 Ma, 95% HPD: 39–25), Pomacentrinae 2 (stem age = 25 Ma, 95% HPD: 32–19 Ma) and *Pomacentrus* (15 Ma, 95% HPD: 19–11 Ma), from which only *Pomacentrus* seems to have origin after the Oligo-Miocene period of tectonic activity in the IWP (Figure 4)

For the labrid tree, three clades used to calibration have age estimation close to the age of the oldest fossil: labrid root = 58 Ma (95% HPD: 62–55 Ma), Hypsigenyines = 51 Ma (95% HPD: 53–50), and Hypsigenyine’s sister group = 54 Ma (95% HPD: 59–50) (Figure 3). The age of 26 Ma estimated to Scaridae (95% HPD: 34-18) indicates it may be a much older clade than suggests the fossil record (15 Ma). Character optimization indicates four derived lineages of species with low-quality diets which have arisen independently at different times, using different food items, with probable radiation during the Miocene (Figure 3).

3.3. Diversification statistics

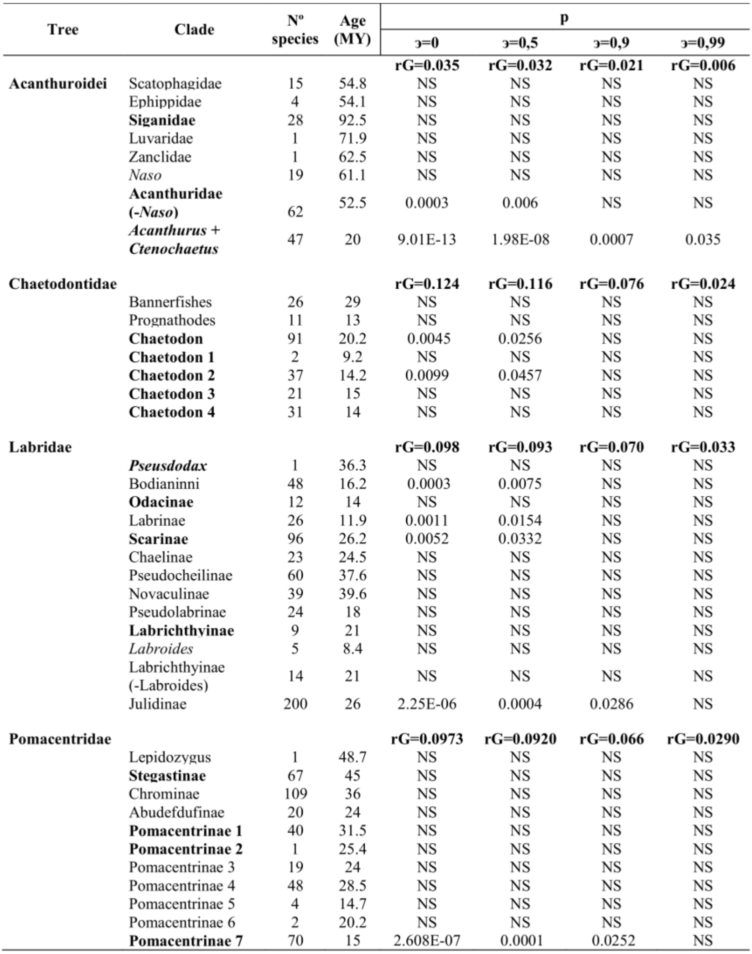
All the CR and MCCR tests did not showed significant *p* values for the gamma values (Acanthuroidei: γ = -1.9806, p = 0.466; Chaetodontidae: γ = 0.0917, p = 0.097; Labridae: γ = -3.7382, p = 0.084; Pomacentridae: γ = -2.9265, p = 0.187). Thus, we cannot ensure decreasing species-level diversification rates because of the amount of missing data.

Global diversification rates (r**G**) estimated with the method of Magallon and Sanderson (2001) decreased with increasing extinction rates, as noted by authors of the method. Significant higher than expected species richness under r**G** conditioned to different values э are found in Table 3. It corresponds to: (1) *Acanthurus* + *Ctenochaetus* (Acanthuroidei, Figure 1); (2) *Chaetodon* (Chaetodontidae, Figure 2); (3) *Pomacentrus* (Pomacentridae, Figure 4); and (4) Bodianinni, (5) Labrinae, (6) Scarinae and (7) Julidinae (Labridae, Figure 3). In Acanthuroidei, we look for the species richness formed by the clade

Acanthuridae (-*Naso*) to conduct the test since all species, but *Paracanthurus hepatus*, shares the same trophic character in this monophyletic group, and we obtained significant values of p only under э = 0.0. Acanthuridae (-*Naso*) has a mean age of 52 Ma, however, 75% of these species belong to the subclade formed by *Acanthurus* + *Ctenochaetus*, originated about 20 Ma. Therefore, we believe that all influence that lead to higher than expected number of extant species in Acanthuridae (-*Naso*) come exclusively from the effects over the *Acanthurus* + *Ctenochaetus* diversification. We applied the test considering *Acanthurus* + *Ctenochaetus* species richness and we obtained significant values of p under even higher extinction rates (э = 0.0 to э = 0.99). For Julidinae (Labridae) and *Pomacentrus* (Pomacentridae) we obtained significant values o p under э = 0.0 to э = 0.9. The remaining clades showed significant p values under э = 0.0 to э = 0.5. From these seven speciose clades, RC test of Nee et al. (1992) indicates higher than expected rates of cladogenesis in *Chaetodon* (Chaetodontidae), *Pomacentrus* (Pomacentridae), Bodianinni and Scarinae (Labridae).

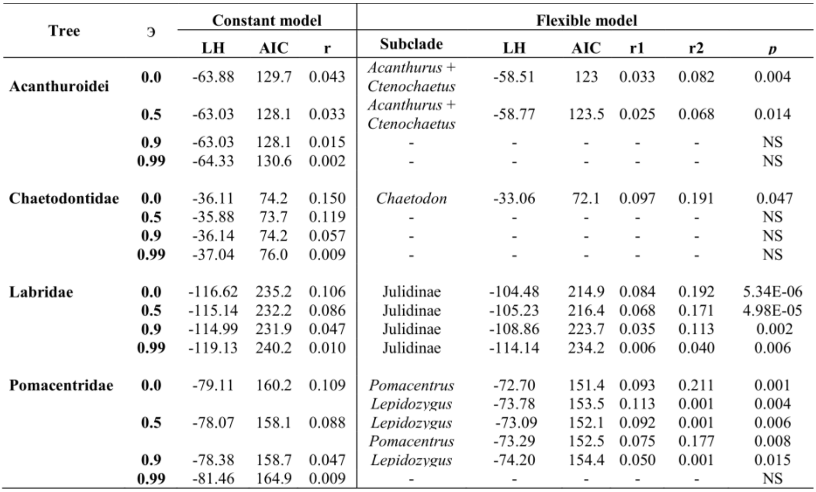
The comparisons between constant model and flexible model following Rabosky (2007) are displayed at the Table 4. As observed in Magallon and Sanderson (2001), r is also conditioned to э (0.0, 0.5, 0.9 and 0.99), and it decreases with э elevation. The flexible model was likely for elevated diversification rate at clades *Acanthurus* + *Ctenochaetus* in Acanthuroidei (э = 0.0 to э = 0.5), *Chaetodon* in Chaetodontidae (э = 0.0), Julidinae in Labridae (э = 0.0 to э = 0.99) and *Pomacentrus* in Pomacentridae (э = 0.0 to э = 0.5). In Pomacentridae were also indicated significant higher likelihoods for a reduced diversification rate in Lepidozygus under values of э = 0.0 to э = 0.9. However, posterior probabilities from Bayesian analysis in this study and in Cooper et al. (2009), both showed uncertain phylogenetic position for this genus which makes its age very doubtful. Rate-decreasing scenario was rejected against flexible model for all clades with elevated diversification rate, which suggests shifting points for increasing diversification rate.

Table 3. Higher than expected species richness of clades pointed in the Figures 1, 2, 3 and 4. rG = estimated global rate of diversification under different values of extinction rate (э). P < 0.05 indicates significant values. NS= not significant. Clade labeled in bold = species within subclades using low-quality diets.



Tree	Clade	Nº species	Age (MY)	p			
				э=0	э=0,5	э=0,9	э=0,99
				rG=0.035	**rG=0.032**	**rG=0.021**	**rG=0.006**
Acanthuroidei	Scatophagidae	15	54.8	NS	NS	NS	NS
	Ephippidae	4	54.1	NS	NS	NS	NS
	Siganidae	28	92.5	NS	NS	NS	NS
	Luvaridae	1	71.9	NS	NS	NS	NS
	Zanclidae	1	62.5	NS	NS	NS	NS
	Naso	19	61.1	NS	NS	NS	NS
	Acanthuridae (-*Naso*)	62	52.5	0.0003	0.006	NS	NS
	Acanthurus* + *Ctenochaetus	47	20	9.01E-13	1.98E-08	0.0007	0.035
Chaetodontidae				**rG=0.124**	**rG=0.116**	**rG=0.076**	**rG=0.024**
	Bannerfishes	26	29	NS	NS	NS	NS
	Prognathodes	11	13	NS	NS	NS	NS
	Chaetodon	91	20.2	0.0045	0.0256	NS	NS
	Chaetodon 1	2	9.2	NS	NS	NS	NS
	Chaetodon 2	37	14.2	0.0099	0.0457	NS	NS
	Chaetodon 3	21	15	NS	NS	NS	NS
	Chaetodon 4	31	14	NS	NS	NS	NS
Labridae				**rG=0.098**	**rG=0.093**	**rG=0.070**	**rG=0.033**
	Pseusdodax	1	36.3	NS	NS	NS	NS
	Bodianinni	48	16.2	0.0003	0.0075	NS	NS
	Odacinae	12	14	NS	NS	NS	NS
	Labrinae	26	11.9	0.0011	0.0154	NS	NS
	Scarinae	96	26.2	0.0052	0.0332	NS	NS
	Chaelinae	23	24.5	NS	NS	NS	NS
	Pseudocheilinae	60	37.6	NS	NS	NS	NS
	Novaculinae	39	39.6	NS	NS	NS	NS
	Pseudolabrinae	24	18	NS	NS	NS	NS
	Labrichthyinae	9	21	NS	NS	NS	NS
	Labroides	5	8.4	NS	NS	NS	NS
	Labrichthyinae (-Labroides)	14	21	NS	NS	NS	NS
	Julidinae	200	26	2.25E-06	0.0004	0.0286	NS
Pomacentridae				**rG=0.0973**	**rG=0.0920**	**rG=0.066**	**rG=0.0290**
	Lepidozygus	1	48.7	NS	NS	NS	NS
	Stegastinae	67	45	NS	NS	NS	NS
	Chrominae	109	36	NS	NS	NS	NS
	Abudefdufinae	20	24	NS	NS	NS	NS
	Pomacentrinae 1	40	31.5	NS	NS	NS	NS
	Pomacentrinae 2	1	25.4	NS	NS	NS	NS
	Pomacentrinae 3	19	24	NS	NS	NS	NS
	Pomacentrinae 4	48	28.5	NS	NS	NS	NS
	Pomacentrinae 5	4	14.7	NS	NS	NS	NS
	Pomacentrinae 6	2	20.2	NS	NS	NS	NS
	Pomacentrinae 7	70	15	2.608E-07	0.0001	0.0252	NS

Table 4. Likelihoods (LH) and Akaike information criterion (AIC) for constant and flexible model of diversification under different extinction rates (э). r is the constant diversification rate estimated across all lineages. $p < 0.05$ indicates significant higher likelihood estimated for the flexible model, in which a diversification rate r1 shift to r2 at the subclade indicated. NS indicates that the flexible model was not significant assuming shifts in any of the subclades. Rate decreasing scenario was not significant in any case, except in Pomacentridae over э = 0.5, which was not considered due the equivocal phylogenetic position of *Lepidozygus*.



Tree	**э**	**Constant model**			**Flexible model**					
		LH	**AIC**	**r**	**Subclade**	**LH**	**AIC**	**r1**	**r2**	***p***
Acanthuroidei	**0.0**	-63.88	129.7	0.043	*Acanthurus + Ctenochaetus*	-58.51	123	0.033	0.082	0.004
	0.5	-63.03	128.1	0.033	*Acanthurus + Ctenochaetus*	-58.77	123.5	0.025	0.068	0.014
	0.9	-63.03	128.1	0.015	-	-	-	-	-	NS
	0.99	-64.33	130.6	0.002	-	-	-	-	-	NS
Chaetodontidae	**0.0**	-36.11	74.2	0.150	*Chaetodon*	-33.06	72.1	0.097	0.191	0.047
	0.5	-35.88	73.7	0.119	-	-	-	-	-	NS
	0.9	-36.14	74.2	0.057	-	-	-	-	-	NS
	0.99	-37.04	76.0	0.009	-	-	-	-	-	NS
Labridae	**0.0**	-116.62	235.2	0.106	Julidinae	-104.48	214.9	0.084	0.192	5.34E-06
	0.5	-115.14	232.2	0.086	Julidinae	-105.23	216.4	0.068	0.171	4.98E-05
	0.9	-114.99	231.9	0.047	Julidinae	-108.86	223.7	0.035	0.113	0.002
	0.99	-119.13	240.2	0.010	Julidinae	-114.14	234.2	0.006	0.040	0.006
Pomacentridae	**0.0**	-79.11	160.2	0.109	*Pomacentrus*	-72.70	151.4	0.093	0.211	0.001
					Lepidozygus	-73.78	153.5	0.113	0.001	0.004
	0.5	-78.07	158.1	0.088	*Lepidozygus*	-73.09	152.1	0.092	0.001	0.006
					Pomacentrus	-73.29	152.5	0.075	0.177	0.008
	0.9	-78.38	158.7	0.047	*Lepidozygus*	-74.20	154.4	0.050	0.001	0.015
	0.99	-81.46	164.9	0.009	-	-	-	-	-	NS

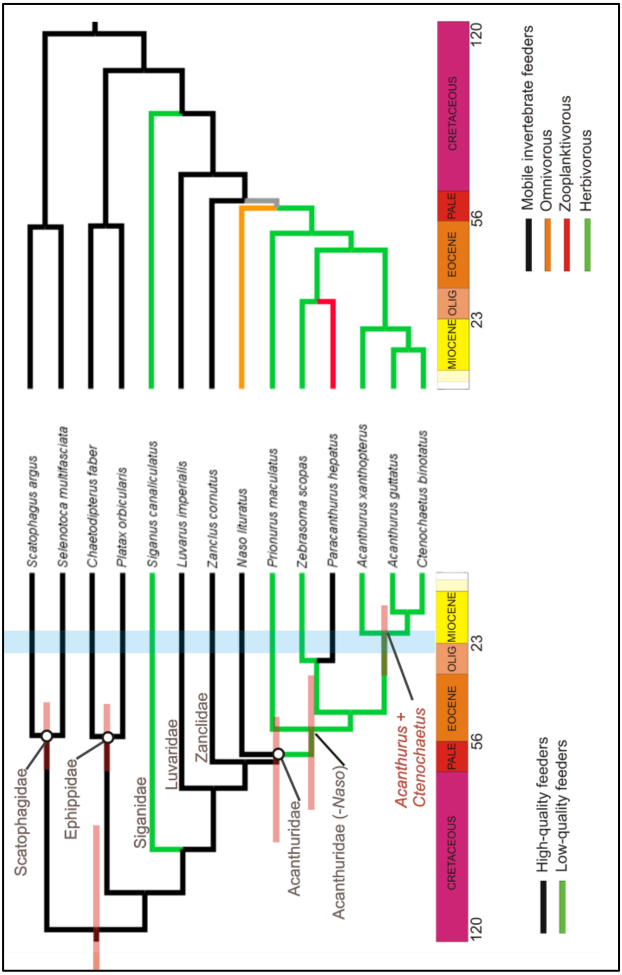


Figure 1. BEAST chronogram of Acanthuroidei showing optimized character under quality (left) and items (right) criteria. Gray branches mean equivocal character. Bars on nodes represent the 95% HPD of subclades mean age. White dots indicate calibration points. The blue bar represents the Oligo-Miocene period among 25–20 Ma in which the collision of Australia with Pacific arcs and the southeastern Asian margin is supposed to have increased the coral-reef carbonate platforms in central IWP. *Acanthurus* + *Ctenochaetus* (labeled on red) was indicated to have higher than expected number of extant species under global rates of diversification in the test of Magallon & Sanderson (2004) and elevated rate of diversification by the test of Rabosky (2007).

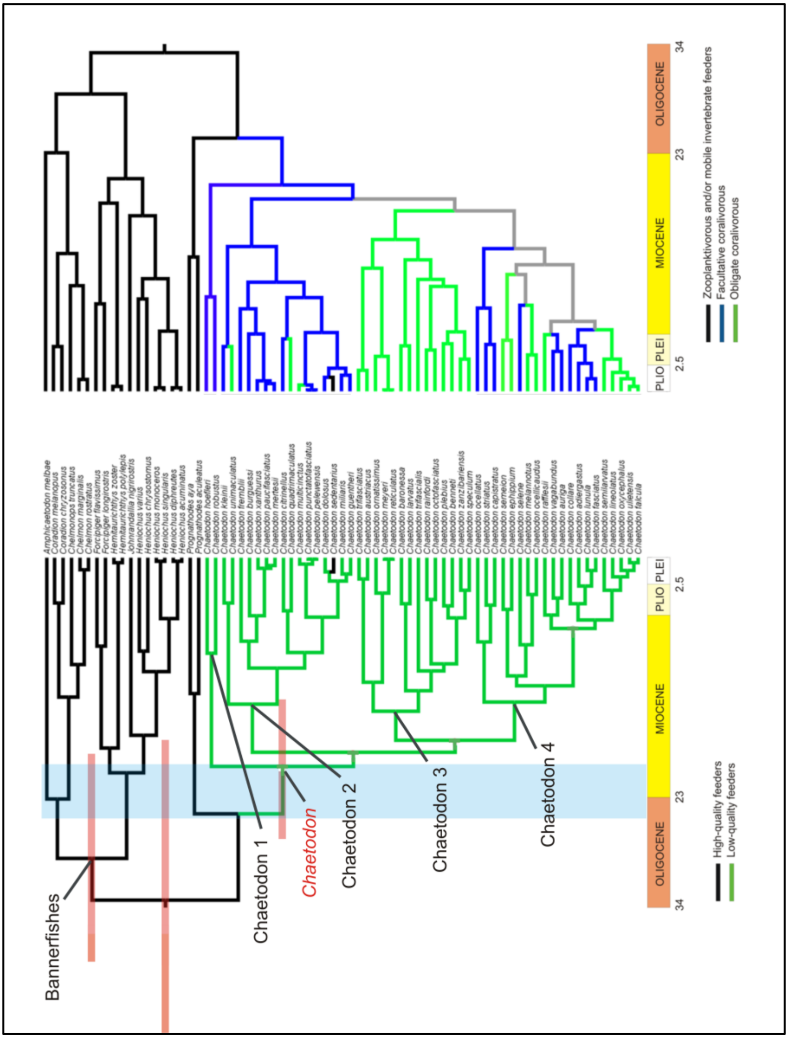


Figure 2. BEAST chronogram of Chaetodontidae showing optimized character under quality (left) and items (right) criteria. Gray branches mean equivocal character. Bars on nodes represent the 95% HPD of subclades mean age. Calibration point is on the root of the outgroup, not contemplated in the figure. The blue bar represents the Oligo-Miocene period among 25–20. *Chaetodon* (labeled on red) was indicated to have higher than expected number of extant species under global rates of diversification in the test of Magallon & Sanderson (2004), and elevated rate of diversification by the tests of Rabosky (2007) and Nee et al. (1992).

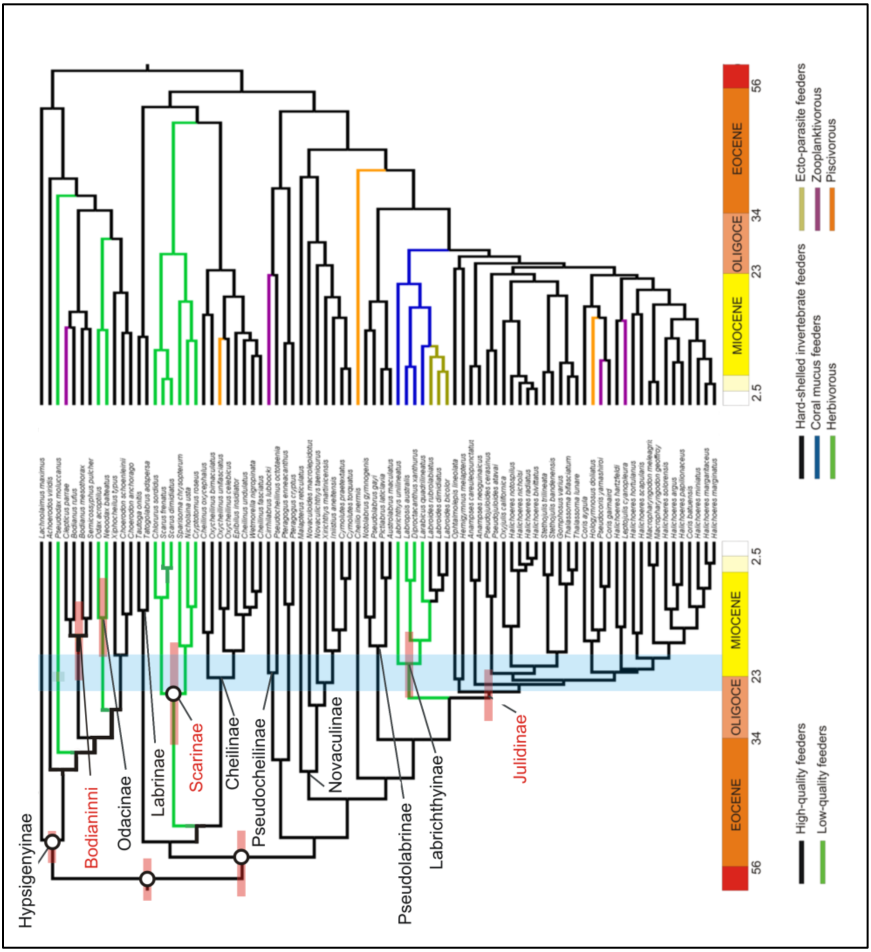


Figure 3. BEAST chronogram of Labridae showing optimized character under quality (left) and items (right) criteria. Bars on nodes represent the 95% HPD of subclades mean age. White dots indicate calibration points. The blue bar represents the Oligo-Miocene period among 25–20. Bodianinni, Scarinae and Julidinae (labeled in red) were indicated to have higher than expected number of extant species under global rates of diversification in the test of Magallon & Sanderson (2004). Bodianinni and Scarinae were indicated to presented elevated diversification rates by the test of Nee et al. (1992); and Julidinae by the test of Rabosky (2007).

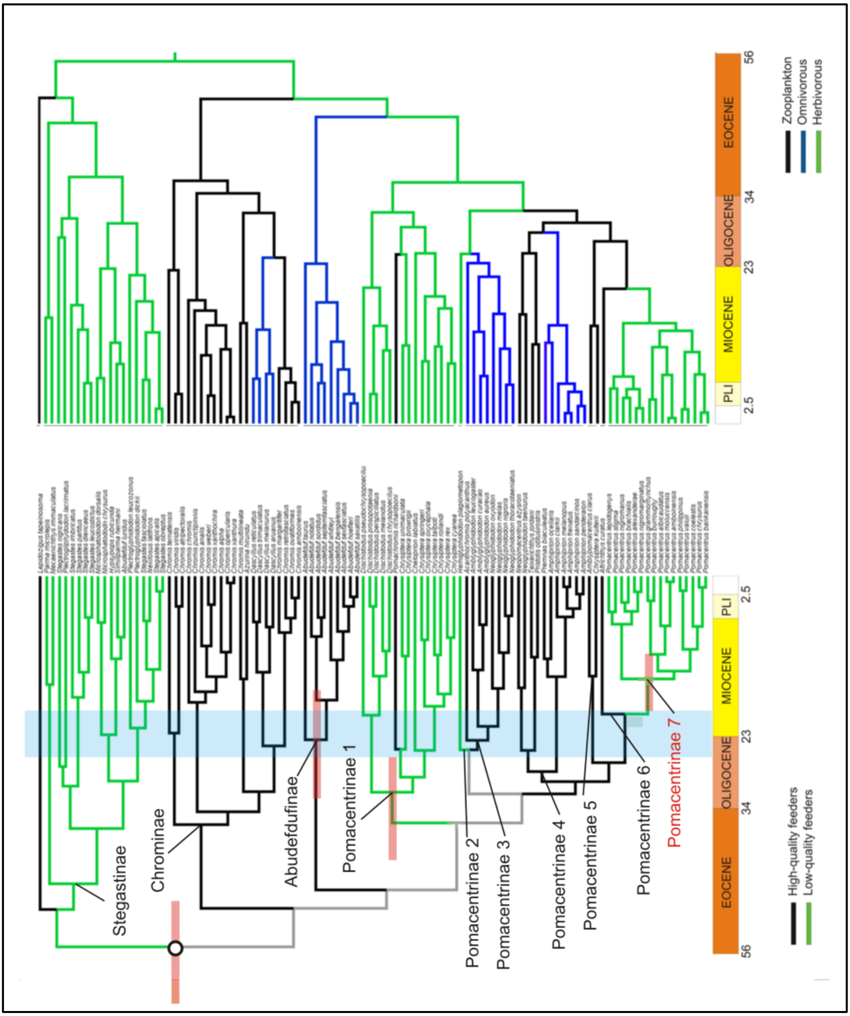


Figure 4. BEAST chronogram of Pomacentridae showing optimized character under quality (left) and items (right) criteria. Gray branches mean equivocal character. Bars on nodes represent the 95% HPD of subclades mean age. White dot indicates the calibration point. The blue bar represents the Oligo-Miocene period among 25–20. *Pomacentrus* (labeled on red) was indicated to have higher than expected number of extant species under global rates of diversification in the test of Magallon & Sanderson (2004), and elevated rate of diversification by the tests of Rabosky (2007) and Nee et al. (1992).

4. Discussion

4.1. Competitive interaction and the rise of low-quality diets

With exception of pomacentrids, the remaining three trees seem to agree with the idea that the use of low-quality food resources is a derived condition which has evolved one or more times independently in clade's history (Kotrshchal, 1987). However, the origin of such condition does not seem to be time-related to periods of increasing species richness as suggested by Harmelinn-Vivien's (2002) evolutionary process. In Acanthuroidei, the origin of diets based on low-quality food resources in Siganidae and Acanthuridae coincides with the origin of main reef fish families (approximately 65-50 Ma), far from the period of origin of most modern reef fish genera at the Miocene (Figure 1). The same apply to pomacentrids, in which the character seems to be already in the root of the tree, with possible independent convergences to high-quality diet (Figure 4). Interesting to note that in Pomacentridae the different food habits (herbivory, omnivory and planktivory) may be related among lineages, distinguishing from each other by different balances between zooplankton and algae in the total ingested biomass.

To the other hand, chaetodontids evolution seem to agree quietly well with Harmelin-Vivien's (2002) predictions. The use of low-quality food resources would be a derived condition originated only when reef communities are expected to reach high levels of species richness, evidenced here by origin and radiation o *Chaetodon* during the Miocene (Figure 2). In addition, the reconstruction of ancestral characters based on food habit (right tree, Figure 2) suggests that the first chaetodons should have more plasticity to use low-quality food items and could count with a little contribution of high-quality food resources in their diet. Later, some derived lineages would become more restricted to feed on corals at least four times independently. Here, as in Pomacentridae, the food habits seem to be related among lineages. All chaetodons bite the substrate to capture the prey, distinguishing from each other by what they are biting. However, the dietary differentiation among chaetodontid's lineages seems to be evolutionarily directed from high to low-quality diets (possibly due competitive interaction according Harmellin-Vivien, 2002), while in pomacentrids, low-quality diet is found among basal, intermediate and derived lineages.

Despite Scarinae, *Pseudodax*, Odacinae and Labrichthyinae to be derived lineages evolved to use low-quality food resources, Labrid's evolution does not seem to by the competitive interactions as inferred based on Harmelin-Vivien's (2002). First, the mean crown age of 26 Ma (95% HPD = 34–18) of Scarinae, and its old stem age about 50 Ma suggest an unlikely origin of the group inside the Miocene, and the same apply to the monotypic genus *Pseudodax*, originated at late Eocene. Second, despite Labrichthyinae mean age fall into the Miocene, in the subclade is observed a regression to high-quality diets among derived species of the genus *Labroides*. Odacinae is a subfamily restricted to temperate waters of southern Australia (Clements et al., 2004), a peripheral region to the center of high diversity in the IWP (Allen, 2002; Briggs, 2003). Plus, only 6 from 12 odacine species are herbivorous. In fact, Odacinae for itself agrees with Harmelin-Vivien (2002) assumptions, which argues that the rise of trophic modes related to low-quality food resources should be uncommon in lineages evolving out of the tropics.

4.2. Low-quality diets and diversification rate

With exception of Labridae, the three remaining clades have confirmed the hypothesis based on density-dependent principles that, clades of species using low-quality diets originated inside periods of high diversity levels in reef communities would present higher than expected number of extant species. Those are *Chaetodon* in Chaetodontidae (Figure 2), *Pomacentrus* in Pomacentridae (Figure 4) and "*Acanthurus* + *Ctenochaetus*" in Acanthuroidei (Figure 1).

It is logical to attribute the high number of extant species in *Chaetodon*, *Pomacentrus* and *Acanthurus* + *Ctenochaetus* to the Oligo-Miocene Tectonic event of the IWP. However, those lineages of species with diets based on high-quality food resources with origin and radiation close to this period does not show significant speciose clades (see Bannerfishes and Prognathodes in Chaetodontidae, Figure 2; Pomacentrinae 3, Pomacentrinae 5, Pomacentrinae 6 and Abudefdufinae in Pomacentridae, Figure 4). The phylogenetic study of Klanten et al. (2004) with all *Naso* (Acanthuridae) extant species shows that from 50 to 25 Ma the rate of origin of new lineages remained constant in the genus history. During the early Miocene there was a boom of cladogenesis followed by a decline in middle Miocene. *Naso* is a subclade of species using high-quality diets, and seems to have increased the diversification rate during Miocene as many others could be have done too. However, principles of density-dependent diversification suggest that for these clades, the species-level diversification rate should decline faster than for *Chaetodon*, *Pomacentrus* and *Acanthurus* + *Ctenochaetu*s. Since the high-quality food items are the base of diet in most reef fish lineages, these resources should be firstly occupied and the ecological opportunities for speciation would decline faster for such clades. Thus, significant higher than expected number of extant species in *Chaetodon*, *Pomacentrus* and *Acanthurus* + *Ctenochaetus* could be attributed to a combination of effects among vicariate events and less competitive interactions, one leading to increasing number of opportunities for speciation, and the other keeping this opportunities in high levels for longer time, respectively.

4.3. The labrid case

The labrid evolution does not seems to fit adequately in our argumentations as the other three groups. Besides we discussed above about Scarinae and Labrichthyinae, the clear statistical indications of increased diversification in Julidinae is totally opposite to the expected result according the hypothesis in this study. Those are evidences that labrid diversification may be influenced by other factors rather than the quality of the food resources.

Scarines are hypothesized to have radiated in stages of divergence along axes of habitat, trophic morphology and communication (Streelman & Danley, 2003). In the first stage they would diverged between lineages of flat seagrass areas and lineages of three-dimensional reef areas. It might be followed by divergence in trophic eco-morphology (browsing, scraping, grazing), and finally, in the communication axes through means of sexual selection of the dichromatic character (Streelman & Danley, 2003). Kazancıoglu et al. (2009) in their phylogenetic study with Scarinae attributed higher diversification rates within taxon radiation starting at the genus *Scarus* (54% of the subfamily) leaded by strong sexual dichromatism, suggesting that sexual selection was a major factor in parrotfish diversification.

Labrichthyines are characterized by thin and long jaws which allow the suction of coral mucus (low-quality diet) or ecto-parasites (high-quality diet) as feeding behavior (Kuiter, 2009). Therefore, one option is that the differentiation of labrichthyines trophic modes may be driven by ecological opportunities related to morphological features instead of alimentary quality.

Julidines, as most labrid species are hard-shelled invertebrate feeders. These fishes are able to live on most different reef habitats and feed on a variety of equinoderms, crustaceans, and molluscians, establishing complex ecological networks with species in the community. It is possible, thus, that the possibility of labrids diversify greatly in their ecological functions may had allowed high diversification rates of labrid lineages even in the use of high-quality resources. That, would be another case of high diversification rates being leaded by less competitive interaction. In the case attributed to acanthuroids, chaetodontids and pomacentrids, the species would avoid competitive interactions by using neglected resources. In the labrid case, such escape would be given by higher morphological disparity leading to more possibilities for speciation.

5. Conclusions

Our study suggest that the diversification of reef fish lineages may be ruled by models of ecological opportunity in which competitive interaction would have an important role. Our inferences do not discarded the Harmelin-Vivien's (2002) evolutionary process, instead, we reinforced it, presenting a new perspective of the role of competition in the speciation process. We propose that a clade might get so specieose as much competition is repealed finding unoccupied by resources to speciation. That would come from two ways: (1) to be a minority, or (2) to be able to find spaces among the majority.

It is important to note that the study look for the data inside a large scale, phylogeneticly, special and, in terms of character analyzed. Another alternative, is to conduct this analysis in the level of species, looking for more specific traits and for species distribution, to be able to argue more consistent inferrences.

Acknowledgements

This work is part of the Master thesis in the Ecology Graduate Program of the Universidade Federal de Santa Catarina (Brazil), which was, in part, financially supported by CNPq (National Counsel of Technological and Scientific Development).

This work benefited from using resources of the Computational Biology Service Unit from Cornell University (CBSU Web Computing Interface) which is partially funded by Microsoft Corporation. We also thanks to Tandy Warnow and the whole team of

the Cyberinfrastructure for Phylogenetic Research (CIPRES) project (http://www.phylo.org) which also allowed us to run faster analysis.

References

Alfaro, M.E., Santini, F., Brock, C.D., 2007. Do reefs drive diversification in marine teleosts? Evidence from the pufferfish and their allies (Order Tetraodontiforms). Evolution 61, 2104–2126.

Alfaro, M.E., Brock, C.D., Banbury, B.L., Wainwright, P.C., 2010. Does evolutionary innovation in pharyngeal jaws lead to rapid lineage diversification in labrid fishes? BMC Evol. Biol. doi:10.1186/1471-2148-9-255.

Allen, G.R., 1991. Damselfishes of the World. Aquarium Systems, Mentor, Ohio.

Allen, G.R., 2002. Indo-Pacific coral-reef fishes as indicators of conservation hotspots. Proc. 9th Int. Coral Reef Symp., Bali, Indonesia 2, 23–27.

Allen, G.R., 2007. Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. Aquat. Conserv.: Mar. Freshwat. Ecosys. 18, 541–556.

Bannikov, A.F., Sorbini, L., 1990. Eocoris bloti, a new genus and species of labrid fish (Perciformes, Labroidei) from the Eocene of Monte Bolca, Italy. Studi e Recereche sui Giacimenti Terziari di Bola, Museo Civico di Storia Naturale. Verona 6, 133–148.

Bannikov, A.F., 2004. Fishes from the Eocene of Bolca, northern Italy, previously classified with the Chaetodontidae (Perciformes). Studie Ricerche sui Giacimenti Terziari di Bolca 13, 55–74.

Bellwood, D.R., 1990. A new fossil fish *Phyllopharyngodon longipinnis* gen. Et sp. nov. (family Labridae) from the Eocene, Monte Bolca, Italy. Studi e Ricerche sui Giacimenti Terziari di Bola, Museo Civico di Storia Naturale. Verona 6, 149–160.

Bellwood, D.R., 1994. A phylogenetic study of the parrotfishes, family Scaridae (Pisces: Labroidei), with revision of genera. Rec. Aust. Mus. 20, 1–86.

Bellwood, D.R., 1996. The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. Coral Reefs 15, 11–19.

Bellwood, D.R., 1997. Reef fish biogeography: habitat associations, fossils and phylogenies. Proc. 8th Int. Coral Reef Symp. 1, 379–384.

Bellwood, D.R., 1998. What are coral reef fishes?—Comment on the report by D.R. Robertson: do coral reef fish faunas have a distinctive taxonomic structure? (Coral Reefs 17: 179–196). Coral Reefs 17, 187–189.

Bellwood, D.R., 1999. Fossil pharyngognath fishes from Monte Bolca, Italy, with a description of a new pomacentrid genus and species. Studi e Recereche sui Giacimenti Terziari di Bola, Museo Civico di Storia Naturale. Verona 8, 207–217.

Bellwood, D.R., Wainwright, P.C., 2002. The history and biogeography of fishes on coral reefs. In: Sale, P.F. (Ed.), Coral reef fishes: dynamics and diversity on a complex ecosystem. Academic Press, San Diego, California, pp. 5–32.

Bellwood, D.R., van Herwerden, L., Konow, N., 2004. Evolution and biogeography of marine angelfishes (Pisces: Pomacanthidae). Mol. Phyloget. Evol. 33, 140–155.

Bellwood, D.R., Klanten, S., Cowman, P.F., Pratchett, M.S., Konow, N., Van Herwerden, L., 2010. Evolutionary history of the butterflyfishes (f: Chaetodontidae) and the rise of coral feeding fishes. J. Evol. Biol. 23, 335–49.

Benson, D.A., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J., Wheeler, D.L., 2005. Genbank. Nucleic Acids Res. 1, 34–38 (http://www.ncbi.nlm.nih.gov).

Blum, S.D., 1988. Osteology and Phylogeny of the Chaetodontidae (Pisces: Perciformes). University of Hawaii, Honolulu.

Bowen, S.H., Lutz, E.V., Ahlgren, M.O. 1995. Dietary protein as determinants of food quality: trophic strategies compared. Ecology 76, 899–907.

Briggs, J.C., 2000. Centrifugal speciation and centres of origin. J. Biogeogr. 27, 1183–1188.

Briggs, J.C., 2003. Marine centers of origin as evolutionary engines. J. Biogeogr. 30, 1–18.

Briggs, J.C., 2005. Coral reefs: Conserving the evolutionary sources. Biol. Conserv. 126, 297–305.

Brown, J.W., Rest, J.S., García-Moreno, J., Sorenson, M.D., Mindell, D.P., 2008. Strong mitochondrial DNA support for a Cretaceous origin of modern avian lineages. BMC Biol. doi:10.1186/1741-7007-6-6.

Bruggemann, J.H., 1994. Parrotfish grazing on coral reefs: a trophic novelty. PhD Thesis, University of Groningen, Netherlands.

Bruggemann, J.H., Begeman, J., Bosna, E.M., Verbug, P., Breeman, A.M., 1994. Foraging by the stoplight parrotfish Sparisoma viride. II. Intake and assimilation of food, protein, and energy. Mar. Ecol. Prog. Ser. 112, 57–71.

Burns, E. & Ilan, M. (2003). Comparison of anti-predatory defenses of Red Sea and Caribbean sponges. II. Physical defence. Mar. Ecol. Progr. Ser. 252, 115–123.

Burns, E., Ifrach, I., Carmeli, S., Pawlik, J.R., Ilan, M., 2003. Comparison of antipredatory defenses of Red Sea and Caribbean sponges. II. Chemical defence. Mar. Ecol. Prog. Ser. 252, 105–114.

Cattin M.F., Bersier, L.F., Banašek-Richter, C., Baltensperger, R., Gabriel, J.P., 2004. Phylogenetic constraints and adaptation explain food-web structure. Nature 427, 835-839.

Clements, K.D., Gray, R.D., Choat, J.H., 2003. Rapid evolutionary divergences in reef fishes of the family Acanthuridae (Perciformes: Teleostei). Mol. Phylogenet. Evol. 26, 190–201.

Carpenter, R.C., 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecolog. Monogr. 56, 345–363.

Choat, J.H., 1991. The biology of herbivorous fishes on coral reefs. In: Sale, P.F. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, California, pp. 120–155.

Choat, J.H., Bellwood, D.R., 1991. Reef fishes: their history and evolution. In: Sale, P.F. (Ed.), The Ecology of Coral Reef Fishes. Academic Press, San Diego, California, pp. 39–60.

Choat, J.H., Clements, K.D., 1993. Daily feeding rates in herbivorous labroid fishes. Mar. Biol. 117, 205–211.

Choat, J.H., Clements, K.D., 1998. Vertebrate herbivores in marine and terrestrial environments: a nutritional ecology perspective. Annu. Rev. Ecol. Syst. 29, 375–403.

Choat, J.H., Clements, K.D., 2002. The trophic status of herbivorous fishes on coral reefs 1: dietary analyses. Mar. Biol., 140, 613–623.

Clements, K.D., Alfaro, M.E., Fessler, J.L., Westneat, M.W., 2004. Relationships of the temperate Australasian labrid fish tribe Odacini. Mol. Phylogenet. Evol. 32, 575– 587.

Cooper, W.J., 2006. The Evolution of the Damselfishes: Phylogenetics, Biomechanics, and Development of a Diverse Coral Reef Fish Family. Organismal Biology and Anatomy. The University of Chicago, Chicago.

Cooper, W.J., Smith, L.L., Westneat, M.W., 2009. Exploring the radiation of a diverse reef fish family: Phylogenetics of the damselfishes (Pomacentridae), with new classifications based on molecular analyses of all genera. Mol. Phylogenet. Evol. 52, 1–16.

Cooper, W.J., Westneat, M.W., 2009. Form and function of damselfish skulls: rapid and repeated evolution into a limited number of trophic niches. BMC Evolut. Biol, doi:10.1186/1471-2148-9-24.

Cowen, R.K. 2002. Larval dispersal and retention and consequences for population connectivity. In: Sale P.F. (Ed.), Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, California, pp. 149–170.

Cowen, R.K., Sponaugle, S., 2009. Larval dispersal and retention and consequences for population connectivity. Annu. Rev. Mar. Sci. 1, 443–466.

Cowman, P.F., Bellwood, D.R., van Herwerden, L., 2009. Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs. Mol. Phylogenet. Evol. 52, 621–63.

Doebeli, M., Dieckmann, U., 2003. Speciation along environmental gradients. Nature 421, 259–263.

Drummond, A.J. & Rambaut, A. 2007. Bayesian evolution analysis by sampling trees. BMC Evol. Biol. 7: 214.

Drummond, A.J., Ho, S.Y.W., Phillips, M.J. & Rambaut, A. 2006. Relaxed phylogenetics and dating with confidence. PLoS Biol. 4: 699–710.

Dunlap, M., Pawlik, J.R., 1996. Video-monitored predation by Caribbean reef fishes on an array of mangrove and reef sponges. Mar. Biol. 126, 117–123.

Elliott, J.P., Bellwood, D.R., 2003. Alimentary tract morphology and diet in three coral reef fish families. J. Fish Biol. 63, 1598–1609.

Emerson, B.C., Gillespie, G.R., 2008. Phylogenetic analysis of community assembly and structure over space and time. Trends Ecol. Evol. 23, 619–630.

Emery, A.R., 1973. Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at alligator reef, Florida Keys. Bull. Mar. Sci. 23, 649–770.

Epifânio, R.A., Martins, D.L., Gabriel, R., Villac, R.C., 1999. Chemical defenses against fish predation in three brazilian octocorals: 11ß,12ß-Epoxypukalide as a feeding deterrent in Phyllogorgia dilatata. J. Chemic. Ecol. 10, 2255–2265.

Eschmeyer, W.N. (Ed.), Catalog of Fishes, http://research.calacademy.org/ichthyology/ catalog/fishcatmain.asp, Version (12 July 2010)

Ferreira, C.E.L., Peret, A.C., Coutinho, R., 1998. Seasonal grazing rates and food processing by tropical herbivorous fishes. J. Fish Biol. 53, 222–235.

Fessler, J.L. & Westneat, M.W. 2007. Molecular phylogenetics of the butterflyfishes (Chaetodontidae): taxonomy and biogeography of a global coral reef fish family. Mol. Phylogenet. Evol. 45: 50–68.

Floeter, S.R., Ferreira, C.E.L., Dominici-Arosemena, A., Zalmon, I.R., 2004. Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. J. Fish Biol. 64, 1680–1699.

Froese, R., Pauly., D. (Eds.), FishBase: World Wide Web electronic publication.
www.fishbase.org, version (05/2010).

Gerking, S.D., 1994. Feeding ecology of fishes. Academic Press, San Diego, California.

Goldschmid, A., Kotrschal, K., Wirtz, P., 1984. Food and gut length of 14 Adriatic Blenniid fish (Blenniidae; Percomorpha; Teleostei). Zoologischer Anzeiger, 213, 145–150.

Halas, D., Winterbottom, R., 2009. A phylogenetic test of multiple proposals for the origins of the East Indies coral reef biota. J. Biogeogr. 36, 1847–1860.

Harmelin-Vivien, M.L., 1981. Trophic relationships of reef fishes in Tuléar (Madagascar). Oceanol. Acta 4, 365–374.

Harmelin-Vivien, M. L. (1989). Reef fish community structure: an Indo-Pacific comparison. In: Harmelin-Vivien, M.L., Bourliere, F. (Eds.) Ecological Studies. Springer-Verlag, New York, pp. 21–60.

Harmelin-Vivien, M.L., 2002. Energetics and fish diversity on coral reefs. In: Sale, P.F. (Ed.), Coral reef fishes: dynamics and diversity on a complex ecosystem. Academic Press, San Diego, California, pp. 265–274.

Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E., Challenger, W., 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24, 129–131.

Hay, M.E., 1991. Fish–seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In: Sale, P.F. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, California, pp. 96–119.

Horn, M.H., 1983. Optimal diets in complex environments: feeding strategies of two herbivorous fishes from a temperate rocky intertidal zone. Oecologia 58, 1432–1939.

Horn, M.H., 1989. Biology of marine herbivorous fishes. Oceanogr. Mar. Biol. Annu. Rev. 27, 167–272.

Horn, M. H., 1998. Feeding and digestion. In: Evans, D.H. (Ed.), The Physiology of Fishes. CRC Press, New York, pp. 41–60.

Huelsenbeck, J.P., Ronquist, F.R., 2001. Mrbayes: Bayesian inference of phylogeny. Bioinformatics 17, 754.

Huelsenbeck, J.P., Ronquist, F., Nielsen, R., Bollback, J.P., 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. Science 294, 2310–2314.

Ihaka, R., Gentleman, R., 1996. R: a language for data analysis and graphics. J. Comput. Graph. Stat. 5, 299–314.

Jones, R.S., 1968. Ecological relationships in Hawaiian and Johnston Island acanthurids (surgeonfishes). Micronesia 4, 310–361.

Kazancioglu, E., Near, T.J., Hanel R., Wainwright, P.C., 2009. Influence of sexual selection and feeding functional morphology on diversification rate of parrotfishes (Scaridae). Proc. R. Soc. B 276, 3439–3446.

Kuiter, R.H., 2010 2002(a). Labroid fishes. Zoonetics, Seaford, Australia.

Kuiter, R.H. 2002(b). Butterflyfishes, Bannerfishes and Their Relatives: A Comprehensive Guide to Chaetodontidae and Microcanthidae. TMC Publishing, Chorleywood.

Kuiter, R.H., Debelius, H., 2007. World Atlas of Marine Fishes. IKAN Unterwasserarchiv.

Mabuchi, K., Miya, M., Azuma, Y., Nishida, M., 2007. Independent evolution of the specialized pharyngeal jaw apparatus in cichlid and labrid fishes. BMC Evol. Biol. 7, 10. doi:10.1186/1471-2148-7-10.

Maddison, D.R., Maddison, W.P., 2000. MacClade 4: Analysis of Phylogeny and Character Evolution, Version 4.0. Sinauer Associates, Sunderland, Massachusetts.

Maddison, W. P., Maddison, D.R., 2009. Mesquite: a modular system for evolutionary analysis, http://mesquiteproject.org, Version 2.72

Magallon, S., Sanderson, M.J., 2001. Absolute diversification rates in angiosperm clades. Evolution 55, 1762–1780.

Meylan, A., 1991. Nutritional characteristics of sponges in the diet of the hawksbill turtle, *Eretmochelys imbricata*. In: Rützler, K. (Ed.), New Perspectives in Sponge Biology. Smithsonian Institution Press, Washington, DC, pp. 472–477.

Miller, T.L., Cribb, T.H., 2007. Phylogenetic relationships of some common Indo-Pacific snappers (Perciformes: Lutjanidae) based on mitochondrial DNA sequences, with comments on the taxonomic position of the Caesioninae. Mol. Phylogenet. Evol. 44 450–60.

Moore, B.R., Chan, K.M.A., Donoghue, M.J., 2004. Detecting diversification rate variation in supertrees. In Bininda-Emonds, O.R.P. (Ed.), Phylogenetic Supertrees: Combining Information to Reveal the Tree of Life, Kluwer Academic, Dordrecht, Netherlands, pp. 487–533.

Myles, B.D., Dunham, E.A, 1993. Historical perspectives in ecology and evolutionary biology: The Use of Phylogenetic Comparative Analyses. Annu. Rev. Ecol. Syst. 24, 587–619.

Myers, R.F., 1991. Micronesian Reef Fishes. Coral Graphics, Barrigada, Guam.

Nee, S., Mooers, O., Harvey, P.H., 1992. Tempo and mode of evolution revealed from molecular phylogenies. Proc. Natl. Acad. Sci. USA 89, 8322–8326.

Nelson, J.S., 1994. Fishes of the world. Wiley, New York.

Liem, K.F., 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. Syst. Zool. 22, 425–441.

Liem, K.F., Greenwood, P.H., 1981. A functional approach to the phylogeny of pharyngognath teleosts. Amer. Zool. 21, 83–101.

Lomolino, M.V., Riddle, B.R., Brown, J.H., 2006. Biogeography. Sinauer, Sunderland, Massachusetts.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformat. 20, 289–290

Parrish, J.D., Callahan, M.W., Norns, J.E., 1985. Fish trophic relationships that structure reef communities. Proc. 5th Int. Coral Reef Congr. 4, 73–78.

Paul, V.J., 1992. Chemical defenses of benthic marine invertebrates. In: Sale, P.F. (Ed.), Ecological Roles of Marine Natural Products. Comstock, Ithaca, New York, pp. 164–188.

Phillimore, A.B., Price, T.D., 2008. Density-Dependent Cladogenesis in Birds. Public. Lib. Sci. Biol. 6, 483–489.

Pratchett, M.S., 2005. Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. Mar. Biol. 148, 373–382.

Puebla, O., 2009. Ecological speciation in marine *v.* freshwater fishes. J. Fish Biol. 75, 960–996.

Purcell, S.W., Bellwood, D.R., 2001. Spatial patterns of epilithic algal and detrital resources on a windward coral reef. Coral Reefs 20, 117–125.

Pybus, O.G. & Harvey, P.H., 2000. Testing macro-evolutionary models using incomplete molecular phylogenies. Philos. Trans. R. Soc. (Lond.) B 267, 2267–2272.

Quenouille, B., Bermingham, E., Planes, S., 2004. Molecular systematics of the damselfishes (Teleostei: Pomacentridae): Bayesian phylogenetic analyses of mitochondrial and nuclear DNA sequences. Mol. Phylogenet. Evol. 31, 66–88.

Rabosky, D.L., 2006a. LASER: a maximum likelihood toolkit for detecting temporal shifts in diversification rates from molecular phylogenies. Evol. Bioinform. 257–260.

Rabosky, D.L., 2006b. Likelihood methods for detecting temporal shifts in diversification rates. Evolution, 60, 1152–1164.

Rabosky, D. L., Donnellan, S. C., Talaba, A. L. & Lovette, I. J., 2007 Exceptional among-lineage variation in diversification rates during the radiation of Australia’s largest vertebrate clade. Proc. R. Soc. B 274, 2915–2923.

Rabosky, D.L., Lovette, I.J., 2008. Density-dependent diversification in North American wood warblers. Proc. R. Soc. B 275, 2363–2371.

Rambaut, A., Drummond, A.J., 2007. Tracer. Available from http://beast.bio.ed.ac.uk/tracer.

Randall, J.E., 2004. Food habits of reef fishes of the west indies. University of Puerto Rico, Mayaguez.

Rezende, E.L., Albert, E.M., Fortuna, M.A., Bascompte, J., 2009. Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. Ecol. Lett. 12, 779–788.

Renema, W., Bellwood, D.R., Braga, J.C., Bromfield, K., Hall, R., Johnson, K.G., Lunt, P., Meyer, C.P., McMonagle, L., Morley, R.J., O’dea, A., Todd, J.A., Wesselingh, F.P., Wilson, M.E.J. & Pandolfi, J.M., 2008. Hopping hotspots: global shifts in marine biodiversity. Science 321, 654–657.

Ricklefs, R.E., 2003. Global diversification rates of passerine birds. Proc. R. Soc. Lond. B 270, 2285–2291.

Robertson, D.R., 1998. Do coral reef fishes have a distinctive taxonomic structure? Coral Reefs 17, 179–186.

Rocha L.A., Bowen, B.W., 2007. Phylogeography and the conservation of coral reef fishes. Coral Reefs 26, 501–512.

Rüber, L., Zardoya, R., 2005. Rapid cladogenesis in marine fishes revisited. Evolution 59, 1119–1127.

Sobel, J.M., Chen, G.F., Watt, L.R, Schemske, D.W, 2009. The biology of speciation. Evolution 64, 295–315.

Sanderson, M.J., 1994. Reconstructing the evolution of genes and organisms using maximum likelihood. In: Fambrough, D. (Ed.), Molecular evolution of physiological processes. Rockefeller, New York, pp. 13–26.

Sepkoski, J.J., 1998. Rates of speciation in the fossil record. Phil. Trans. R. Soc. B 353, 315–326.

Schluter D., 2000. The ecology of adaptive radiation. In Oxford University Press New York, NY: Oxford University Press.

Smith, L.L., Fessler, J.L., Alfaro, M.E., Streelman, J.T., Westneat, M.W., 2008. Phylogenetic relationships and the evolution of regulatory gene sequences in the parrotfishes. Mol. Phylogenet. Evol. 49,136–152.

Stiassny, M.L.J., Jensen, J.S., 1987. Labroid intrarelationships revisited: morphological complexity, key innovations, and the study of comparative diversity. Bull. Mus. Comp. Zool. Harv. 151, 269–319.

Streelman, J.T., Danley, P.D., 2003. The stages of vertebrate evolutionary radiation. Trends Ecol. Evol. 18, 126–131

Thacker, C.E., Roje, D.M., 2009. Phylogeny of cardinalfishes (Teleostei: Gobiiformes: Apogonidae) and the evolution of visceral bioluminescence. Mol. Phylogenet. Evol. 52, 735–745.

Tang, K.L., 2001. Phylogenetic relationships among damselfishes (Teleostei: Pomacentridae) as determined by mitochondrial DNA data. Copeia 2001, 591–601.

Tang, K.L., Berendzen, P.B., Wiley, E.O., Morrissey, J.F., Winterbottom, R., Johnson, G.D., 1999. The phylogenetic relationships of the suborder Acanthuroidei (Teleostei: Perciformes) based on molecular and morphological evidence. Mol. Phylogenet. Evol. 11, 415–425.

Taylor, M.S. Hellberg, M.E, 2005. Marine radiations at small geographic scales: speciation in Neotropical reef gobies (*Elacatinus*). Evolution, 59, 374–385.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. Higgins, D.G., 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research, 24, 4876–4882.

Tyler, J.C., Bannikov, A.F., 1997. Relationships of the fossil and recent genera of rabbitfishes (Acanthuroidei: Siganidae). Smiths. Contrib. Paleobiol. 84, 1–35.

Wainwright, P.C., Bellwood, D.R., 2002. Ecomorphology of Feeding in Coral Reef Fishes. In: Sale, P.F. (Ed.), Coral reef fishes: dynamics and diversity on a complex ecosystem. Academic Press, San Diego, California, pp. 33–55.

Wainwright, P.C., Bellwood, D.R., Westneat, M.W., Grubich, J.R., Hoey, A.S., 2004. A functional morphospace for the skull of labrid fishes: patterns of diversity in complex biomechanical systems. Biol. J. Linn. Soc. 82, 1–25.

Williams, S.T., Duda, T.F., 2008. Did tectonic activity stimulate speciation in the Oligo-Miocene Indo-West Pacific? Evolution 62, 1618–1634.

Winterbottom, R., McLennan, D.A., 1993. Cladogram versatility: Evolution and biogeography of acanthuroid fishes. Evolution 47, 1557–1571.

Westneat, M.W., Alfaro, M.E., 2005. Phylogenetic relationships and evolutionary history of the reef fish family Labridae. Mol. Phylogenet. Evol. 36, 370–390.

White, J.W., Samhouri, J.F., Stier, A.C. Wormald, C.L., Hamilton, S.L. Sandin, S.A., 2010. Synthesizing mechanisms of density dependence in reef fishes: behavior, habitat configuration, and observational scale. Ecology 91, 1949–1961.

Woodland, D.J., 1990. Revision of the fish family Siganidae with descriptions of two new species and comments on distribution and biology. Indo-Pacific Fishes 19, 1–136.

Yamanoue, Y., Miya, M., Matsuura, K., Sakai, H., Katoh, M., Nishida, M., 2009. Unique patterns of pelvic fin evolution: A case study of balistoid fishes (Pisces: Tetraodontiformes) based on whole mitochondrial genome sequences. Mol. Phylogenet. Evol. 50, 179–189.

CONCLUSÕES

Foi atingido o principal objetivo do trabalho que era utilizar ferramentas de análise filogenética para investigar a história das linhagens e testar hipóteses que explicam as diferenças de diversidade entre regiões e grupos taxonômicos.

A explanação dos resultados juntamente com informações da história biogeográfica do Pacifico Indo-Oeste sugere que taxas de diversificação de linhagens de peixes recifais podem ser reguladas, dentre outros fatores, por modelos de oportunidade ecológica onde o uso de dietas de baixa qualidade pode ter implicado em queda mais lenta das taxas de diversificação em relação às taxas de linhagens de alta qualidade na dieta, provavelmente devido à ocupação primária dos recursos de alta qualidade. Tomados em conjunto as evidências, o estudo sugere que a utilização dos recursos de baixa qualidade é provavelmente mais relacionada com a menor velocidade de queda das taxas de diversificação em ambientes ricos em espécies do que acelerar as taxas de diversificação. Nossos resultados também concordam com a hipótese de Harmelin-Vivien (2002) que explica o gradiente latitudinal de diversidade de peixes recifais pela melhor utilização dos recursos alimentares nos trópicos.

Seria apropriado que estudos futuros utilizem filogenias ao nível e espécie de cada um dos subclados apontados nesse estudo para comparar o comportamento de declínio na taxa diversificação desses grupos ao longo de suas radiações, e verificar se quedas menos acentuadas correspondem a linhagens de espécies com dietas de baixa qualidade.

Estudos similares que avaliem a influência de outros fatores ambientais e ecológicos também se fazem necessários; por exemplo, qual a diferença entre o comportamento das taxas de diversificação de grupos que evoluíram nos trópicos e outros que evoluíram em regiões subtropicais e temperadas? Ou ainda, entre grupos que evoluíram em ambientes recifais e outros que evoluíram em ambientes mais homogêneos? É provável que se encontre evidências desses ou outros fatores também influenciando na diversificação das espécies, o que é esperado tendo em vista a complexa rede de influencias que regem os ecossistemas. Logo todos estes estudos tenderiam a se complementarem explicando as partes que cada um em particular não pode explicar, como é o caso da família Labridae neste trabalho.

REFERÊNCIAS BIBLIOGRÁFICAS

Allen, A.P., Gillooly, J.F., 2006. Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. Ecol. Lett. 9, 947–954.

Barraclough, T.G., Vogler, A.P., Harvey, P.H., 1998. Revealing the factors that promote speciation. Philos. Trans. R. Soc. Lond. B 353, 241–249.

Barraclough, T.G., Vogler, A.P., 2000. Detecting the geographical pattern of speciation from species-level phylogenies. Nature 155, 419–434.

Briggs, J.C., 1987. Biogeography and Plate Tectonics. Elsevier Publishing Company, New York.

Briggs, J.C., 2000. Centrifugal speciation and centres of origin. J. Biogeogr. 27, 1183–1188.

Briggs, J.C., 2003. Marine centres of origin as evolutionary engines. J. Biogeogr. 30, 1–18.

Briggs, J.C., 2005. Coral reefs: Conserving the evolutionary sources. Biol. Cons. 126, 297–305.

Cardillo, M., 1999. Latitude and rates of diversification in birds and butterflies. Proc. R. Soc. Lond. B. 266, 1221–1225.

Cardillo, M., Orme, C.D.L., Owens, I.P.F., 2005. Testing for latitudinal bias in diversification rates: an example using new world birds. Ecology 86, 2278–2287.

Carnaval, A.C., Hickerson, M.J., Haddad, C.F., Rodrigues, M.T., Moritz, C., 2009. Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. Science 323, 785–789

Cavender-Bares, J., Kozak, K., Fine, P., Kembel S., 2009. The merging of community ecology and phylogenetic biology. Ecol. Lett. 12, 693–715.

Davies, T.J., Barraclough, T.G., Savolainen, V., Chase, M.W., 2004. Environmental causes for plant biodiversity gradients. Philos. Trans. R. Soc. Lond. B Biol. Sci. 359, 1645–1656.

Dieckmann, U., Doebeli, M., 1999. On the origin of species by sympatric speciation. Nature 400, 354–357

Doebeli, M., U. Dieckmann, J. A. J. Metz, D. Tautz. 2005. What we have also learned: adaptive speciation is theoretically plausible. Evolution 59:692–696.

Donoghue, M.J., 2005. Key innovations, convergence, and success: macroevolutionary lessons from plant phylogeny. Paleobiol. 31, 77–93.

Engen, S., Lande, R., Saether, B.E., 2002. The spatial scale of population fluctuations and quasi-extinction risk. Am. Nat. 160, 439–451.

Felsenstein, J., 1973. Maximum likelihood and minimum-steps methods for estimating evolutionary trees from data on discrete characters. Syst. Zool. 22, 240–249.

Felsenstein, J., 1985. Phylogenies and the comparative method. Amer. Nat. 125, 1–15.

Felsenstein, J., 1988. Phylogenies from molecular sequences: inference and reliability. Annu. Ver. Genet. 22, 521–565.

Fine, P.V.A., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M., Stevens, M.H.H., 2006. The growth-defense trade-off and habitat specialization by plants in Amazonian forests. Ecology 87, 150–162.

Fry, J.D., 2003. Multilocus models of sympatric speciation: bush versus rice versus Felsenstein. Evolution 57, 1735–1746.

Gavrilets, S. 2003. Models of speciation: what have we learned in 40 years? Evolution 57: 2197–2215.

Gavrilets, S. 2005. ‘‘Adaptive speciation’’ – it is not that easy: a reply to Doebeli et al.. Evolution 59: 696–699.

Gillespie, R., 2004. Community assembly through adaptive radiation in Hawaiian spiders. Science 303, 356–359

Halas, D., Winterbottom, R., 2009. A phylogenetic test of multiple proposals for the origins of the East Indies coral reef biota. J. Biogeogr. 36, 1847–1860.

Harmelin-Vivien, M.L., 2002. Energetics and fish diversity on coral reefs. In: Sale, P.F. (Ed.), Coral reef fishes: dynamics and diversity on a complex ecosystem. Academic Press, San Diego, California, pp. 265–274.

Hey, J., 1992. Using phylogenetic trees to study speciation and extinction. Evolution 46, 627–640.

Hillebrand, H., 2004. On the generality of the latitudinal diversity gradient. Am. Nat. 163, 192–211.

Huston, M., 1994. Biological Diversity: The Coexistence of Species on a Changing Landscape. Cambridge University Press, Cambridge.

Jokiel, P., Martinelli, F.J., 1992. The vortex model of coral reef biogeography. J. Biogeogr. 19, 449–458.

Karlson, R.H., Cornell, H.V., Hughes, T.P., 2004. Coral communities are regionally enriched along an oceanic biodiversity gradient. Nature 429, 867-870.

Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. Am. Nat. 142, 911–927.

Magallon, S., Sanderson, M.J., 2001. Absolute diversification rates in angiosperm clades. Evolution 55, 1762–1780.

Mittelbach, G.G., Schemske, D.W., Cornell, M.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton,N., Lessios, H.A., McCain, C.M., McCune, A.R., McDade, M.A., McPeek, M.A., Near, T.J, Price. T.D., Ricklefs, R.E., Roy, K., Sax, D.F., Schluter, D., Sobel, H.J., Turelli, M., 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol.Lett.10, 315–331.

Nee, S., Mooers, O., Harvey, P.H., 1992. Tempo and mode of evolution revealed from molecular phylogenies. Proc. Natl. Acad. Sci. USA 89, 8322–8326.

Nee, S., 2006. Birth-death models in macroevolution. Annu. Rev. Ecol. Evol. Syst. 37, 1–17.

Paradis, E., 2005. Statistical analysis of diversification with species traits. Evolution 59, 1–12.

Puebla, O., 2009. Ecological speciation in marine *v.* freshwater fishes. J. Fish Biol. 75, 960–996.

Ree, R.H., Moore, B.R., Webb, C.O. & Donoghue, M.J., 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. Evolution 59, 2299–2311.

Ricklefs, R.E., 2007a. History and Diversity: Explorations at the Intersection of Ecology and Evolution. Amer. Nat. 170, 56–70.

Ricklefs, R.E., 2007b. Estimating diversification rates from phylogenetic information. Ecol. Lett. 22, 601–610.

Ricklefs, R.E., Schluter, D., 1997. Species diversity in ecological communities. Historical and geographical perspectives. The University of Chicago Press, Chicago.

Roberts, C.M., 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295, 1280–1284.

Rosenzweig, M.L., 1995. Species Diversity in Time and Space. Cambridge University Press, Cambridge, UK.

Siddall, M., Rohling, E. J., Almogi-Labin, A., Hemleben, Ch., Meischner, D., Schmelzer, I., Smeed, D.A., 2003. Sea-level fluctuations during the last glacial cycle. Nature 423, 853–858.

Material suplementar

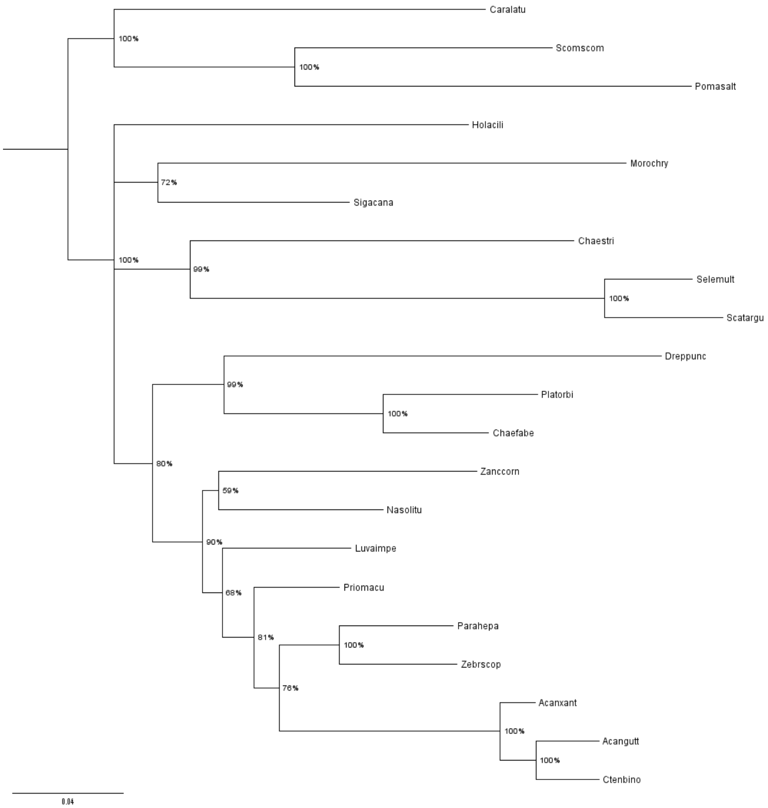


Figure 1. Bayesian post burn-in consensus phylogram of the Acanthuroidei. Numbers at nodes are posterior probabilities of nodes.

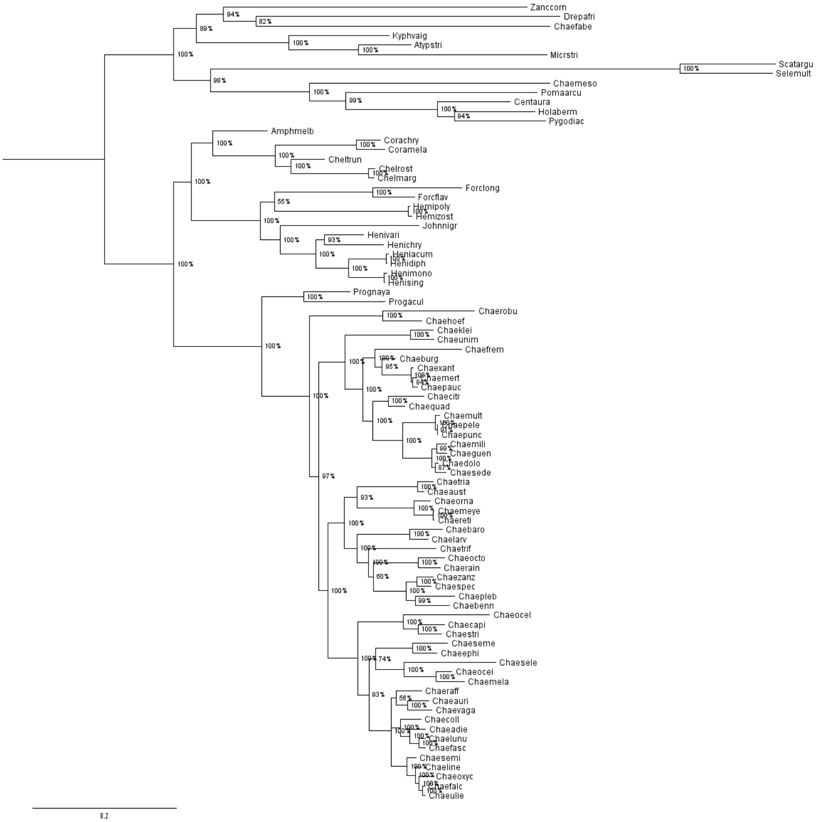


Figure 2. Bayesian post burn-in consensus phylogram of the Chaetodontidae. Numbers at nodes are posterior probabilities of nodes.

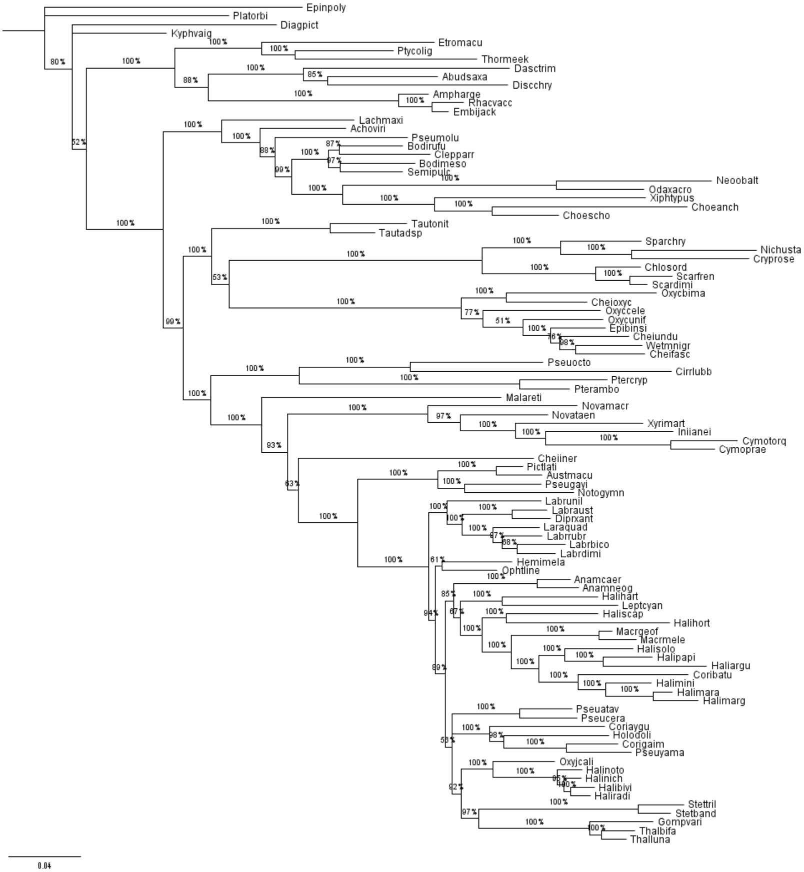


Figure 3. Bayesian post burn-in consensus phylogram of the Labridae. Numbers at nodes are posterior probabilities of nodes.

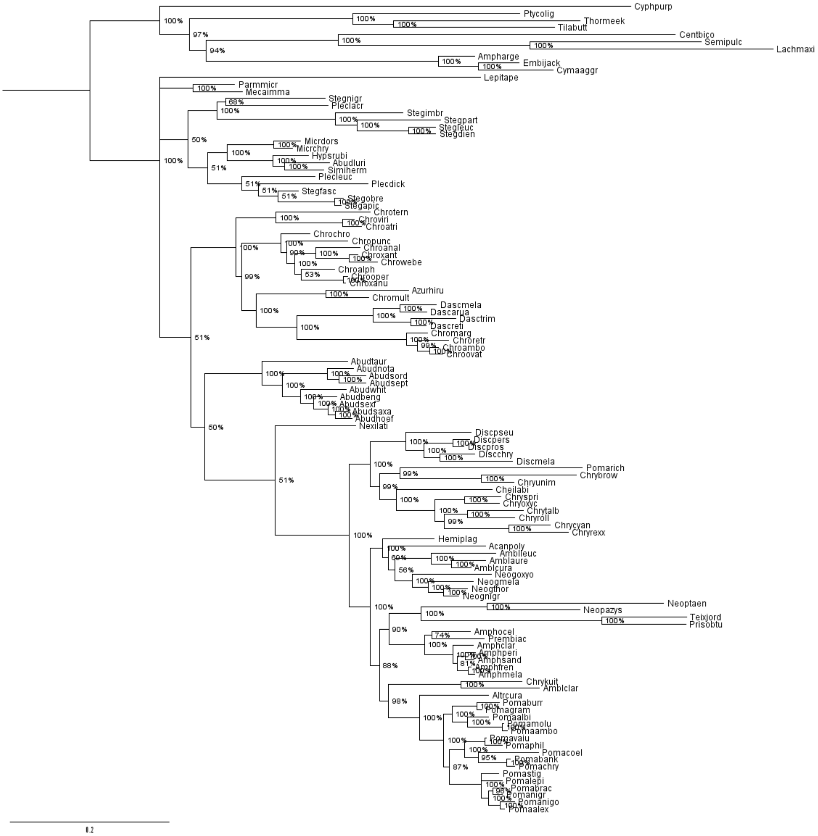


Figure 4. Bayesian post burn-in consensus phylogram of the Pomacentridae. Numbers at nodes are posterior probabilities of nodes.

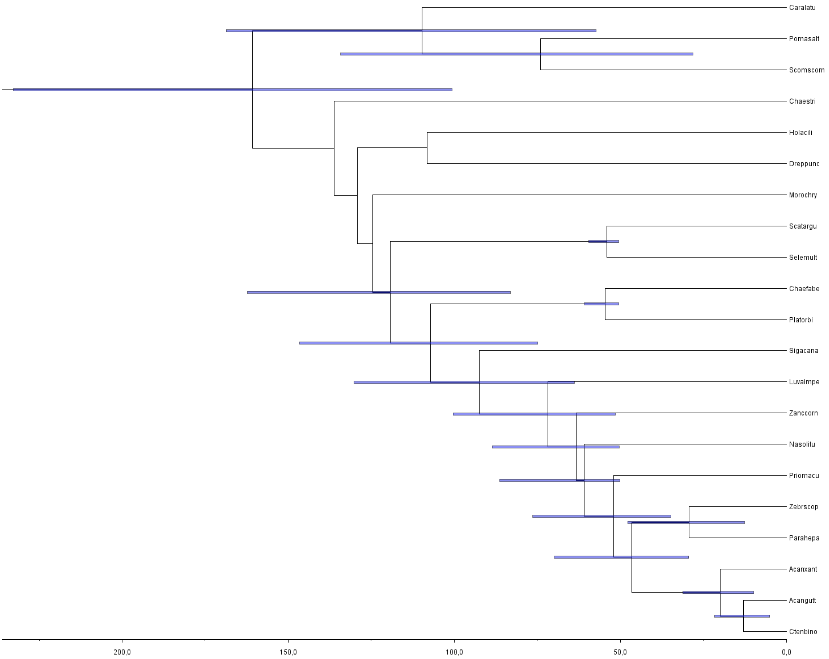


Figure 5. BEAST chronogram of Acanthuroidei showing mean node heights and 95% HPD at bars.

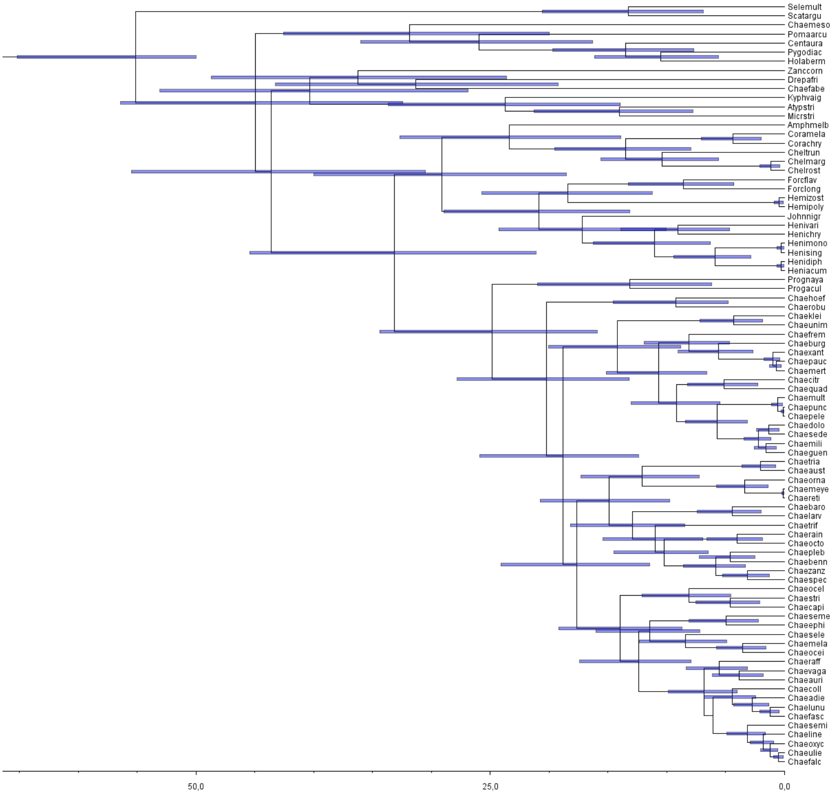


Figure 6. BEAST chronogram of Chaetodontidae showing mean node heights and 95% HPD at bars.

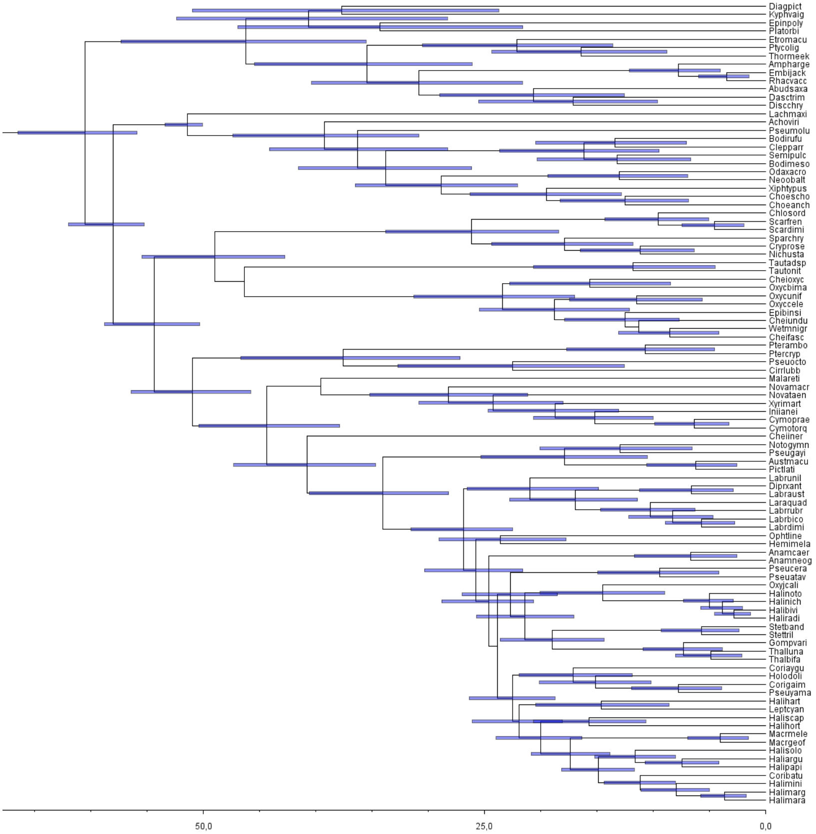


Figure 7. BEAST chronogram of Labridae showing mean node heights and 95% HPD at bars.

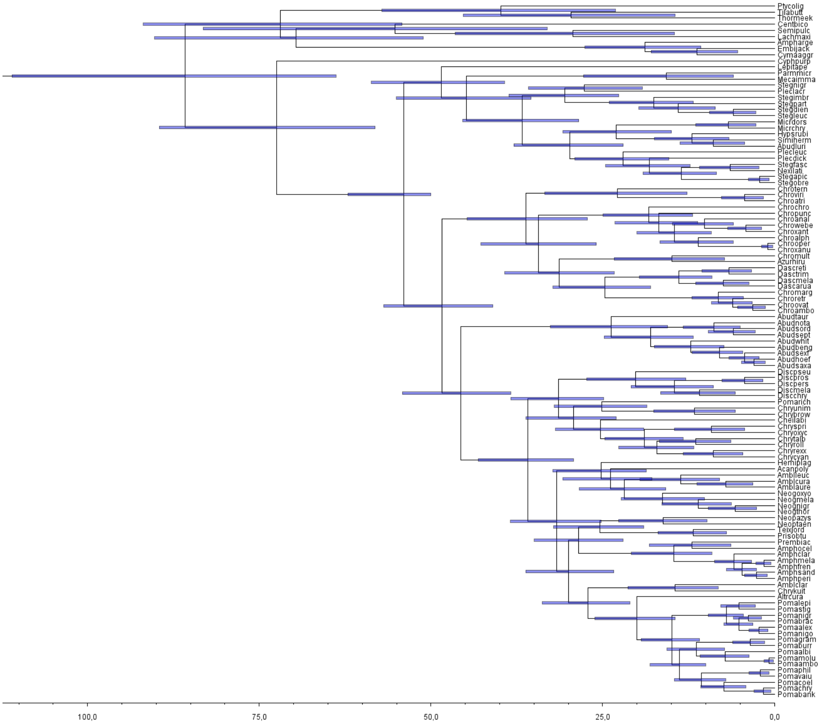


Figure 8. BEAST chronogram of Pomacentridae showing mean node heights and 95% HPD at bars.