UNICAMP

Instituto de Biologia

NAYARA FERNANDA HACHICH

ESTRUTURA ESPACIAL DA BIODIVERSIDADE DE ORGANISMOS RECIFAIS NO OCEANO ATLÂNTICO

CAMPINAS

2014

UNIVERSIDADE ESTADUAL DE CAMPINAS

INSTITUTO DE BIOLOGIA

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

NAYARA FERNANDA HACHICH

ESTRUTURA ESPACIAL DA BIODIVERSIDADE DE ORGANISMOS RECIFAIS NO OCEANO ATLÂNTICO

Dissertação apresentada ao Instituto de Biologia da Universidade Estadual de Campinas como parte dos requisitos exigidos para obtenção do título de Mestre em Ecologia.

Orientador: Dr. THOMAS MICHAEL LEWINSOHN

Co-orientador: Dr. SERGIO RICARDO FLOETER

Esse exemplar corresponde à versão final da dissertação defendida pela aluna Nayara Fernanda Hachich e orientada pelo professor Dr. Thomas Michael Lewinsohn.

CAMPINAS - 2014

Ficha catalográfica
Universidade Estadual de Campinas
Biblioteca do Instituto de Biologia
Mara Janaina de Oliveira - CRB 8/6972

H115e
Hachich, Nayara Fernanda, 1987-
Estrutura espacial da biodiversidade de organismos recifais no Oceano Atlântico / Nayara Fernanda Hachich. – Campinas, SP : [s.n.], 2014.

Orientador: Thomas Michael Lewinsohn.
Coorientador: Sergio Ricardo Floeter.
Dissertação (mestrado) – Universidade Estadual de Campinas, Instituto de Biologia.

1. Diversidade beta. 2. Estrutura da comunidade ecológica. 3. Grupos funcionais. 4. Filogenia. 5. Peixes recifais. I. Lewinsohn, Thomas Michael,1952-. II. Floeter, Sergio Ricardo. III. Universidade Estadual de Campinas. Instituto de Biologia. IV. Título.

Informações para Biblioteca Digital

Título em outro idioma: Spatial structure of reef biodiversity in the Atlantic Ocean
Palavras-chave em inglês:
Beta diversity
Ecological community structure
Functional groups
Phylogeny
Reef fishes
Área de concentração: Ecologia
Titulação: Mestra em Ecologia
Banca examinadora:
Thomas Michael Lewinsohn [Orientador]
Paulo Inácio de Knegt López de Prado
Carlos Eduardo Ferreira Leite
Data de defesa: 13-08-2014
Programa de Pós-Graduação: Ecologia

Campinas, 13 de Agosto de 2014

COMISSÃO EXAMINADORA

Prof. Dr. Thomas Michael Lewinsohn
(assinatura)

Prof. Dr. Paulo Inácio de Knegt López de Prado
(assinatura)

Prof. Dr. Carlos Eduardo Leite Ferreira
(assinatura)

Prof. Dr. Martin Francisco Pareja Piaggio
(assinatura)

Prof. Dr. Milton Cezar Ribeiro
(assinatura)

RESUMO

Os recifes são ecossistemas marinhos fortemente ameaçados. Pressões antrópicas desencadeiam mudanças ambientais e climáticas que interferem direta ou indiretamente na qualidade dos recifes. Estudos sobre ecossistemas marinhos ainda são escassos se comparados à vasta literatura acerca de ecossistemas terrestres. Compreender como a biodiversidade recifal está distribuída e quais os processos que agem sobre a estruturação das comunidades recifais é essencial para a conservação destes ecossistemas. Esta dissertação tem como objetivo investigar os padrões espaciais da distribuição da biodiversidade de organismos recifais no oceano Atlântico. Tais padrões possibilitam inferências acerca dos processos que estruturam as comunidades estudadas.

O primeiro capítulo é composto por uma introdução geral da dissertação, que apresenta um referencial teórico e contextual para a compreensão das pesquisas desenvolvidas durante o mestrado. Nessa introdução, apresento brevemente as teorias sobre processos estruturadores de comunidades ecológicas e a contribuição da Biogeografia de Ilhas, Ecologia Funcional e Ecologia Filogenética para o estudo de padrões e processos em comunidades ecológicas. Em seguida, contextualizo a região de estudo, apresentando brevemente a história do oceano Atlântico e o conhecimento dos processos ecológicos e histórico-evolutivos que influenciam a estruturação das comunidades de peixes recifais desse oceano.

O segundo capítulo, em forma de artigo científico, trata de padrões de biogeografia de ilhas de peixes recifais, gastrópodes e macroalgas. Neste estudo investiguei como a área de plataforma rasa, isolamento e idade geológica das ilhas oceânicas do Atlântico influenciam a riqueza de espécies e endemismo de organismos recifais que as compõem. Mostrei que os padrões de biogeografia de ilhas de organismos recifais são distintos daqueles encontrados para organismos terrestres e, ainda, que há especificidade taxonômica nos padrões de biogeografia de ilhas entre grupos de organismos recifais.

O terceiro capítulo, também em forma de artigo científico, trata de padrões qualitativos da distribuição de duas famílias de peixes recifais (Labridae e Pomacentridae). O objetivo foi compreender a contribuição relativa do ambiente e posição espacial dos recifes na variação da diversidade de peixes recifais entre os recifes do Atlântico ocidental. Neste estudo, investigo como a betadiversidade taxonômica, funcional e filogenética desses organismos varia entre recifes, de acordo com a distância geográfica e a dissimilaridade ambiental entre eles. Os resultados mostraram que a variação na composição de peixes entre recifes do Atlântico ocidental é influenciada principalmente por filtros ambientais e fracamente influenciada por processos que causam autocorrelação espacial na distribuição da biodiversidade. Ainda, as variáveis ambientais que melhor explicaram a diversidade beta de peixes entre os recifes variou fortemente, principalmente entre escalas e regiões biogeográficas, mas também entre famílias de peixes recifais.

A dissertação se completa com uma conclusão geral que sintetiza as principais fontes de variação nos padrões de distribuição de organismos recifais no oceano Atlântico (entre escalas, regiões biogeográficas, grupos taxonômicos ou aspectos da biodiversidade) e apresenta um resumo das evidências de processos ecológicos, histórico-evolutivos ou neutros na estruturação das comunidades recifais do oceano Atlântico.

Palavras-chave: Diversidade beta, Estrutura da comunidade ecológica, Grupos funcionais, Filogenia, Peixes recifal

ABSTRACT

Reefs are among the most threatened marine systems on earth. Anthropic pressures lead to environmental and climate changes that are able to affect reefs quality, directly or indirectly. Compared to terrestrial ecosystems, marine ones are barely studied. The conservation of reef ecosystems requires the comprehension of reef biodiversity distributional patterns and the processes that modulate them. The aim of this study was to investigate spatial patterns on the distribution of reef biodiversity in the Atlantic Ocean. The study of these patterns allows the inference of processes that structure these communities.

The first chapter comprises a general introduction that contextualizes and gives a theoretical framework for the comprehension of the research conducted in this thesis. In this introduction I briefly show the theories concerning processes that structure ecological communities and the potential contribution of Island Biogeography, Functional Ecology and Phylogenetic Ecology to the study of patterns and processes on ecological communities. Then, I contextualize the study region, briefly covering the history of the Atlantic Ocean and the knowledge on the ecological and historical-evolutionary processes that affect the structure of reef fish community in the Atlantic Ocean.

In the second chapter, formatted in scientific paper style, I investigate the island biogeographic patterns of reef fish, gastropods and seaweeds. I tested how the shallow shelf area, isolation and geological age of Atlantic oceanic islands influence species' richness and endemism of reef organisms. I showed that the patterns observed in reef organisms are different from those observed in the terrestrial ones and, furthermore, that for reef organisms the patterns are taxon-dependent.

The third chapter, also formatted in scientific paper style, explore qualitative patterns on the distribution of two families of reef fish (Labridae e Pomacentridae) in the Atlantic Ocean. The aim of this study was to understand the relative contribution of reef environment and spatial location to variation of fish diversity between reefs in the Western Atlantic Ocean. To this end I investigated how the taxonomic, functional and phylogenetic aspects of biodiversity of the two reef fish families vary with spatial distance or environmental dissimilarity between reefs. Results showed that the variation of reef fish composition in Western Atlantic reefs is mainly driven by environmental filters and weakly influenced by processes that cause spatial autocorrelation of species distributions. However, the environmental variables that best explained reef fish beta diversity varied strongly, especially between scales and biogeographical regions, but also between reef fish families.

This thesis ends with a general conclusion about the main sources of variation in the patterns of distribution of reef organisms in the Atlantic Ocean (including variation due to scale, biogeographic region, taxonomic group or aspect of biodiversity), as well as with a summary of the evidences of ecological, historical-evolutionary and neutral processes in structuring reef communities in the Atlantic Ocean.

Keywords: Beta diversity, Community structure, Functional groups, Phylogeny, Reef fishes

Ao MAR e aos VENTOS que dele sopram dedico esta dissertação..

..em agradecimento à imensa e constante PAZ e INSPIRAÇÃO que me trazem.

AGRADECIMENTOS

Esta dissertação foi submetida ao Programa de Pós-graduação em Ecologia, da Universidade Estadual de Campinas, para a obtenção do título de Mestre em Ecologia. Embora no início tenha contado com financiamento da Coordenação de Aperfeiçoamento de Pessoal de nível Superior (CAPES), esse trabalho, incluindo participações em congressos e o estágio no exterior, foi financiado principalmente pela Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), à qual sou muito grata. Todo o conteúdo apresentado é baseado na pesquisa realizada em maioria no Laboratório de Interações Inseto-Planta (LIIP), do Departamento de Biologia Animal da Unicamp, e em parte no Mathematical Ecology Research Group, do Departamento de Zoologia da Universidade de Oxford.

Se neste momento eu recomeçasse as pesquisas apresentadas nesta dissertação, eu certamente mudaria muito do que fiz. Isso de maneira alguma me chateia e sim me alegra, pois percebo o quanto aprendi com os caminhos que tracei. A mudança mais fundamental seria em conhecer de fato o ecossistema que estudei, ou seja, mergulhar. Embora os livros e artigos tenham sido essenciais, sinto que eles não substituem o olhar do observador, o conhecimento prático de assistir às interações entre espécies e das espécies com o ambiente. E embora sejam encantadores os livros, eles tampouco substituem a emoção de vivenciar as cores, formas, texturas e sons da natureza. Ao mesmo tempo, valorizo muito a experiência que tive com os livros, artigos, e discussões com outros pesquisadores. Percebo que adquiri uma ampla base teórica em ecologia.

Estou muito feliz com tudo o que se passou nesse período. Estou enormemente feliz com a escolha (e aceite recíproco) do meu orientador. Esse estudo não poderia ter sido realizado sem a preciosa assistência do Dr. Thomas Michael Lewinsohn, a quem sou imensamente grata. O Thomas é para mim um grande exemplo e me ensinou uma nova maneira de olhar para a ciência. Além disso, se mostrou um amigo muito agradável e pessoa culta e correta.

Sou igualmente grata à assistência concedida pelo meu co-orientador, Dr. Sergio Ricardo Floeter, que muito me incentivou e auxiliou no estudo de organismos recifais. Valorizo também o vínculo que, através do Sergio, pude manter com a maravilhosa equipe do LBMM. Sou grata também ao meu supervisor no exterior, Dr. Michael Bonsall, pela contribuição direta na dissertação, mas também por ter me permitido vivenciar uma comunidade e cultura científica diferentes da que estava habituada; além, é claro, da incrível experiência de conhecer Oxford.

De uma forma geral, agradeço ao Programa de Pós-Graduação (PPG) em Ecologia, a todos os professores, servidores e colegas que contribuíram para minha formação. Sou muito grata aos pesquisadores que aceitaram compor minha banca examinadora, pois são pessoas a quem eu admiro e que estão contribuindo bastante para o meu desenvolvimento acadêmico. Aos colaboradores dos artigos científicos sou grata pela imensa contribuição nesse processo árduo e importante de publicação.

Agradeço ao meu namorado, Dr. Eduardo Arraut, por ter me sugerido procurar o professor Thomas para me orientar e por ter me incentivado a fazer intercambio, pois foram esses os melhores componentes do meu mestrado. Sou muitíssimo grata a meus pais, Flávio Hachich e Maria Inez Buosi Hachich, e ao meu irmão, Rafael Hachich, principalmente pelo apoio emocional (mas também pelo apoio financeiro) e por sempre acreditarem em mim, mesmo não entendendo muito bem o sentido da carreira acadêmica. E, em especial, agradeço ainda ao Edu e à minha família por constantemente me apoiarem na busca daquilo que me cativa e me faz feliz.

Por fim, e de maneira alguma menos importante, agradeço ao Infinito, por tudo e todos que colocou na minha vida durante essa etapa, e por sua imensa beleza...sem suas variadas cores não seriam tão encantadores os recifes!!

E para encerrar essa etapa de mestrado, nada mais adequado do que a frase de Raquel de Queiroz:

"Cada coisa tem sua hora e cada hora o seu caminho"

Campinas, Agosto de 2014.

Nayara Fernanda Hachich

SUMÁRIO

1. INTRODUÇÃO GERAL

1.1. ESTUDO DE PADRÕES PARA INFERÊNCIA DE PROCESSOS EM ECOLOGIA DE COMUNIDADES

Um dos grandes objetivos da ecologia de comunidades é identificar e quantificar os processos que determinam a distribuição espacial da biodiversidade. Desde a década de 1980, ecólogos investigam os mecanismos e efeitos distintos de processos ecológicos e processos histórico-evolutivos distribuição da biodiversidade (Ricklefs 1987). Os processos ecológicos são aqueles relacionados ao nicho, ou seja, às condições e recursos ambientais que um indivíduo necessita para viver e seus atributos fenotípicos (físicos ou comportamentais), que moldam a sua interação imediata com esse ambiente, e até mesmo o alteram (Chase and Leibold 2003). Tais processos ecológicos são, portanto, mediados por interações bióticas (como competição, mutualismo e predação) ou pela interação de espécies com o ambiente (i.e. filtros ambientais; Cavender-Bares et al., 2009). Os processos histórico-evolutivos, que incluem também processos biogeográficos, são aqueles relacionados à geração de novas linhagens filogenéticas (especiação) e sua resposta adaptativa ao ambiente (dispersão, seleção ao longo do tempo evolutivo ou extinção; Cavender-Bares et al. 2009). De certa maneira, eles refletem processos ecológicos em uma maior escala temporal, no tempo evolutivo. Assim, a montagem de uma comunidade local pode ser influenciada pelo modo em que os atributos ecológicos e de nicho de cada espécie evoluíram na filogenia, pela história geológica dos diversos habitats e da região de estudo como um todo, e pela história e composição do pool regional de espécies (Wiens and Donoghue 2004).

Além dos processos ecológicos e histórico-evolutivos, também processos neutros podem influenciar a distribuição da biodiversidade. Em modelos neutros, as espécies são vistas como equivalentes, respondendo igualmente a estímulos bióticos ou abióticos (Hubbell 2001). Assim, em modelos de dinâmica estocástica neutra a incorporação ou perda de espécies decorrem apenas de eventos randômicos de nascimento, mortalidade, migração e especiação. Tais eventos, portanto, controlam a distribuição espacial das espécies por meio de deriva ecológica (Hubbell, 2001).

Processos ecológicos, histórico-evolutivos e neutros podem agir simultaneamente na estruturação de uma comunidade, e a intensidade desses processos pode ser distinta em diferentes escalas espaciais e temporais (Lawton et al. 1993, Emerson and Gillespie 2008, Cavender-Bares et al. 2009). Processos histórico-evolutivos tendem a ser mais evidentes em grandes escalas espaciais e temporais, enquanto que processos ecológicos mediados pelo ambiente predominam em escalas intermediárias e processos ecológicos denso-dependentes em escalas menores (Lawton et al. 1993, Cavender-Bares et al. 2009).

Uma abordagem frequentemente usada para inferir os processos estruturadores de comunidades é estudar os próprios padrões de distribuição da biodiversidade. Abaixo descreverei a contribuição da biogeografia de ilhas, ecologia funcional e ecologia filogenética para esse fim.

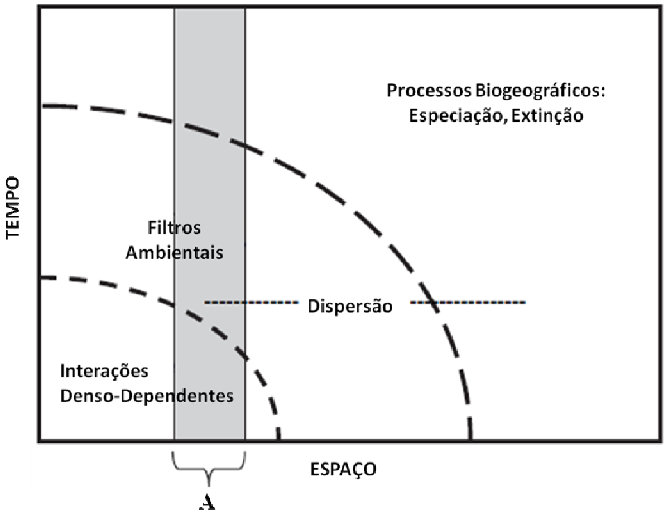


Figura 1. Adaptada de Cavender-Bares *et al.* (2009). Escalas espaciais e temporais de operação de processos distintos. “A” representa uma determinada escala espacial na qual múltiplos processos determinam a montagem das comunidades, porém em diferentes escalas de tempo.

1.2. BIOGEOGRAFIA DE ILHAS

A Teoria de Biogeografia de Ilhas (MacArthur and Wilson 1967), desenvolvida no final da década de 60, foi um marco importante para o estudo da distribuição da biodiversidade. Os estudos biogeográficos, que até então tinham um caráter mais descritivo, passaram a incorporar uma abordagem preditiva. A teoria prevê um equilíbrio determinado pelas taxas de imigração e de extinção de espécies, que mantém constante o número de espécies nas ilhas (Fig 2a). Entretanto, sempre que as taxas de imigração e extinção forem maiores que zero, a identidade das espécies que compõem as ilhas irá variar ao longo do tempo, pois constantemente novas espécies são acrescentadas por imigração, e outras se extinguem localmente (MacArthur and Wilson 1967). Dessa maneira, a taxa de substituição de espécies é decorrente dos valores das taxas de imigração e extinção quando essas se equiparam (Fig 2a).

A Teoria de Biogeografia de Ilhas supõe (a) que a taxa de imigração de espécies será menor quanto mais isolada a ilha, visto a capacidade limitada de dispersão das espécies, e (b) que a taxa de extinção será menor em ilhas maiores, visto que elas possuem maior heterogeneidade de habitats e capacidade de manter populações maiores (MacArthur and Wilson 1967). Se atendidas essas premissas, a riqueza de espécies de uma ilha será maior quanto menor seu isolamento (padrão espécie-isolamento) e maior sua área (padrão espécie-área; Fig 2a). Isto posto, a Teoria de Biogeografia de Ilhas prevê que a relação espécie-área siga uma função potência, em que $R=c*A^z$, sendo R a riqueza de espécies, A a área da ilha e c e z duas constantes que variam com a região e grupo de estudo (Fig 2b; MacArthur and Wilson 1967). A diminuição na taxa de aumento da riqueza de espécies com a área da ilha, prevista pelo modelo, é justificada por restrições ambientais que geram uma relação não-linear entre heterogeneidade de habitats e área da ilha (MacArthur and Wilson 1967).

Embora vários outros modelos matemáticos tenham sido propostos para representar a relação espécie-área (e.g. linear, logarítmico, Kobayashi) o modelo função potência tem se mostrado bastante adequado para a maioria dos sistemas estudados (Triantis et al. 2012). Entretanto, esse modelo não é geral: estudos realizados com diferentes táxons ou em escalas distintas têm apresentado padrões de biogeografia de ilhas variados (Crawley and Harral 2001, Storch et al. 2012).

Desde sua concepção, a Teoria de Biogeografia de Ilhas tem sido amplamente testada e aprimorada (Welter-Schultes and Williams 1999, Roos et al. 2004, Badano et al. 2005, Sandin et al. 2008, Stracey and Pimm 2009, Hart and Pearson 2010, Spengler et al. 2011). Recentemente, Whittaker e colaboradores propuseram uma Teoria Dinâmica Geral de Biogeografia de Ilhas Oceânicas (Whittaker et al. 2008). Essa teoria pressupõe um padrão unimodal de complexidade topográfica em ilhas, desde o seu surgimento até seu desaparecimento por imersão (Fig 3a). Logo que emergem, as ilhas apresentam baixa complexidade topográfica (Fig 3a; Whittaker et al. 2008). Ao longo do tempo, a complexidade topográfica vai aumentando devido à atividade vulcânica e também à erosão, de maneira que sua máxima complexidade topográfica coincide com muita atividade vulcânica e certa erosão (Fig 3a; Whittaker et al. 2008). Porém, quando a atividade vulcânica cessa e à medida que a erosão se intensifica, as ilhas oceânicas vão perdendo complexidade topográfica até imergirem (Fig 3a; Whittaker et al. 2008). A heterogeneidade de habitats numa ilha aumenta com sua complexidade topográfica, e, por sua vez, o número de espécies de um local aumenta com a heterogeneidade de habitats (Whittaker et al. 2008). Assim, a teoria prediz que a riqueza de espécies de uma ilha será uma função unimodal da idade geológica, combinada com uma função linear da área da ilha (Fig 3b; Whittaker et al. 2008).

Por predizer como a riqueza de espécies deve variar com características físicas das ilhas, a Biogeografia de Ilhas contribui para a inferência de processos que estruturam quantitativamente as comunidades ecológicas. Ou seja, ela permite compreender porque um determinado número de espécies ocorre numa ilha. Entretanto, essa teoria ou suas variantes recentes não permitem inferir processos que estruturam qualitativamente as comunidades ecológicas. Ou seja, não se explica porque certas espécies estão restritas a determinados lugares ou habitats, enquanto outras estão mais espalhadas ou restritas a lugares distintos. Já a ecologia funcional e a ecologia filogenética propõem explicações para tais fenômenos.

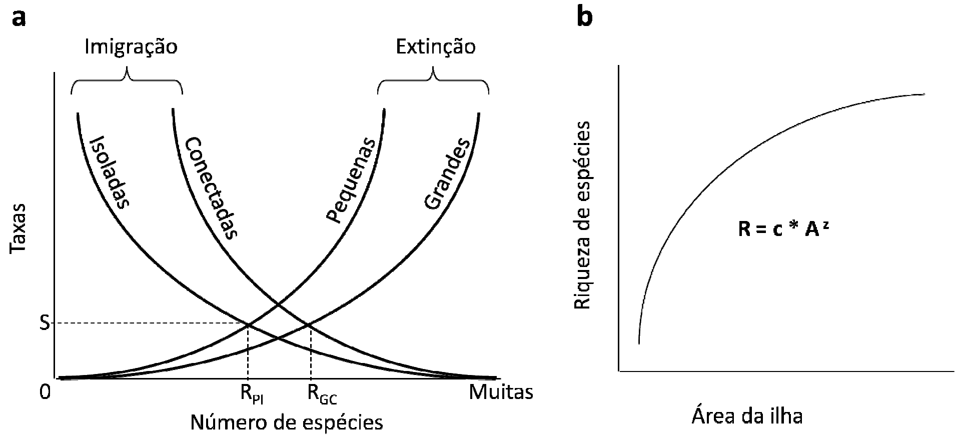


Figura 2. Modelo da Teoria de Biogeografia de Ilhas (adaptado de MacArthur and Wilson 1967). a) Taxas de imigração e extinção variam respectivamente com o isolamento e o tamanho da ilha. Taxas de imigração e extinção estabelecem uma riqueza de espécies (R) para a ilha, na qual há uma taxa de substituição de espécies (S). R_{PI}: riqueza de ilhas pequenas e isoladas; R_{GC}: riqueza de ilhas grandes e conectadas. b) Riqueza de espécies (R) aumenta com área da ilha (A) segundo uma função potência ($R=c*A^z$) em que c e z representam constantes.

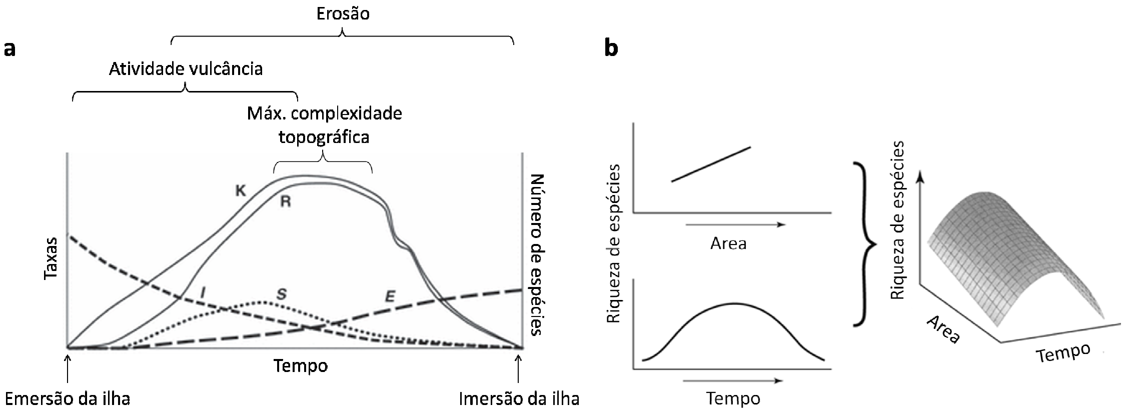


Figura 3. Teoria Dinâmica Geral de Biogeografia de Ilhas Oceânicas (adaptado de Whittaker et al. 2008). a) Mecanismos reguladores da riqueza de espécies em ilhas oceânicas. I: taxa de imigração; S: taxa de especiação; E: taxa de extinção; K: capacidade de suporte; R: riqueza de espécies realizada. b) Padrões previstos pela teoria.

1.3. ECOLOGIA FUNCIONAL

A abordagem de categorizar espécies em diferentes grupos funcionais, com base em seus atributos fenotípicos (morfológicos, fisiológicos ou comportamentais), fornece um caminho importante para distinguir entre diferentes processos ecológicos estruturadores de comunidades. Visto que, por definição, espécies pertencentes ao mesmo grupo funcional ocupam nichos ecológicos semelhantes ou idênticos, sua distribuição espacial pode resultar em padrões distintos de coocorrência de espécies e de grupos funcionais, devido a pressões seletivas divergentes (Cavender-Bares et al. 2009). Por um lado, espécies funcionalmente similares, ao ocuparem o mesmo nicho, podem ser selecionadas para os mesmos tipos de habitats e, portanto, tender a coocorrerem com maior frequência (i.e. filtros ambientais estruturando as comunidades; Webb et al. 2002). Por outro lado, justamente por ocuparem nichos similares, elas irão explorar os mesmos recursos e tenderão a se excluir competitivamente (Webb et al. 2002).

Quando filtros ambientais forem mais importantes, locais com ambientes mais parecidos tenderão a ser mais similares na sua composição de grupos funcionais (Webb et al. 2002), embora possam variar na composição de espécies em cada grupo funcional. Entretanto, se a competição interespecífica for intensa e contínua, características ambientais poderão influenciar a ocorrência de grupos funcionais, mas a composição de espécies nas comunidades mostrará coocorrência reduzida intragrupos.

1.4. ECOLOGIA FILOGENÉTICA

O grau de parentesco entre táxons reflete a medida de compartilhamento de suas histórias evolutivas. Consequentemente, a disposição espacial de linhagens filogenéticas permite inferir processos históricos ou evolutivos que estruturam as comunidades (a não ser que a dispersão de espécies seja tão extensa e efetiva a ponto de anular sinais evolutivos no espaço). Se comunidades ecológicas forem estruturadas unicamente por limitação de dispersão, linhagens estarão espacialmente restritas, independentemente das características ambientais de cada local (Eiserhardt et al. 2013). Por outro lado, se a composição de linhagens se ajustar às características ambientais das comunidades, independentemente da distância geográfica entre elas, pode-se inferir ou a especiação adaptativa ao ambiente ou a evolução limitada de nichos (Eiserhardt et al. 2013).

Quando há uma convergência nos atributos ecológicos de linhagens distantes que ocorrem em ambientes similares, há especiação adaptativa ao ambiente. Dessa maneira, comunidades ambientalmente mais similares serão mais distintas na composição de linhagens (Eiserhardt et al. 2013). Por outro lado, a evolução limitada de nicho implica que espécies mais aparentadas também serão ecologicamente mais similares, resultando numa composição de linhagens mais parecida em comunidades ambientalmente mais semelhantes (Eiserhardt et al. 2013).

O estudo da distribuição dos atributos funcionais das espécies na filogenia e no espaço geográfico, juntamente com o estudo da distribuição espacial de linhagens filogenéticas – portanto, a fusão da ecologia funcional e filogenética - deverão permitir um melhor entendimento dos processos estruturadores de comunidades ecológicas (Cavender-Bares et al. 2009).

1.5. REGIÕES BIOGEOGRÁFICAS DO OCEANO ATLÂNTICO

O oceano Atlântico é composto por quatro principais regiões biogeográficas, delimitadas por afinidades na biodiversidade e pelo grau de endemismo: Atlântico Noroeste, Atlântico Sudoeste, Cordilheira Meso-Atlântica e Atlântico Leste (Fig 4; Briggs 1974). Essas regiões estão delimitadas por barreiras biogeográficas com diferentes permeabilidades (Fig 4; Briggs 1974, Floeter et al. 2008). O Atlântico Noroeste, composto pelo Caribe e a província Carolínea, está separado do Atlântico Sudoeste (costa do Brasil à Patagônia) pelo deságue do rio Amazonas, que forma uma pluma semipermeável de água doce carregada de sedimentos (Floeter et al. 2008). A Cordilheira Meso-Atlântica se separa das demais regiões biogeográficas devido ao vasto oceano de águas profundas, sendo que essa Barreira Meso-Atlântica também isola o Atlântico leste do Atlântico oeste (Fig 4; Floeter et al. 2008). Além disto, conforme a composição da fauna de peixes recifais, o Atlântico Leste pode ser dividido em três sub-regiões: o Atlântico Nordeste, composto pelo mar Mediterrâneo e as ilhas Macaronésias; o Atlântico Leste Tropical, na costa norte da África; e a África do Sul (Floeter et al. 2008). O fechamento do Mar de Tétis e as águas frias da corrente de Benguela, ao sul da África, desconectam o oceano Atlântico do oceano Índico; assim como o fechamento do Istmo do Panamá desconectou o oceano Atlântico do oceano Pacífico (Fig 5; Floeter et al. 2008).

O oceano Atlântico é bem menos rico na sua fauna de peixes recifais do que o oceano Indo-Pacífico, provavelmente devido à sua menor extensão e às mudanças ambientais que frequentemente impactaram os recifes do Atlântico, tais como glaciações e alterações nas correntes oceânicas (Floeter et al. 2008). O Atlântico Noroeste constitui a região de maior biodiversidade taxonômica de peixes recifais do oceano Atlântico (Floeter et al. 2008). Embora o Atlântico Sudoeste apresente pouco mais de metade da riqueza do Atlântico Noroeste, essas são as regiões biogeográficas do Atlântico mais parecidas entre si em relação ao número de espécies compartilhadas. Por sua vez, a composição de espécies de peixes recifais da Cordilheira Meso-Atlântica é intermediária entre o leste e oeste do Atlântico. Acredita-se que o oeste do Atlântico tenha sido o centro de origem de espécies para todo o oceano, pois muitas espécies que evoluíram no oeste se mostraram capazes de colonizar o leste, enquanto que bem menos espécies têm a origem e trajetória inversas (Briggs 2003).

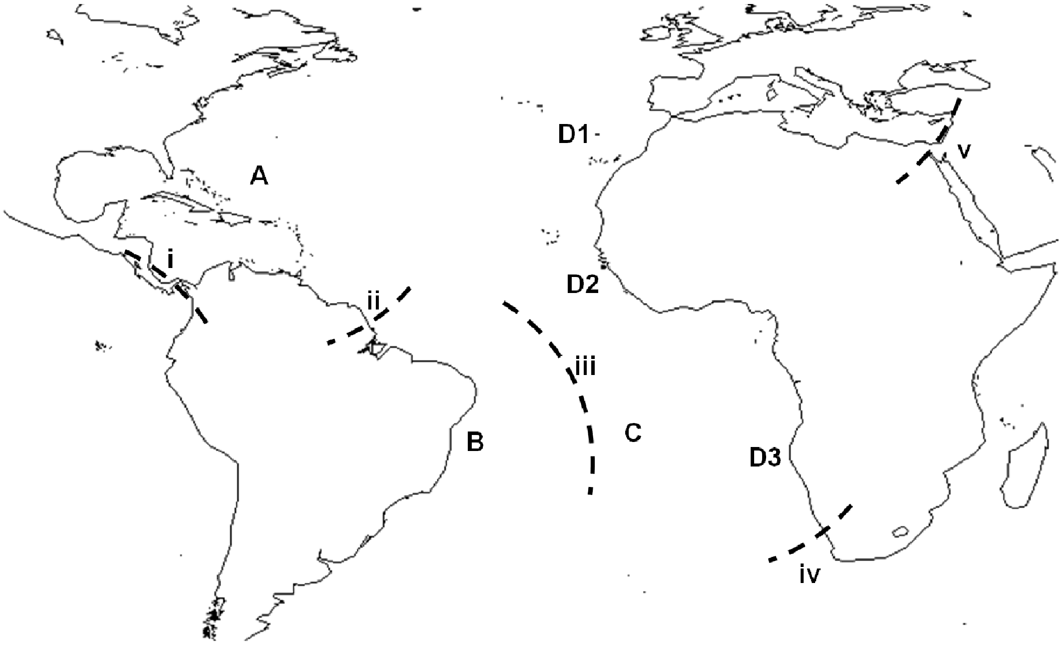


Figura 4. Regiões (A-D) e barreiras (i-v) biogeográficas do oceano Atlântico. A: Atlântico Noroeste; B: Atlântico Sudoeste; C: Cordilheira Meso-Atlântica; D1: Atlântico Sudeste, D2: Atlântico Leste Tropical e D3: África do Sul compõem o Atlantico Leste. i: Fechamento do Istmo do Panamá; ii: Deságue do Rio Amazonas; iii: Barreira Meso-Atlântica; iv: Corrente de Benguela; v: Fechamento do mar de Tétis.

1.6. TEORIA DA TEMPERATURA PLEISTOCÊNICA

A Teoria da Temperatura Pleistocênica postula que a porção norte do oceano Atlântico tenha sido fortemente influenciada pela queda acentuada da temperatura nos períodos glaciários do Pleistoceno (Briggs 1966). Essa queda de temperatura teria acarretado uma extinção em massa nessa região, de maneira que os recifes do Atlântico Norte teriam sido repovoados após as ultimas glaciações, a partir de 12 mil anos atrás. Dessa maneira, não teria decorrido tempo suficiente para mudanças evolutivas marcantes. Espera-se portanto que os recifes do Atlântico norte, embora tenham recuperado sua riqueza de espécies, apresentem reduzido nível de endemismo (Briggs 1996). Por outro lado, flutuações de temperatura também poderiam ter estimulado o processo de especiação, de maneira que, mesmo que algumas espécies endêmicas tivessem se extinguido, outras teriam surgido (Briggs 2003).

Há controvérsias a respeito da Teoria da Temperatura Pleistocênica, principalmente em relação ao lado Leste do Atlântico. Briggs (2003) sugere que o leste do Atlântico tenha sido mais atingido pelas glaciações, pois sua biodiversidade é composta principalmente por espécies transatlânticas de gêneros do Atlântico oeste, com poucos gêneros típicos do próprio Atlântico leste. Entretanto, embora na costa atlântica dos Estados Unidos a hipótese de extinção tenha sido corroborada por um estudo de moluscos bivalves (Stanley 1986), outro estudo no Atlântico Leste (arquipélago de Açores) não encontrou evidências de extinção de espécies endêmicas de moluscos durante as glaciações (Ávila et al. 2008).

1.7. PROCESSOS HISTÓRICO-EVOLUTIVOS E ECOLÓGICOS NA ESTRUTURAÇÃO DE COMUNIDADES DE PEIXES RECIFAIS DO ATLÂNTICO

Há indícios tanto de processos histórico-evolutivos como de processos ecológicos recentes na distribuição de peixes recifais no oceano Atlântico (Floeter et al. 2008, Bender et al. 2013).

Processos histórico-evolutivos

A variação da permeabilidade de barreiras biogeográficas ao longo do tempo parece ter permitido uma recente diversificação de linhagens no oceano Atlântico (Floeter et al. 2008). Algumas espécies teriam se dispersado para outras regiões em períodos em que as barreiras foram mais permeáveis, porém as populações teriam ficado isoladas pela redução de permeabilidade subsequente dessas barreiras.

Outra marca histórica na distribuição de peixes recifais no Atlântico é a maior riqueza de espécies por família nos locais de origem de cada clado (Floeter et al. 2008, Bender et al. 2013). Por exemplo, os gêneros *Sparisoma* e *Diplodus* são mais diversificados no Atlântico Oeste e Leste, respectivamente, onde se acredita que eles tenham se originado (Floeter et al. 2008).

Processos ecológicos

Um possível indício de processos ecológicos na distribuição de peixes recifais é dado por espécies que, embora tenham cruzado a barreira amazônica no sentido Caribe-Brasil e colonizado ilhas como Fernando de Noronha e Atol das Rocas, não lograram colonizar as regiões costeiras, que apresentam características ambientais muito distintas dos recifes caribenhos (Floeter et al. 2008). Isto apoia a suposição de que o tipo de recife (coralíneo ou rochoso) e a latitude têm grande influência sobre a estrutura trófica das comunidades de peixes recifais do Atlântico (Floeter et al. 2004, Ferreira and Gonçalves 2006, Bender et al. 2013). Por exemplo, a distribuição de peixes herbívoros no Atlântico diminui com a latitude, provavelmente devido a variações na temperatura (Floeter et al. 2005). Entretanto, diferentes famílias de peixes geram esse padrão latitudinal no Atlântico Noroeste e Sudoeste (Floeter et al. 2005).

Devido ao seu caráter semipermeável, as barreiras biogeográficas do oceano Atlântico implicam na ação concomitante de processos ecológicos e histórico-evolutivos. A distribuição de uma linhagem pode estar restrita ao local em que se originou caso ela não tenha meios de transpor determinada barreira. Atributos ecológicos das espécies afetam sua capacidade de transpor diferentes barreiras biogeográficas do Atlântico (Luiz et al. 2012). O potencial para uma espécie cruzar a Barreira Meso-Atlântica, por exemplo, depende de sua capacidade de ser transportada por objetos ou outros indivíduos (*rafting;* Luiz et al. 2012). Por outro lado, a capacidade de uma espécie usar múltiplos habitats está diretamente correlata com seu potencial de cruzar a pluma Amazônica (Luiz et al. 2012). Ambas as barreiras são mais facilmente transpostas por espécies maiores e com distribuição latitudinal mais extensa (Luiz et al. 2012), porque o maior tamanho corporal em peixes recifais está associado a um maior sucesso de colonização, devido a rápido crescimento, maior capacidade competitiva, maior capacidade de evitar predadores e maior tolerância fisiológica de variações ambientais (Luiz et al. 2012). A amplitude de distribuição latitudinal indica a capacidade de tolerância de variações ambientais (Luiz et al. 2012).

1.8. OBJETIVOS DA DISSERTAÇÃO

Essa dissertação tem como objetivo investigar os padrões espaciais da distribuição da biodiversidade de organismos recifais no oceano Atlântico. Com base no reconhecimento desses padrões serão feitas inferências acerca dos processos que estruturam tais comunidades.

O primeiro capítulo trata de padrões de biogeografia de ilhas de peixes recifais, gastrópodes e macroalgas; ou seja, padrões qualitativos da distribuição desses organismos recifais. O segundo capítulo trata de padrões quantitativos da distribuição de duas famílias de peixes recifais (Labridae e Pomacentridae). Neste estudo, mostro como a betadiversidade desses organismos recifais varia entre recifes de acordo com a distância geográfica ou dissimilaridade ambiental entre eles.

A dissertação se completa com uma conclusão geral que aponta para as principais fontes de variação nos padrões de distribuição (entre escalas, regiões biogeográficas, grupos taxonômicos ou aspectos da biodiversidade) e um resumo das evidências de processos ecológicos, histórico-evolutivos ou neutros na estruturação de comunidades recifais do oceano Atlântico.

1.9. REFERÊNCIAS BIBLIOGRÁFICAS

Ávila, S. P. et al. 2008. Mass extinctions in the Azores during the last glaciation: fact or myth? - J. Biogeogr. 35: 1123–1129.

Badano, E. I. et al. 2005. Species richness and structure of ant communities in a dynamic archipelago: effects of island area and age. - J. Biogeogr. 32: 221–227.

Bender, M. G. et al. 2013. Biogeographic, historical and environmental influences on the taxonomic and functional structure of Atlantic reef fish assemblages. - Glob. Ecol. Biogeogr. 22: 1173–1182.

Bolker, B. M. 2007. Ecological Models and Data in R. - Ecology: 408.

Briggs, J. C. 1966. Oceanic islands, endemism, and marine paleotemperatures. - Syst. Biol. 15: 153–163.

Briggs, J. C. 1974. Marine Zoogeography. - McGraw-Hill.

Briggs, J. C. 1996. Tropical Diversity and Conservation. - Conserv. Biol. 10: 713–718.

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

Cavender-Bares, J. et al. 2009. The merging of community ecology and phylogenetic biology. - Ecol. Lett. 12: 693–715.

Chase, J. M. and Leibold, M. A. 2003. Ecological Niches. Linking Classical and Contemporary Approaches. - The University of Chicago Press.

Crawley, M. J. and Harral, J. E. 2001. Scale dependence in plant biodiversity. - Science. 291: 864–868.

Eiserhardt, W. L. et al. 2013. Dispersal and niche evolution jointly shape the geographic turnover of phylogenetic clades across continents. - Sci. Rep. 3: 1164.

Emerson, B. C. and Gillespie, R. G. 2008. Phylogenetic analysis of community assembly and structure over space and time. - Trends Ecol. Evol. (Personal Ed. 23: 619–30.

Ferreira, C. E. L. and Gonçalves, J. E. a. 2006. Community structure and diet of roving herbivorous reef fishes in the Abrolhos Archipelago, south-western Atlantic. - J. Fish Biol. 69: 1533–1551.

Floeter, S. R. et al. 2004. Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. - J. Fish Biol. 64: 1680–1699.

Floeter, S. R. et al. 2005. Geographical gradients of marine herbivorous fishes: patterns and processes. - Mar. Biol. 147: 1435–1447.

Floeter, S. R. et al. 2008. Atlantic reef fish biogeography and evolution. - J. Biogeogr. 35: 22–47.

Hart, P. and Pearson, E. 2010. An application of the theory of island biogeography to fish speciation on seamounts. - Mar. Ecol. Prog. Ser. 430: 281–288.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography.

Lawton, J. H. et al. 1993. Patterns of diversity for the insect herbivores on bracken. - In: Species diversity in ecological communities: historical and geographical perspectives. pp. 178–184.

Luiz, O. J. et al. 2012. Ecological traits influencing range expansion across large oceanic dispersal barriers: insights from tropical Atlantic reef fishes. - Proc. R. Soc. B Biol. Sci. 279: 1033–1040.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of Island Biogeography. - Princeton University Press.

Ricklefs, R. E. 1987. Community Diversity: relative roles of local and regional processes. - Science. 235: 167–171.

Roos, M. C. et al. 2004. Species diversity and endemism of five major Malesian islands: diversity–area relationships. - J. Biogeogr. 31: 1893–1908.

Sandin, S. A. et al. 2008. Island biogeography of Caribbean coral reef fish. - Glob. Ecol. Biogeogr. 17: 770–777.

Spengler, A. et al. 2011. How island size and isolation affect bee and wasp ensembles on small tropical islands: a case study from Kepulauan Seribu, Indonesia. - J. Biogeogr. 38: 247–258.

Stanley, S. M. 1986. Anatomy of a regional mass extinction: Plio- Pleistocene decimation of the Western Atlantic Bivalve Fauna. - Palaios 1: 17–36.

Storch, D. et al. 2012. Universal species–area and endemics–area relationships at continental scales. - Nature 488: 78–81.

Stracey, C. M. and Pimm, S. L. 2009. Testing island biogeography theory with visitation rates of birds to British islands. - J. Biogeogr. 36: 1532–1539.

Triantis, K. A. et al. 2012. The island species-area relationship: biology and statistics. - J. Biogeogr. 39: 215–231.

Webb, C. O. et al. 2002. Phylogenies and Community Ecology. - Annu. Rev. Ecol. Syst. 33: 475–505.

Welter-Schultes, F. and Williams, M. 1999. History, island area and habitat availability determine land snail species richness of Aegean islands. - J. Biogeogr. 26: 239–249.

Whittaker, R. J. et al. 2008. A general dynamic theory of oceanic island biogeography. - J. Biogeogr. 35: 977–994.

Wiens, J. J. and Donoghue, M. J. 2004. Historical biogeography, ecology and species richness. - Trends Ecol. Evol. 19: 639–644.

2. ISLAND BIOGEOGRAPHY: PATTERNS OF MARINE SHALLOW-WATER ORGANISMS IN THE ATLANTIC OCEAN

Nayara F. Hachich[1,2], Michael B. Bonsall[2], Eduardo M. Arraut[4], Diego R. Barneche[5], Thomas M. Lewinsohn[1], Sergio R. Floeter[3]

1. Programa de Pós-Graduação em Ecologia, Departamento de Biologia Animal, Universidade Estadual de Campinas, Rua Monteiro Lobato, 255 - Cidade Universitária, Campinas-SP. CEP: 13083-970, Brazil.
2. Mathematical Ecology Research Group, Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK.
3. Laboratório de Biogeografia e Macroecologia Marinha, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Campus Universitário, Trindade, Florianópolis-SC. CEP: 88.040-900, Brazil.
4. Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxfordshire OX13 5QL, UK.
5. Department of Biological Sciences, Macquarie University, Sydney, NSW2109, Australia.

ABSTRACT

Aim To understand whether species-area, species-island age and species-isolation large-scale biogeographic patterns of marine shallow-water groups in the Atlantic Ocean differ from those of terrestrial habitats and among marine taxa.

Location Atlantic Ocean

Methods Reef fish, gastropod and seaweed species richness as well as reef fish endemic species data were obtained for eleven Atlantic oceanic islands. Using a multi-model inference approach based on linear and non-linear regressions we tested hypotheses regarding the variation of species richness and endemism as a function of island area, age and isolation. Best models were selected using ratios between Akaike weights corrected for small sample size (AICc). Results were compared among the three shallow-water species groups and contrasted against previous studies on marine and terrestrial systems.

Results Island area explained richness in all taxa and was the best single predictor of gastropod richness. Age was the best single predictor of reef fish richness and an important predictor of seaweed richness, though the latter was equally explained by area, age and isolation. Although isolation was a good predictor of seaweed richness, it did not explain fish and gastropod richness, due to their overall higher dispersal capacity. Whittaker's General Dynamic Model explained fish and seaweed richness adequately, but was the best model only for fish.

Main conclusions We show that island biogeography patterns differ between marine and terrestrial ecosystems, among different oceanic ecosystems, and, importantly, that within marine shallow-water environments biogeographical patterns are highly taxon-dependent.

Keywords age, area, Atlantic ocean, endemism, gastropod, island biogeography, isolation, reef fish, richness, seaweed

INTRODUCTION

The Theory of Island Biogeography (MacArthur & Wilson, 1967) postulates that larger islands should maintain larger populations and offer more habitat heterogeneity, therefore experiencing lower extinction rates and maintaining higher richness. At the same time, isolated islands receive fewer immigrants and consequently maintain lower richness (MacArthur & Wilson, 1967), and, due to decreased gene flow, are expected to have more endemic species (Whittaker & Fernández-Palacios, 2007). Furthermore, older islands are expected to hold increased richness and endemism since there is more time for migrant arrival and speciation (Whittaker & Fernández-Palacios, 2007). Although island biogeographical patterns have been well documented and accepted, to date research has focused largely on terrestrial organisms. Differently from terrestrial, marine groups are in general able to disperse over much greater distances (Kinlan & Gaines, 2003). Marine species have complex life cycles and disperse mainly via propagules, whose dispersion is probably facilitated by the fluid dynamic of the seas (Kinlan & Gaines, 2003).

Biogeographical patterns can be scale-dependent (Crawley & Harral, 2001; Triantis et al., 2012). Oceanic systems differ in scale: the Indo-Pacific Ocean occupies 239 million km² and inter-island distances are large. In contrast, the Atlantic Ocean is smaller (106 million km²) and its oceanic islands are less isolated from each other (Luiz et al., 2012). Previous island biogeography studies on marine systems, although corroborating the species-area and species-isolation patterns found in studies on terrestrial habitats, spanned spatial scales that were not comparable (either larger or smaller) to the Atlantic Ocean (Mora et al., 2003; Sandin et al., 2008; Parravicini et al., 2013). Moreover, to our knowledge, the relationship between species richness and island geological age (hereafter called species-age pattern) has not been investigated in marine systems. Moreover, mechanisms can contribute differentially to island biogeographical processes, leading to taxon-specific patterns (Whittaker & Fernández-Palacios, 2007), hence the need of studying multiple taxa in marine systems.

In this study we investigated whether species-area, species-age and species-isolation large-scale biogeographic patterns of marine shallow-water groups in the Atlantic Ocean differ from those of terrestrial habitats and among marine taxa. Our cross-taxon analyses encompassed shallow-water reef fish, gastropods and seaweeds.

METHODS

Study region

This study spanned a large scale in the Atlantic Ocean, covering its tropical and subtropical zones. When focusing on marine shallow-water systems, and on such a macroscale analysis, an archipelago can be considered a continuous community for reef life and be treated as an island on island biogeography studies of reef biodiversity. Thus, eleven oceanic islands or archipelagos of the Atlantic Ocean were included in this study, namely: Saint Helena Island, Ascension Island, Sao Tome & Principe Islands, Cape Verde Archipelago, Canaries Islands, Archipelago of Azores, Archipelago of Madeira, Bermuda Island, Trindade Island, Saint Paul's Rocks Archipelago and Fernando de Noronha Ridge (Fig 1). This sites are distributed over five biogeographical provinces, according to their biota affinity: South-western Atlantic, North-western Atlantic, Tropical-eastern Atlantic, North-eastern Atlantic and Mid-Atlantic Ridge (Fig. 1; Floeter et al., 2008).

The advantage about studying island biogeographical patterns based on oceanic islands is that, since they arise from the ocean basins floor and were never connected to the continental shelfs, different from the continental island they do not show a tricky history about varying connectivity and continuous habitat area. Our study comprised almost all the oceanic islands of the Atlantic Ocean within the sea surface temperature range that could be considered tolerable for reef organisms. The only oceanic islands that satisfy these conditions and were left behind were Bioko and Annobon Islands, for which we couldn't find reasonable data.

Among the eleven Atlantic oceanic islands studied, three of them – Bermuda, Azores and Canaries - are considered to had suffered effects of the Pleistocene glaciations. The drop of temperature could have extinct these islands' local biota, and although the elapsed time (12 myr) could have been enough so they recover they species richness by immigration events, it is considered not to be enough to allow much evolutionary change (Briggs, 1996). Given that, these islands are expected to show reduced levels of endemism (Briggs, 1996).

Biotic and abiotic data

We used reef fish, gastropods and seaweeds as marine shallow-water groups. The term "reef fish" encompasses fish of shallow marine waters that are consistently associated with hard substrates or occupy adjacent sand substrate (Floeter et al., 2008). Reef fish richness and endemism data were obtained for the eleven islands in Floeter et al. (2008) and Simon et al (2013). Although, endemism was only analysed for fish, excluding those islands that are likely to have suffered higher extinction rates during the last glaciation - Bermuda, Azores and Canaries (Briggs, 1966).

Data on gastropods richness were compiled for 10 of the 11 islands, excluding São Tomé & Príncipe. Richness data for nine of the ten sites (except for Cape Verde) were obtained from the online database Malacolog (Rosenberg, 2009). Data from Gomes et al. (2006) was also used for Brazilian islands, Cervera et al. (2004) for the Canaries and Azores, and Rosewater (1975) for Ascension and Saint Helena. These data were compiled including all gastropods and then synonymies were eliminated following Rosenberg (2009) and a strong effort was put into excluding species that do not live in shallow marine waters. Data on Cape Verde gastropods richness were compiled from Rolán (2005) and, following Dr. Emilio Rolán expertise (personal communication), those species that live on deep water or that probably do not occur on the archipelago were removed from the species list. Marine shallow-water gastropods represent at least 80% of gastropods data.

All shallow-water macroalgae belonging to Rhodophyta, Chlorophyta and Phaeophyta were grouped as ‘seaweeds’. Richness data were obtained for 10 of the 11 islands (excluding São Tomé & Príncipe). This data was kindly provided by Dr. Paulo A. Horta (Universidade Federal de Santa Catarina – Brazil, unpublished data) and Dr. Craig W. Schneider (Trinity College – USA, unpublished data) and obtained from Villaça et al. (2006) and Guiry & Guiry (2014).

We defined island area as shallow shelf surface of islands (<200m deep), age as time since islands originated and isolation as distance to the nearest reef habitat. These abiotic data were obtained from Floeter et al (2008).

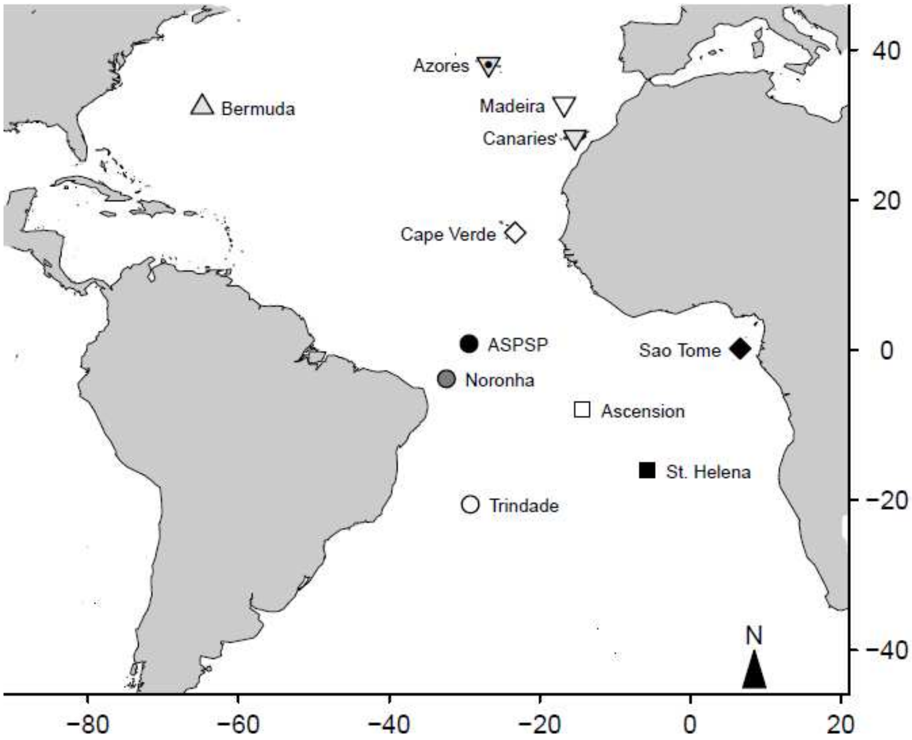


Figure 1. Atlantic biogeographical regions (after Floeter et al. 2008) included in the study: South-western (circles), North-western (triangle), Tropical-eastern (diamonds) North-eastern (inverted triangles) and Mid-Atlantic Ridge (squares). Light-grey coloured islands suffered significant extinctions due to glaciations (Briggs, 1966) and were excluded from endemism analyses.

Hypotheses

We were not only interested on elucidate whether richness or endemism of marine shallow-water groups vary with island area, age or isolation, but we were also interested on the pattern in which this relationship occurs, which can reveal the processes shaping them.

In the absence of ecological constraints, the increase of habitat heterogeneity with area or of niche partitioning with age may allow species richness and endemism to increase linearly with island area or age. On the other hand, if ecological constraints reduce the pace of increase of habitat availability or niche partitioning, the increase os species richness or endemism should slow down on bigger or older islands. However, despite the ecological constraints, there is no limit to species richness and endemism since speciation events and niche subdivision can always add or accommodate new species (Cornell, 2013).

Isolation restricts immigration rates and gene flow and is predicted to cause a constant decrease of species richness and increase of endemism. However, if the distribution of species dispersal capacity is skewed to the right, that is, if the majority of species show low dispersal capacity and only a few are capable of long dispersal, one can expect the pace of the decrease on the number of colonisers or the pace of increasing the number of endemics to slow down on very isolated islands. Still, the variation of richness or endemism with area, age or isolation can be negligible on very small, young and barely isolated islands.

Besides these hypotheses on the variation of richness with each island feature, species richness is expected to vary as a unimodal function of island age combined with a positive linear function of area. This species-age humped pattern reflects the degeneration of very ancient islands (deep seamounts when it comes to marine shallow-water habitats; Hart & Pearson, 2010), which lose area and complexity of suitable habitats. This hypothesis is determined by Whittaker's General Dynamic Model (GDM; Whittaker et al., 2008).

Analysis

We used different mathematical models to test the null hypotheses of richness or endemism being independent of area, age or isolation. The four alternative hypotheses were tested using univariate linear and non-linear regressions. The models and functions applied to test each hypothesis is shown on Table 1.

Except for the GDM, which combines area and age in a single model, for each taxonomic group we tested each model separately for each predictor variable (area, age and isolation), so as to best explore the relationships between each response and predictor variable. Models were fitted by minimising residual sums of squares. Best models were selected using ratios between Akaike Information Criterion weights (w_i) corrected for small sample size (AICc; Burnham & Anderson, 2002; Wagenmakers & Farrell, 2004). When an AICc weight was less than two, we considered that both models described equally well the data and used *y-model* averaging to infer a consensus response curve (Burnham & Anderson, 2002). We also selected the overall best predictors of richness and endemism using the same procedure as above (based on AICc values) but comparing all models of all predictors. However, in the latter analysis, we only calculated w_i between models that showed AICc values that exceeded the smallest AICc of each response variable by less than two units.

Although we used the power model non-linear equation on the species-area model selection, we also fitted its log-log form so the coefficient values could be comparable to the literature. We used t-tests to evaluate whether z-values were within the range (0.2–0.4) expected according to previous studies (MacArthur & Wilson, 1967). To explore patterns of endemism we analysed the variation in number and proportion of endemic fish.

To corroborate the results of the predictors of each group richness and endemism we also fitted multiple regression models, based on power relationships between the response and predictor variables (Appendix S2). Correlations among predictor variables were not significant (Appendix S2). All analyses were run in R (R Development Core Team, 2013).

RESULTS

Island area was positively correlated with species richness of all taxa. The species-area relationship (SAR) was best described by log-linear and power models (Table 2). However, there were noteworthy differences among taxa. For gastropods the simpler linear model also provided a robust fit to SAR (Table 2). Although gastropod and seaweed z-values were within the expected range, the z-value for reef fish was much lower (Table 3). Graphical representations of the best model(s) are shown in Figure 2. There was no relationship between proportion of endemic fish and area.

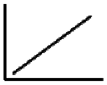
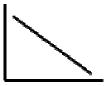
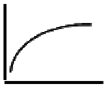
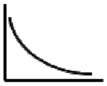
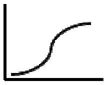
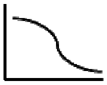
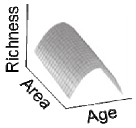
Island age was positively correlated with species richness of reef fish and seaweeds. However, for gastropod richness, the model with age did not improve on the null model (Table 2). Both linear and power models fit the reef fish species-age relationship equally, and these models together with the logarithmic one better represented the seaweed species-age relationship (Table 2). The number of endemic fish did not vary significantly with age, whereas age had a negative, but not significant, effect on the proportion of endemic species (Table 2; Fig 2).

Isolation by distance was negatively correlated with seaweed richness (Fig 2; Table 2). Other taxa richness were unaffected by isolation. Proportion of endemic fish species, though not their number, did increase with isolation (Fig 2; Table 2). Other variables did not affect endemic reef fish.

On the whole the single best predictors were: isolation for reef fish endemism, age for reef fish richness and area for gastropod richness (Table 2). Interestingly, there was no single best predictor for seaweed richness (Table 2). Although Whittaker's GDM was significant for reef fish species richness, it was not the best model for any of the marine shallow-water groups (Table 2).

The multiple regressions corroborated simple regression results concerning the predictors of each group richness or fish endemism (Appendix S1). Interestingly, the power model of richness increase with both area and age together improved on the GDM model, which predicts that richness should increase linearly with area together with a unimodal variation with island age. This indicates the prevalence of a monotonic relationship between richness and age over the unimodal relationship.

Table 1. Models for the variation in species richness or endemism (y) as a function of island area, age or isolation (x) that were compared by model selection.

Model	Function	Relationship	Graph
Null	y = a	Species-Area, Species-Age, Species-Isolation, Endemism-Area, Endemism-Age, Endemism-Isolation	
Linear	y = a + b.x	Species-Area, Species-Age, Endemism-Area, Endemism-Age, Endemism-Isolation	
		Species-Isolation	
Logarithmic or Power	y = a + b.log(x) or $y = b.x^a$	Species-Area, Species-Age, Endemism-Area, Endemism-Age, Endemism-Isolation	
		Species-Isolation	
Logistic	$y=\frac{a}{1 + e^{(xmid-x)/b}}$	Species-Area, Species-Age, Endemism-Area, Endemism-Age, Endemism-Isolation	
		Species-Isolation	
General Dinamic Model (GDM)	y = a + b.log(area) + c.age + d.age²	Species richness with Area and Age	

,Table 2. Akaike Information Criterion values of each model corrected for small sample sizes (AICc). Best models for each predictor (area, age and isolation) are in bold letters, overall best models are highlighted. NC: no convergence.

		Fish richness		**Gastropod richness**		**Seaweed richness**		**Endemic fish (%)**		**Endemic fish (n)**	
	Model	**AICc**	wi	**AICc**	wi	**AICc**	wi	**AICc**	wi	**AICc**	wi
Area	Null	128.35	0.17	132.61	0.08	137.54	0.12	**50.02**	0.62	**52.26**	0.31
	Linear	129.89	0.08	**129.49**	0.38	137.84	0.11	53.75	0.10	**51.26**	0.50
	Logarithmic	**126.51**	0.42	**130.50**	0.23	**135.00**	0.44	53.03	0.14	54.79	0.09
	Power	**126.92**	0.34	**129.95**	0.31	**134.93**	0.45	53.02	0.14	54.45	0.10
	Logistic	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
Age	Null	128.35	0.00	**132.61**	0.18	137.54	0.11	**50.02**	0.24	**52.26**	0.60
	Linear	**119.05**	0.49	**132.09**	0.23	**136.49**	0.18	**49.33**	0.33	55.20	0.14
	Logarithmic	123.11	0.06	**131.91**	0.26	**135.21**	0.35	**49.88**	0.25	55.21	0.14
	Power	**119.79**	0.34	**131.62**	0.30	**135.13**	0.36	50.61	0.18	55.30	0.13
	Logistic	122.08	0.11	136.20	0.03	NC	NC	NC	NC	NC	NC
Isolation	Null	**128.35**	0.50	**132.61**	0.62	137.54	0.10	50.02	0.04	**52.26**	0.61
	Linear	130.72	0.15	135.81	0.13	138.33	0.06	**46.47**	0.23	55.50	0.12
	Logarithmic	130.52	0.17	135.79	0.13	135.92	0.21	**45.27**	0.42	55.26	0.14
	Power	130.49	0.17	135.81	0.13	**133.78**	0.63	**45.95**	0.30	55.32	0.13
	Logistic	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
GDM		**121.72**	-	137.61	-	136.71	-	-	-	-	-

Table 3. Power-model species-area relationship coefficients for fish, gastropods and seaweeds (C: intercept; z: exponent) and t-values of t-tests of the z-values against 0 and 0.2. Significant values of t are in bold letters.

Group	**C**	**z**	**t (0)**	**t (0.2)**
Reef fish	62.85	0.12	**9.16**	**-5.96**
Gastropods	34.36	0.24	**10.11**	1.82
Seaweeds	42.67	0.23	**9.76**	1.35

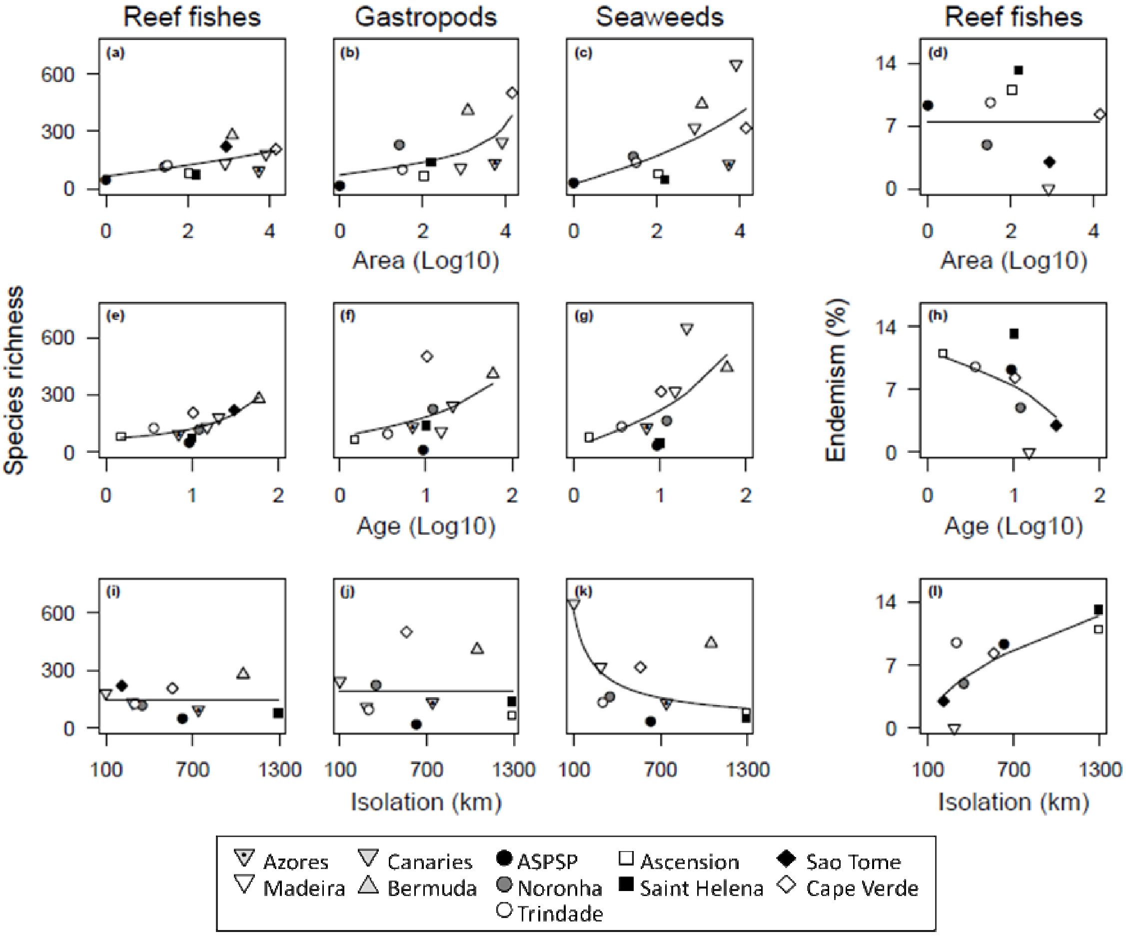


Figure 2. Model averaging curves of best models - in cases in which several models fitted the data equally well (a-c, e-h an l) - or single best models (d, i-k) for effects of island area, age or isolation on richness of three taxa and on endemic fish. The predictor-response relationships that had alternative models that improved in the null model are those represented in a-c, e, g, k and l. Atlantic islands can be identified by symbols in Figure 1.

DISCUSSION

We explored island biogeographical patterns in reef fish, seaweeds and gastropods across oceanic islands in the Atlantic. The increase of species richness with island area and the prevalence of power and logarithmic convex-shape models for describing SARs of all three marine taxa supports findings from previous studies (MacArthur & Wilson, 1967; Mora et al., 2003; Sandin et al., 2008; Triantis et al., 2012; Parravicini et al., 2013). The increase of species richness with island area has been attributed to reduced extinction rates, greater niche variability and higher chance of migrants reaching larger islands (MacArthur & Wilson, 1967). Niche subdivision and speciation events enable continuous increases of richness with island area, so that there is no limit to species richness to increase with area (Cornell, 2013). However, the prevalence of the convex-shape models indicates that niche availability does not increase linearly with area.

The z-value of the power-law SAR was lower for the group with highest dispersal capacity (Table 3). This is in agreement with higher z-values reflecting greater effective isolation (Triantis et al., 2012).

In contrast with findings from terrestrial studies (Storch et al., 2012), there was no direct effect of island area on endemism. Reef fish have high dispersal capacity (Kinlan & Gaines, 2003) and thus may not suffer intra-island allopatric speciation events.

As for terrestrial species (Badano et al., 2005), species richness increased with island age for reef fish and seaweeds. The erosion of rocks and growth of coral colonies through time increases substrate surface complexity and habitat heterogeneity (Hart & Pearson, 2010). Complexity added by corals promotes reef species evolution (Price et al., 2011) and, additionally, older islands accumulate species over longer periods (Whittaker & Fernández-Palacios, 2007). Nonetheless, according to the “damped increase hypothesis” (Cornell, 2013) the increase of richness with age should slow down on older islands due to ecological constraints that reduce immigration and speciation. The linear and convex-shape curves describing the species-age relationship for reef fish and seaweeds agree with these hypotheses.

The number of endemic fish did not increase with age, as would be expected by the general increase in total fish richness; hence, contrasting biogeographical processes may maintain constant levels of endemism (Emerson & Oromi, 2005). On one hand, endemic fish species are likely to arise continually (through localised speciation events), but reef fish high dispersal capacity may allow them to spread rapidly to other islands. Moreover, endemic species are more vulnerable to extinction and may be lost through competition with new colonizers (Emerson & Oromi, 2005). In such cases, the negative relationship between proportion of endemics and age is expected if overall richness increases through time. Evidence of opposing forces shaping endemism-age patterns have also been shown in terrestrial habitats (Emerson & Oromi, 2005).

Although isolation explained seaweed richness, it was a poor predictor of fish or gastropod species richness. These taxon-specific differences occur because distances between Atlantic Ocean islands are not sufficient to isolate groups with higher dispersal capacities (Kinlan & Gaines, 2003; Luiz et al., 2012). This contrasts with patterns observed in the Indo-Pacific Ocean (Mora et al., 2003), where islands can be much more isolated (Luiz et al., 2012), and patterns observed in terrestrial organisms, which have smaller scales of dispersal and for which isolation is often strongly correlated with richness (Badano et al., 2005; Stracey & Pimm, 2009). The larger percentage of endemic fish on more isolated islands corroborates previous studies and presumably reflects reduced gene flow in more isolated populations (Whittaker & Fernández-Palacios, 2007).

Our finding that island age was the best single predictor of reef fish richness is likely due to *i)* historical-evolutionary processes such as accumulation of colonizers and speciation events and *ii)* ecological mechanisms associated with higher habitat complexity in older islands. This evidence of age as the key determinant of reef fish richness, together with the fact that age also explained seaweed richness, strengthens the importance of incorporating an evolutionary dimension into the Theory of Island Biogeography (Whittaker et al., 2008). However, the relationship between species richness and island age seems not to be unimodal, as proposed by the General Dynamic Theory of Oceanic Island Biogeography (Whittaker et al., 2008). This is most likely due to the absence of atols or even seamounts in this study, so the reefs studied have not suffered much degeneration and consequently no reduction of available niches. Nonetheless, such long-term processes are likely to be taxon-specific since, as we show, there is no clear evidence that gastropod richness is affected by island age. This clearly warrants further investigation.

In conclusion, we show that marine shallow-water organisms in the Atlantic reveal that island biogeographical patterns differ between marine and terrestrial ecosystems and that many island biogeographical patterns are both taxon- and scale-dependent and vary across different oceans. This has important implications for understanding the structure, function and conservation of marine ecosystems.

ACKNOWLEDGEMENTS

We are grateful to Paulo Horta and Craig Schneider for providing access to seaweed data, Emilio Rolán for help in organizing Cape Verde gastropods data, Osmar Luiz, Leonardo Jorge and Robert Colwell for insights and methodology discussions, Paulo Inácio Prado, Carlos Ferreira and Martin Pareja for a critical review of the text, and for financial support provided by FAPESP, CAPES, CNPQ, Rede Clima and INCT Mudanças Climáticas.

REFERENCES

Badano E.I., Regidor H.A., Núñez H.A., Acosta R., & Gianoli E. (2005) Species richness and structure of ant communities in a dynamic archipelago: effects of island area and age. *Journal of Biogeography*, **32**, 221–227.

Briggs J.C. (1966) Oceanic islands, endemism, and marine paleotemperatures. *Systematic Biology*, **15**, 153–163.

Briggs J.C. (1996) Tropical Diversity and Conservation. *Conservation Biology*, **10**, 713–718.

Burnham K.P. & Anderson D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach.* Springer, London.

Cervera J.L., Calado G., Gavaia C., Malaquias M.A.E., Templado J., Ballesteros M., García-Gómez J.C., & Megina C. (2004) An annotated and updated checklist of the opisthobranchs (Mollusca: Gastropoda) from Spain and Portugal (including islands and archipelagos). *Boletín Instituto Español de Oceanografía*, **20**, 1–132.

Cornell H. V (2013) Is regional species diversity bounded or unbounded? *Biological reviews of the Cambridge Philosophical Society*, **88**, 140–65.

Crawley M.J. & Harral J.E. (2001) Scale dependence in plant biodiversity. *Science*, **291**, 864–868.

Emerson B.C. & Oromi P. (2005) Diversification of the forest beetle genus Tarphius on the Canary Island, and the evolutionary origins of island endemics. *Evolution*, **59**, 586–598.

Floeter S.R., Rocha L.A., Robertson D.R., Joyeux J.C., Smith-Vaniz W.F., Wirtz P., Edwards A.J., Barreiros J.P., Ferreira C.E.L., Gasparini J.L., Brito A., Falcón J.M., Bowen B.W., & Bernardi G. (2008) Atlantic reef fish biogeography and evolution. *Journal of Biogeography*, **35**, 22–47.

Gomes R.S., Costa P.M.S., Monteiro J.C., Coelho A.C.S., & Salgado N.C. (2006) Moluscos das ilhas oceânicas brasileiras. *Ilhas oceânicas brasileiras: da pesquisa ao manejo.* pp. 298. Ministério do Meio Ambiente, Secretaria de Biodiversidade e Florestas,

Guiry M.D. & Guiry G.. (2014) *AlgaeBase.* World-wide electronic publication. National University of Ireland, Galway.

Hart P. & Pearson E. (2010) An application of the theory of island biogeography to fish speciation on seamounts. *Marine Ecology Progress Series*, **430**, 281–288.

Kinlan B.P. & Gaines S.D. (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology*, **84**, 2007–2020.

Luiz O.J., Madin J.S., Robertson D.R., Rocha L.A., Wirtz P., & Floeter S.R. (2012) Ecological traits influencing range expansion across large oceanic dispersal barriers: insights from tropical Atlantic reef fishes. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1033–1040.

MacArthur R.H. & Wilson E.O. (1967) *The theory of Island Biogeography.* Princeton University Press, Princeton.

Mora C., Chittaro P., Sale P., Kritzer J., & Ludsin S. (2003) Patterns and processes in reef fish diversity. *Nature*, **421**, 933–936.

Parravicini V., Kulbicki M., Bellwood D.R., Friedlander a. M., Arias-Gonzalez J.E., Chabanet P., Floeter S.R., Myers R., Vigliola L., D'Agata S., & Mouillot D. (2013) Global patterns and predictors of tropical reef fish species richness. *Ecography*, **36**, 1254–1262.

Price S.A., Holzman R., Near T.J., & Wainwright P.C. (2011) Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. *Ecology letters*, **14**, 462–9.

R Development Core Team (2013) R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, **739**, .

Rolán E. (2005) *Malacological fauna from the Cape Verde archipelago, Part 1: Polyplacophora and Gastropoda.* ConchBooks, Hackenheim.

Rosenberg G. (2009) *Malacolog 4.1.1: A database of Western Atlantic marine Mollusca.* http://www.malacolog.org,

Rosewater J. (1975) An annotated list of the marine mollusks of Ascension Island, South Atlantic Ocean. *Smithsonian Contributions to Zoology*, 1–41.

Sandin S.A., Vermeij M.J.A., & Hurlbert A.H. (2008) Island biogeography of Caribbean coral reef fish. *Global Ecology and Biogeography*, **17**, 770–777.

Simon T., Macieira R.M., & Joyeux J.-C. (2013) The shore fishes of the Trindade-Martin Vaz insular complex: an update. *Journal of fish biology*, **82**, 2113–27.

Storch D., Keil P., & Jetz W. (2012) Universal species–area and endemics–area relationships at continental scales. *Nature*, **488**, 78–81.

Stracey C.M. & Pimm S.L. (2009) Testing island biogeography theory with visitation rates of birds to British islands. *Journal of Biogeography*, **36**, 1532–1539.

Triantis K.A., Guilhaumon F., & Whittaker R.J. (2012) The island species-area relationship: biology and statistics. *Journal of Biogeography*, **39**, 215–231.

Villaça R., Pedrini A.G., Pereira S.M.B., & Figueiredo M.A. (2006) Flora marinha bentônica das Ilhas Oceânicas Brasileiras. *Ilhas oceânicas brasileiras: da pesquisa ao manejo* pp. 298. Ministério do Meio Ambiente, Secretaria de Biodiversidade e Florestas,

Wagenmakers E.-J. & Farrell S. (2004) AIC model selection using Akaike weights. *Psychonomic bulletin & review*, **11**, 192–196.

Whittaker R. & Fernández-Palacios J. (2007) *Island biogeography: ecology, evolution, and conservation.* Oxford University Press, Oxford.

Whittaker R.J., Triantis K. a., & Ladle R.J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, **35**, 977–994.

2.1. APPENDIX S1. CORRELATIONS AMONG THE PREDICTOR VARIABLES AND MULTIPLE REGRESSIONS ON BIODIVERSITY PATTERNS

There were no correlations among island area, age and isolation (Table 1).

To corroborate the results we also conducted multiple regressions combining the predictor variables two by two (Area-Age, Area-Isolation, Isolation-Age) and with all three predictor variables together (Isolation-Area-Age), based on power relationships. The conclusion based on multiple regression results (last four models of Table 2) remained the same as those of the simple regressions. The variables that best fit richness were island area and island age for reef fish, island area alone for gastropod and all three variables for seaweed. Island isolation best fit reef fish endemism.

Table 1. Pearson correlation values (r) and their coeficient of significance (p).

Pair of variables	**r**	**p**
Area-Age	-0.05	>0.05
Area-Isolation	-0.22	>0.05
Age-Isolation	0.02	>0.05

Table 2. Akaike values of each model corrected for small sample sizes (AICc). Best models for each predictor, Area (Ar), Age (A) and Isolation (I) are in bold letters, overall best single and multiple models are highlighted. wi: Akaike weights; NC: no convergence.

		Fish richness	**Gastropod richness**	**Seaweed richness**	**Endemic fish (%)**	**Endemic fish (n)**
	Model	**AICc**	**AICc**	**AICc**	**AICc**	**AICc**
Area	Null	128.35	132.61	137.54	**50.02**	**52.26**
	Linear	129.89	**129.49**	137.84	53.75	**51.26**
	Logarithmic	**126.51**	**130.50**	**135.00**	53.03	54.79
	Power	**126.92**	**129.95**	**134.93**	53.02	54.45
	Logistic	NC	NC	NC	NC	NC
Age	Null	128.35	**132.61**	137.54	**50.02**	**52.26**
	Linear	**119.05**	**132.09**	**136.49**	**49.33**	55.20
	Logarithmic	123.11	**131.91**	**135.21**	**49.88**	55.21
	Power	**119.79**	**131.62**	**135.13**	50.61	55.30
	Logistic	122.08	136.20	NC	NC	NC
Isolation	Null	**128.35**	**132.61**	137.54	50.02	**52.26**
	Linear	130.72	135.81	138.33	**46.47**	55.50
	Logarithmic	130.52	135.79	135.92	**45.27**	55.26
	Power	130.49	135.81	**133.78**	**45.95**	55.32
	Logistic	NC	NC	NC	NC	NC
GDM		**121.72**	137.61	136.71	-	-
Area-Age		**118.37**	**131.11**	**130.52**	55.88	56.05
Area-Isolation		130.65	133.41	**132.12**	51.02	**52.50**
Isolation-Area		**123.36**	135.90	**124.87**	51.54	59.26
Isolation-Area-Age		**126.60**	134.74	**119.50**	58.88	66.59

3. ENVIRONMENTAL FILTERING AND SPATIAL STRUCTURE OF REEF FISH DIVERSITY VARIATION AMONG ATLANTIC REEFS

Nayara F. Hachich[1,2], Sergio R. Floeter[2] & Thomas M. Lewinsohn[1]

1. Laboratório de Interação Inseto-Planta, Programa de Pós-Graduação em Ecologia, Departamento de Biologia Animal, Universidade Estadual de Campinas, Cidade Universitária, Campinas-SP. CEP: 13083-970, Brazil.
2. Laboratório de Biogeografia e Macroecologia Marinha, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Campus Universitário, Trindade, Florianópolis-SC. CEP: 88.040-900, Brazil.

ABSTRACT

Reefs are among the most threatened marine systems on earth and little is known about the processes structuring reefs ecological communities. Inferences about the role of these processes can be based on biodiversity distribution patterns, and exploring various aspects of biodiversity can facilitate this comprehension.

When beta diversity is explained by environmental differences between sites, one can assume that environmental filters are influencing diversity distribution. On the other hand, when beta diversity is best explained by the spatial distance between communities, biotic processes related to demographic events, ecological drift and spatialization may be acting.

In this study we aimed to understand the relative contribution of the reef environment and spatial location to variation of fish diversity between reefs in the Western Atlantic Ocean. To this end we explored the taxonomic, functional and phylogenetic aspects of biodiversity of two reef fish families, Labridae and Pomacentridae. We partitioned reef fish beta diversity into environmental and spatial components using distance-based Redundancy Analysis.

Results showed that the variation of reef fish composition in Western Atlantic reefs is mainly driven by environmental filters and weakly influenced by processes that cause spatial autocorrelation of species distributions. However, the environmental variables that best explained reef fish beta diversity varied strongly, especially between scales and biogeographical regions, but also between reef fish families.

Keywords: functional diversity, phylogenetic diversity, variation partition, beta diversity, reef fish, Atlantic, environmental filters, spatial autocorrelation

INTRODUCTION

Similarity between communities can be influenced by the spatial distance between them, due to dispersal limitation or to ecological drift, either of which can produce spatial autocorrelation (neutral theory; Hubbell 2001). At the same time, communities that are environmentally similar may be composed of similar species, due to environmental filtering (a mechanism of niche-related processes; Keddy 1992). However, environmental variables also can be spatially structured (environmental spatial autocorrelation; Hubbell 2001), and, to some degree, there is a continuum between the influence of neutral and niche-related processes in shaping biodiversity spatial distributional patterns.Thus, the causal factors of beta diversity, that is the biodiversity variation between communities, can be disentangled into a pure spatial (PS), a pure environmental (PE), and a spatially structured environmental (SSE) component through variation partitioning (Peres-Neto et al. 2006). The first two components may be directly related to neutral processes and environmental filtering, respectively. Variation not explained by these three components (the residuals of variation partitioning) may be due to other sources of stochasticity (e.g. environmental stochasticity) if one can assume that, when analysing the data, no important environmental variable was left out (Sattler et al. 2010).

The importance of neutral processes, niche-related processes and stochasticity for taxononomic diversity variation between communities, gauged in this way, is known to vary across scales (Jombart et al. 2009) and taxa (Lindo and Winchester 2009, Sattler et al. 2010, Leduc et al. 2012). Furthermore, biodiversity is a multifaceted concept. Instead of investigating taxonomic diversity in itself, it is more informative to explore it together with functional and phylogenetic biodiversity (Cavender-Bares et al. 2009, Pavoine and Bonsall 2011). The distribution of diversity of functional traits can enlighten the ecological processes shaping biodiversity patterns, in the sense that individuals carrying these traits could be selected by environmental filters or by interspecific interactions, e.g. competition (Cavender-Bares et al. 2009, Pavoine and Bonsall 2011). Likewise, inferences on the evolutionary history of species and their adaptive response to environment can be based on the spatial distribution of phylogenetic lineages (Webb et al. 2002).

Coral reefs are among the most threatened marine systems. Reef fish are crucial to reef ecosystem maintenance, and humans hugely profit of them as food and for economic purposes, including recreation (Sale 2006). Although many studies have been searching for processes that contribute most to diversity variation between communities, few have focused on marine systems.

In this study our main goal was to understand the relative contributions of spatial variation and environmental heterogeneity to reef fish composition in the Western Atlantic Ocean. To reach this goal we explored the taxonomic, functional and phylogenetic aspects of biodiversity. We focused on answering the following questions: (1) How do reef fish functional traits and phylogenetic lineages vary between reefs compared to their taxonomic variation? (2) What portion of reef fish taxonomic, functional and phylogenetic variation between assemblages is due to Pure Spatial, Pure Environmental and Spatially Structured Environmental components? (3) Which environmental variables contribute more to explaining taxonomic, functional and phylogenetic fish beta diversity between reefs?

METHODOLOGY

Study Region

The study comprised 24 Western Atlantic (WA) reefs, distributed over two biogeographic regions, the South-Western Atlantic (which we will refer here as Brazil, BRA, to distinguish it from the entire Western Atlantic) and the Caribbean (CAR; Fig.1; Briggs 1974). The Brazilian reefs studied were: Abrolhos, Arraial do Cabo, Atol das Rocas, Guarapari Islands, Hump of Brazil, Ilha Grande, Laje de Santos, North of Bahia, Parcel Manuel Luiz, Noronha, Santa Catarina, São Paul’s Rocks, Trindade Island and Zumbi. The Caribbean reefs were: Bahamas, Bermuda, Cuba, Florida Keys, Georgia, Mexican Caribbean, Navassa, Pelican Cays, Saba and Tobago.

We analysed reef fish diversity variation in two spatial scales, in which the study extent varies but the grain remained the same. The larger scale included all WA reefs and the smaller scale focused on each biogeographical region in turn.

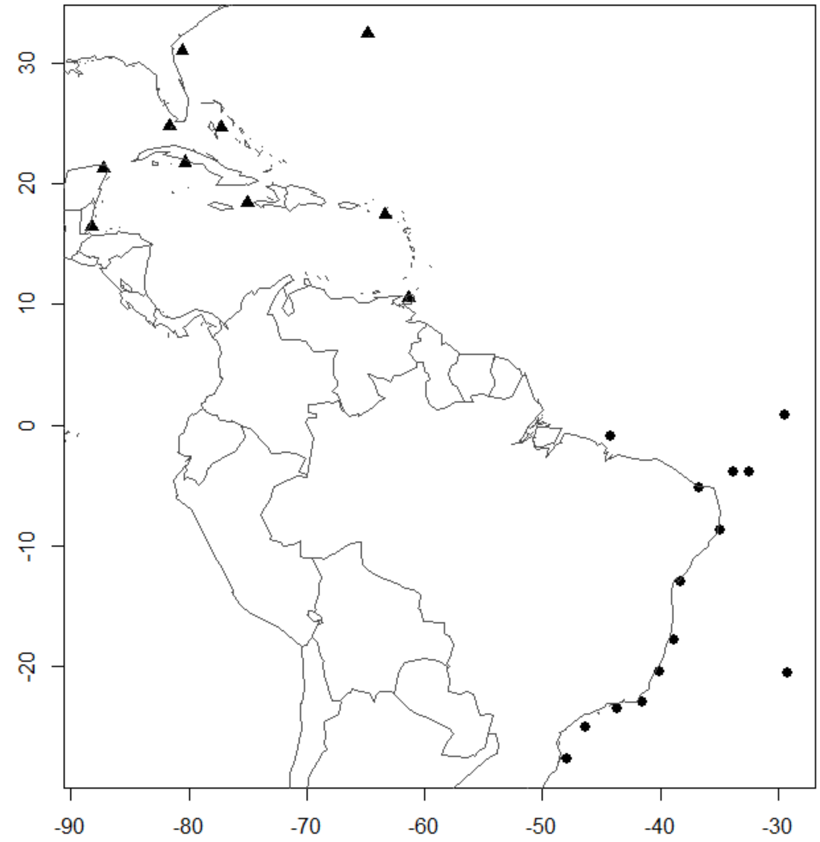


Figure 1. The ten Caribbean (CAR) reefs are represented by triangles and the fourteen Brazilian (BRA) reefs are represented by circles. Caribbean reefs are: Bahamas, Bermuda, Cuba, Florida Keys, Georgia, Mexican Caribbean, Navassa, Pelican Cays, Saba, Tobago; Brazilian reefs are: Abrolhos, Arraial do Cabo, Atol das Rocas, Guarapari Islands, Hump of Brazil, Ilha Grande, Laje de Santos, North of Bahia, Parcel Manuel Luiz, Noronha, Santa Catarina, São Paul’s Rocks, Trindade Island and Zumbi.

Biotic data

Knowledge of all reef fish phylogenetic relationships is uneven, so we focused on two reef fish families, Labridae (wrasses) and Pomacentridae (damselfish). These are among the major reef fish families, found in almost all reef environments and quite abundant (Bellwood 1996). There is much information available on their species functional traits and phylogenetic relatedness. Moreover, Labridae and Pomacentridae are ecologically quite distinct. Labridae species show great morphological variability, such as in body shape, size, mouth apparatus and coloration (Wainwright and Bellwood 2002). This variability suggests the occupancy of different niches, mainly related to diet and habitat preferences. In contrast, Pomacentridae species are more homogeneous in ecological traits and present less specialized dietary habits (Wainwright and Bellwood 2002).

The data on species composition of Labridae and Pomacentridae were extracted from the most comprehensive database on Atlantic reef fish to date (Halpern and Floeter 2008, Floeter et al. 2008). In total we analysed 51 species of Labridae and 22 species of Pomacentridae.

Data on species functional traits

Functional beta diversity was measured based on the maximum depth registered to a species, its maximum size and trophic group. Nevertheless, other important attributes may be considered in the future, such as mobility and position in the water column.

Many environmental conditions vary with sea depth, such as ultraviolet radiation, luminosity, temperature and dissolved oxygen concentration (Lalli and Parsons 1997, Brokovich et al. 2008). These can interfere directly or indirectly (via food and refuge availability) on reef fish survival and distribution (Brokovich et al. 2008). Given that, the maximum depth of a species represents its physiological and behavioural ability to deal with these environmental variations. Body size is related to organisms' temperature resistance, food intake and metabolism (Peters 1983). Furthermore, reef fish maximum body size has proved to be correlated with dispersal capacity, range sizes, demographic rates and association with the reef matrix (Munday and Jones 1998, Luiz et al. 2013). Therefore maximum living depth, maximum size and trophic group are very important in determining reef fish niches and their function in reef communities.

Data on reef fish species traits come from an ongoing compilation by Dr. Sergio Floeter and collaborators. Trophic groups were classified according to Mouillot et al. (2014). In Labridae and Pomacentridae only four of their seven categories are represented: Herbivore-detritivores, Omnivores, Planktivores and Mobile Invertebrates eaters.

Phylogenetic data

Phylogenetic beta diversity was calculated based on the phylogenetic composite tree for each family (Fig. 2). These dated trees were produced by combining phylogenies or relying on indication of sister-species, in the scientific literature or obtained by personal communication (Appendix 1).

Abiotic data

Data on several environmental variables were made available by Dr. Sergio Floeter. We assessed this data and selected those variables that, although not covering all relevant aspects, were the most likely to affect fish diversity variation between reefs. These are: 1) coral richness, 2) reef area, 3) sea surface temperature (SST) and 4) diffuse attenuation of light (DA; Table 1).

Beta diversity measures

We measured the taxonomic, functional and phylogenetic beta diversity between pairs of reefs for each fish family (Fig. 2).

In order to calculate the functional betadiversity between communities we constructed a matrix of functional distances between each pair of species using the Mixed-variable coefficient of distance (Fig. 2;Pavoine et al. 2009). This coefficient is a generalization of Gower distance (Gower and Legendre 1986) which allows calculating distances between objects based on different types of descriptor variables (quantitative and qualitative).

Table 1. Description of environmental variables used to compute for diversity variation partition.

Variable Class	**Variable Measured**	**Description**
Coral	**Richness (n)**	Number of coral species.
Area	**Total shelf (km²)**	Area of the sea-bottom down to 200m depth. Obtained using SRTM30_PLUS bathymetry (Shuttle Radar Topography Mission).
	Coast length (km)	Coastline length. Obtained using SRTM30_PLUS bathymetry (Shuttle Radar Topography Mission).
SST	**Mean (ºC)**	Average of annual means from 2002 to 2009, calculated from monthly averages. Obtained from the Bio-ORACLE database (Tyberghein et al. 2012).
	Range (ºC)	Average of annual ranges from 2002 to 2009, calculated from monthly averages. Obtained from the Bio-ORACLE database (Tyberghein et al. 2012).
DA	**Mean (m^{-1})**	Monthly mean diffuse attenuation of light from 2002 to 2009, obtained from Aqua-MODIS (Feldman & McClain; 2010).

Based on (1) the species incidence matrices, (2) the phylogenetic composite trees and (3) the first two axes of a Principal Coordinates Analysis (PCOA) of the functional distances, we used the Jaccard index of beta diversity and its turnover component (Baselga 2010) to account for taxonomic, functional and phylogenetic diversity variation between reefs (Fig. 2). The Jaccard index of beta diversity emphasizes variation among the terminal branches of the phylogeny or functional dendogram (Swenson 2011), whereas its turnover component adjusts for differences in richness between communities (Baselga 2010). From here on, "Turnover component" will stand for this "Turnover component of the Jaccard index of beta diversity". Both the Jaccard index and the Turnover component were calculated using the R code provided by Leprieur et al. (2012).

The functional and phylogenetic beta diversity measures were rescaled to each potential maximum value. Given that, each pair of islands can show functional and phylogenetic beta diversity values that are higher than the taxonomic one.

Analysis

In order to test for differences on the Beta diversity values between each aspect of biodiversity (taxonomic, functional and phylogenetic) we ran permutation tests on the difference between medians.

We partitioned fish diversity variation between reefs into environmental and spatial components using distance-based Redundancy Analysis (Fig. 3; Legendre and Anderson 1999). We tested only for environmental and spatial linear effects on beta diversity and ran a separate analysis for each reef fish family.

We ran a PCOA with the beta diversity values and used all its vectors as the measure of reef fish compositional variation (Fig. 3). The spatial components were analysed as Distance-based Moran's eigenvector maps (dbMEM) vectors, which are flexible for the distance measures to be used and more appropriate for irregular sampling designs (Fig. 2; Legendre and Legendre 2012). Since we were only interested in analysing the effect of positive spatial correlation on beta diversity partitioning, following Legendre and Legendre (2012) we retained only the eigenfunctions whose Moran's I value exceeded E(I), their expected value (Fig. 2).

To represent the environmental component we used axes of a Principal Component Analysis (PCA) of the standardized environmental variables (Fig. 2). The same methodology was employed twice, with a small modification. The first instance was used to assess the influence of environmental and spatial components on diversity variation. For this, we included in the PCA all the environmental variables and used the axes which cumulatively explained more than the same number of variables in a broken-stick random partitioning of the data (MacArthur 1957). The second instance was used to identify the most important environmental variables on shaping beta diversity patterns. We ran this analysis separately for each class of environmental variable (coral, area and SST). In each one we included in the PCA only the variables of the environmental class in question and used the axes that accounted for at least 80% of the explained variance. Finally, we tested the significance of the fractions by running permutation tests of the simple and partial Redundancy Analysis (Legendre and Legendre 2012).

RESULTS

Reef fish beta diversity

Reef fish taxonomic composition varied greatly between reefs. Taxonomic beta diversity was greater than phylogenetic beta diversity, which in turn was greater than functional beta diversity (Fig. 4). There were two exceptions: first, the Turnover component for both families in the Caribbean (CAR), where all beta diversity measures were very close to zero; second, the full Jaccard index for Pomacentridae in the Brazilian region (BRA), in which the values of functional and phylogenetic beta diversities were equivalent (Fig. 4). The most prominent difference between families is the functional beta diversity in the full index, which were strikingly higher for pomacentriids than for labriids.

Similarly to the partition of the Turnover component of all diversity aspects in the Caribbean, functional beta diversity showed values very close to zero when accounting for the Turnover component, in the entire Western Atlantic or in either biogeographical region. In such cases, due to these low values, we deemed it inappropriate to partition the fish diversity variation between reefs based on the Turnover component. Therefore we will only show the results of variation partition of the Turnover component when it attained a sizeable value, i.e. for Taxonomic and Phylogenetic beta diversity in WA and BRA.

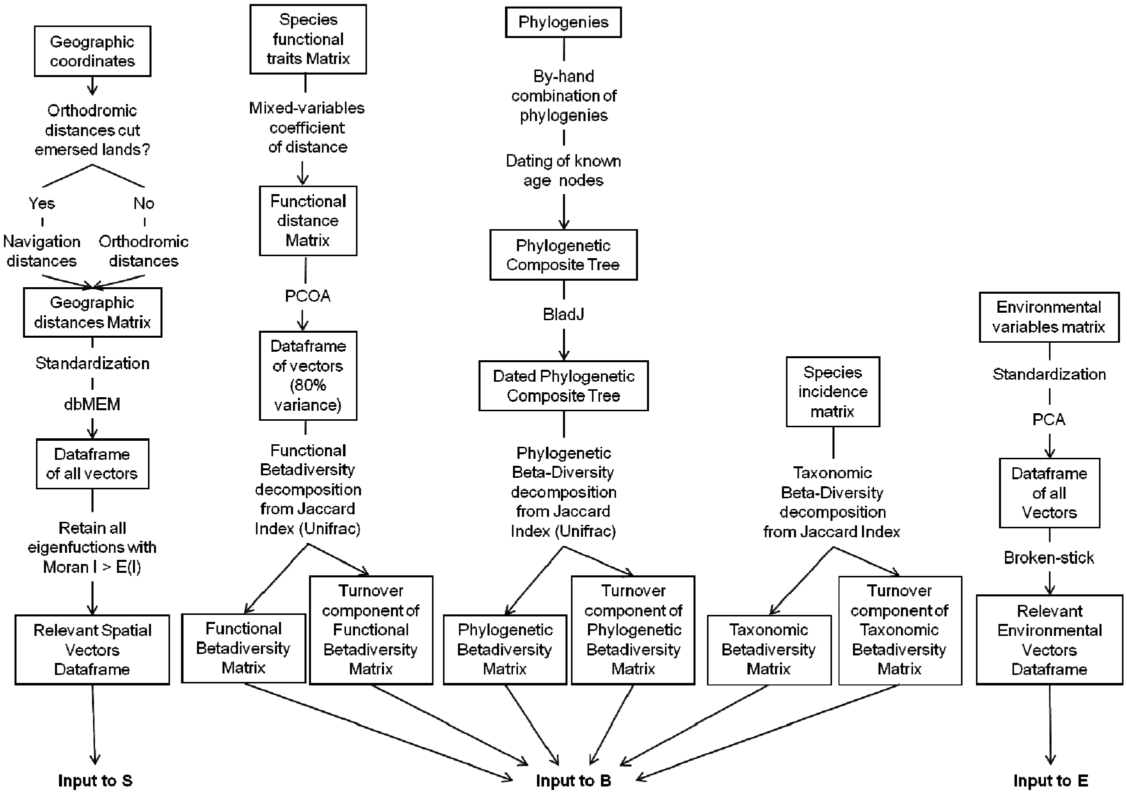


Figure 2. Flow chart of organization of data of beta diversity, environmental and spatial position prior to analysis. The final dataframes or matrices of this flow chart were inputed in the respective places in Figure 3, being S for Spatial, B for Beta diversity and E for Environment.

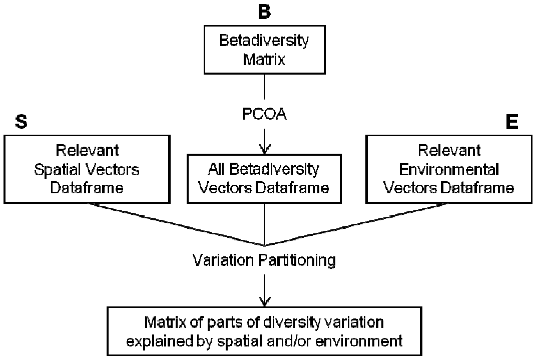


Figure 3. Flow chart of analyses in the study. The letters S (Spatial), B (Beta diversity) and E (Environment) represent the origin of the initial dataframes or matrices used in this analysis, which were produced through the methodology showed on Figure 2.

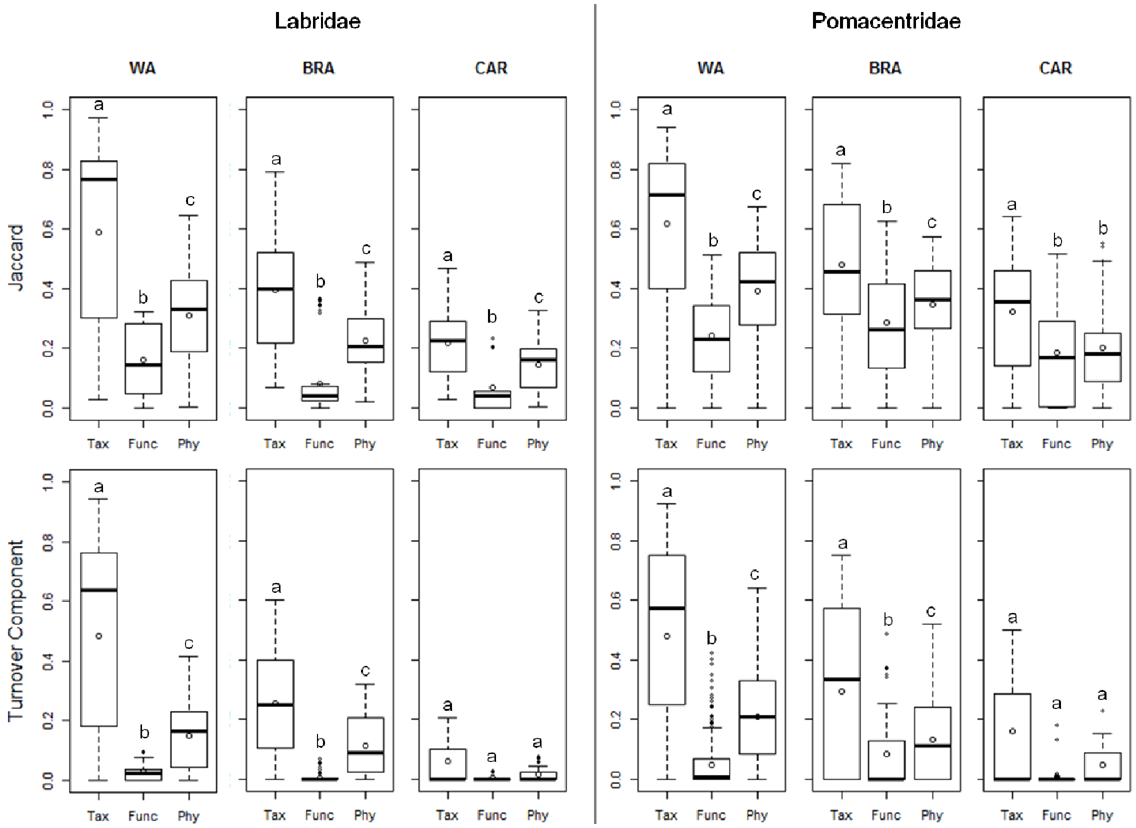


Figure 4. Box plot of the distribution of Labridae and Pomacentridae taxonomic (Tax), functional (Func) and phylogenetic (Phy) beta diversities measured between each pair of reefs in the Western Atlantic (WA), Brazil (BRA) and Caribbean (CAR). The first row shows the full Jaccard index of beta diversity and the second one shows its Turnover component. Different letters (a, b and c) in each frame represent differences on the beta diversity measures between each aspect of biodiversity (taxonomic, functional and phylogenetic).

Effects of space and environment on reef fish diversity variation partitioning

With few exceptions, environment and/or space significantly explained a large portion of Labridae and Pomacentridae beta diversity (Fig. 5). As a rule, the PE component explained proportionally more of reef fish diversity variation than the spatial component (Fig. 5).

In the Western Atlantic and Brazil, the Spatially Structured Environment (SSE) represented a large share in Labridae variation partitioning and in Pomacentridae, taxonomic and phylogenetic variation partitioning (Fig. 5). However, for all beta diversity measures in the Caribbean and for Pomacentridae functional beta diversity (at both scales and in either biogeographical region), the SSE component showed negligible values, most of them negative (Appendix 2).

When comparing the two families, within the full Jaccard index there was a noticeable difference in the amount of functional beta diversity explained by the environment in the Western Atlantic and Caribbean. In the Western Atlantic, functional beta diversity was best explained for Labridae (residuals were 0.19) and much less so for Pomacentridae (residuals were 0.69; Appendix 2, Fig. 5), especially due to the lack of a SSE component in the functional diversity variation of Pomacentridae. In the Caribbean, environmental factors also explained a sizable fraction of Labrid functional beta diversity, whereas they did not explain any variation of Pomacentrid functional beta diversity.

Patterns were the same when partitioning the full Jaccard or its Turnover component.

Best environmental predictor

Reef coral richness explained a major portion of beta diversity of both Labridae and Pomacentridae in the Western Atlantic (Fig. 6). Compared to other beta diversity measures of both families, Pomacentridae functional beta diversity was less explained by coral (Fig. 6). More than half of the variation explained by corals in the WA was spatially structured (Fig. 6). Reef area also significantly explained diversity variation between reefs in the WA. However, the effect of area disappeared when partitioning the Turnover component.

In the Brazilian province, environmental predictors that best explained diversity variation greatly differed between families and beta diversity measures. Taxonomic beta diversity of both fish families was significantly related to all variables when partitioning the full Jaccard index; however, coral richness did not explain taxonomic beta diversity for the Turnover component (Fig. 6). Labrid functional beta diversity was significantly explained by coral richness, reef area and SST, whereas Pomacentridae functional beta diversity was explained only by coral richness and SST (Fig. 6). Labrid phylogenetic beta diversity was only related to reef area in the full Jaccard index. However, no environmental variable explained the Turnover component of Labrid phylogenetic beta diversity (Fig. 6). Pomacentrid phylogenetic beta diversity was significantly related to all variables, regardless of the measure of beta diversity applied (full Jaccard or Turnover component; Fig. 6). However, the fraction of the Turnover component of Pomacentrid phylogenetic beta diversity explained by SST was quite low (Fig. 6).

In the Caribbean, all aspects of Labrid beta diversity were strongly and solely influenced by reef area (Fig. 6). On the other hand, for Pomacentridae only taxonomic beta diversity was significantly explained by an environmental variable, which was also reef area (Fig. 6).

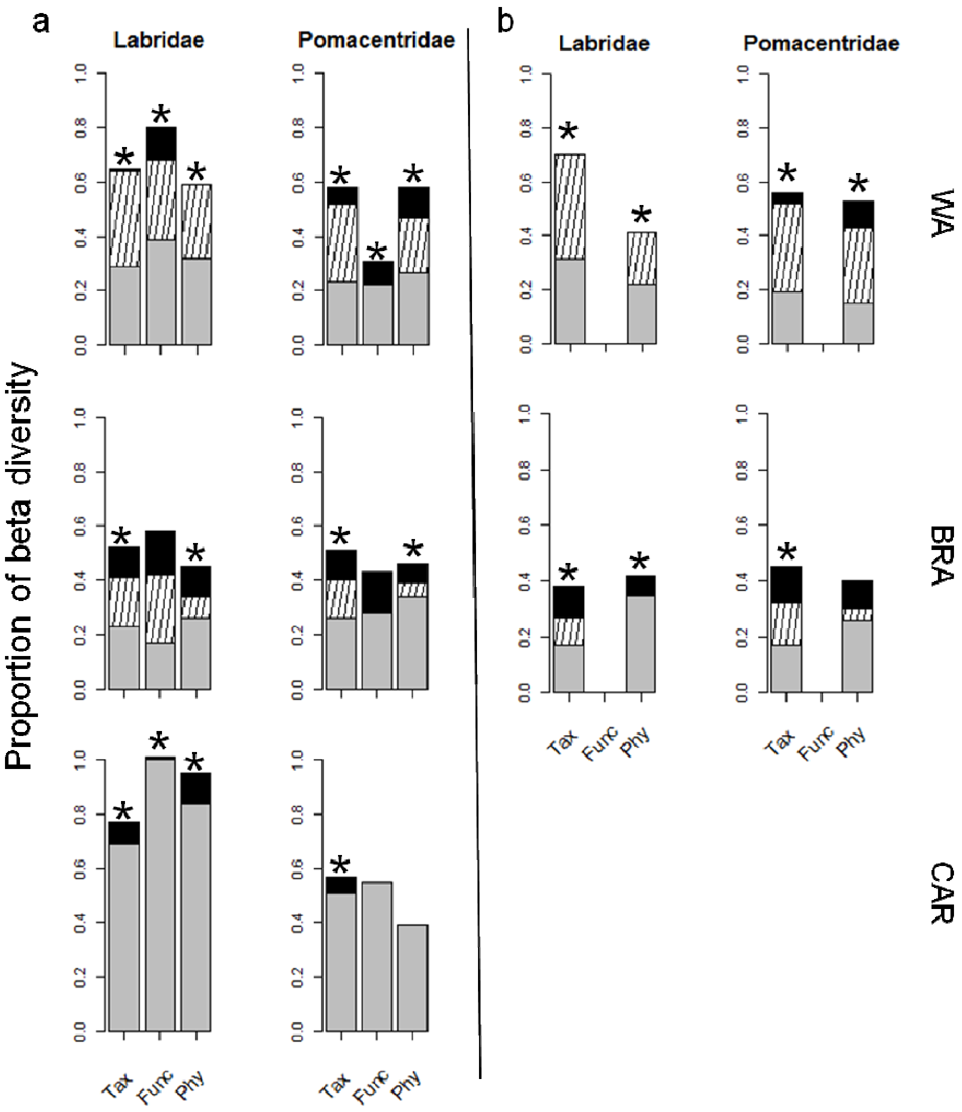


Figure 5. Proportion of Labridae and Pomacentridae taxonomic (Tax), functional (Func) and phylogenetic (Phy) beta diversity explained by a pure environmental (grey), spatially structured environmental (crosshatched) and pure spatial (black) components in the Western Atlantic (WA), Brazil (BRA) and Caribbean (CAR). Stars represent significant values of the set of components of each bar. (a) Partitioning of the full Jaccard index of beta diversity; (b) Partitioning of the Turnover component in cases where the median was considerably different from zero, that is, for Taxonomic and Phylogenetic beta diversity in WA and BRA.

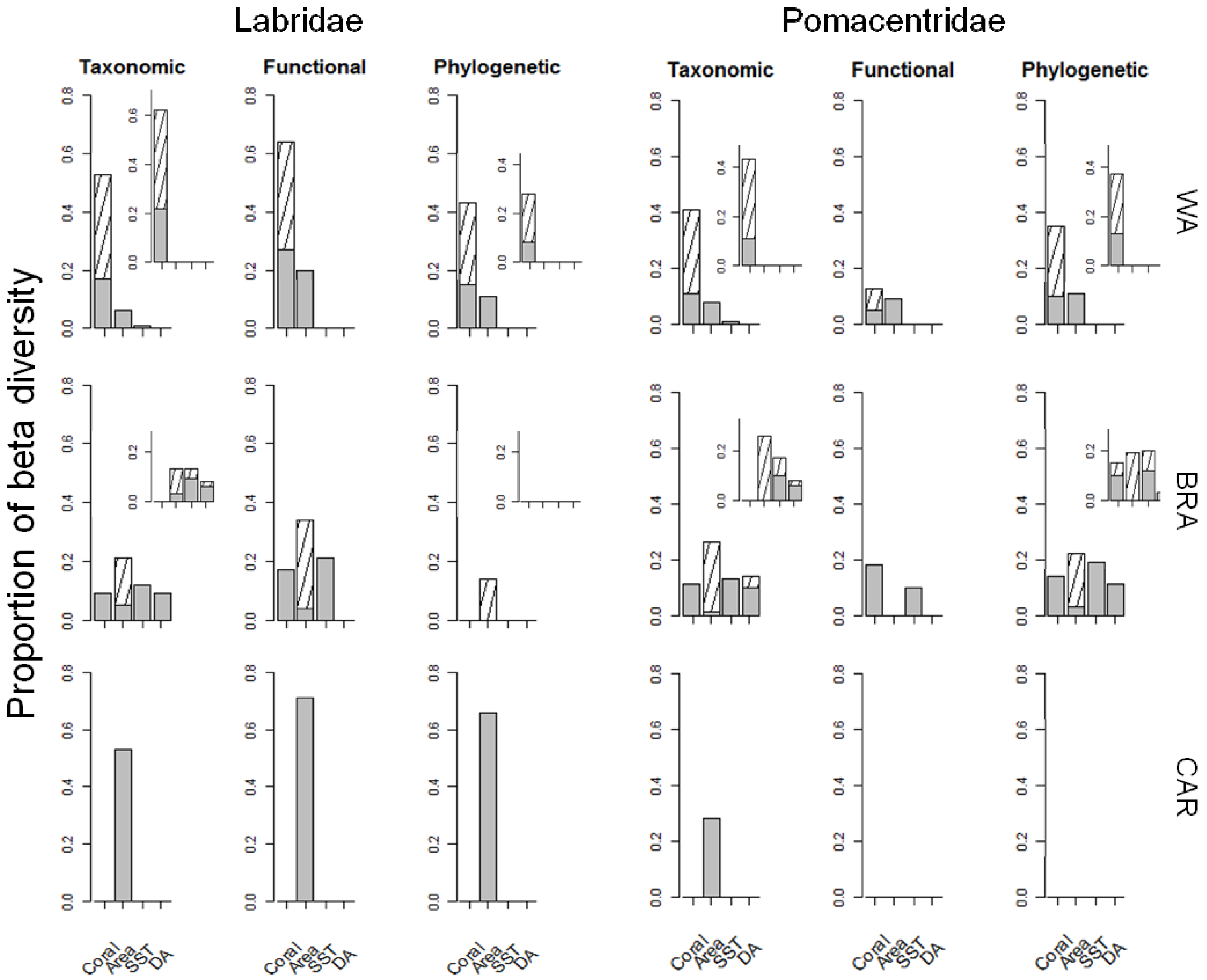


Figure 6. Proportion of Labridae and Pomacentridae taxonomic, functional and phylogenetic beta diversity explained by a pure environmental (grey) or spatially structured environment (crosshatched) components in the Western Atlantic (WA), Brazil (BRA), and Caribbean (CAR). Environmental variables considered were Coral, Area, Sea Surface Temperature (SST) and Diffuse Attenuation of light (DA). Large graphs show components of the full Jaccard beta diversity partition. The inserts represent the components of the Turnover component partition when applicable.

DISCUSSION

Reef fish beta diversity

The low values of functional beta diversity between reefs, despite high taxonomic beta diversity values indicate that, even with changes in species composition, the ecological niches these species occupy tend to be more preserved among reef fish assemblages. This also applies to variation of lineages between assemblages, although less markedly, which suggests that lineages are not strongly restricted to the places where they arose.

When compared to pomacentrids, labriids showed lower values of functional beta diversity inside each biogeographic region when considering the full Jaccard index. We ascribe this low values of labriid beta diversity inside each biogeographic region to the labriids greater variability of body sizes and maximum depths (about 6 and 3 times more variation respectively), and to their higher feeding behaviour specialization, which may allow greater sympatry between labriid species (Longnecker, 2007), since they are able to explore more diverging niches. Among the labriid species included in this study, about 50% have specialized habits of foraging for mobile invertebrates, 36% are herbivores/detritivores that belong to different specialized subgroups (scrapers, excavators and browsers) and the remaining 14% are planktivores. On the other hand, 20% of the Pomacentridae species in this study are omnivores, 34% planktivores and the remaining 48%, although being classed as herbivores, are less specialized, feeding on algae and/or detritus. However, it is not cautious to make inferences about the cooccurance of feeding behaviours based only on beta diversity patterns, and this work will, in the near future, explore patterns of alfa and gama diversity.

The smaller values of the Turnover component suggest that the variation of species, ecological traits and lineages between reefs is partly driven by differences in species richness. However, in the

WA and Brazil, except for functional diversity, there is still substantial beta diversity independent of richness.

Processes shaping diversity distribution in the Caribbean seem to be quite distinctive. There is less diversity variation between Caribbean reefs in comparison to other regions and the Turnover component is virtually nil.

Spatial and environmental effects on reef fish diversity variation partitioning

Reef spatial location and/or their environmental features explained a large share of fish diversity variation between assemblages. The influences of environment and spatial location on reef fish diversity variation could not be fully disentangled when analysing the WA or Brazil, due to high spatial autocorrelation of environmental variables. However, the observed result that the pure environmental (PE) component exceeds the pure spatial component (PS) suggests that the environment is locally filtering species for which each combination of reef conditions is more suitable. Furthermore, this also suggests that the pressure exerted by environmental filters is probably stronger than that exerted by dispersal limitation or ecological drift. It has already been shown that reef fish have wide dispersal capacity (Kinlan and Gaines 2003) and their species richness on islands is not restricted by island isolation (Hachich et al. in press). Thus, our results indicate that although reef fish species successfully disperse to other Atlantic reefs, they fail to colonize unsuitable environments (Floeter et al. 2008).

The PE also accounted for a larger share of functional and phylogenetic diversity variation than PS. Ecological traits are also being filtered by the environment, though at different intensity comparing the two families, as discussed below. The influence of environment on reef fish evolutionary lineages, together with the previously reported lack of evidence for adaptative radiation on wrasses (Alfaro et al. 2009), may denote a faster diversification of lineages when compared to the pace of niche evolution, so that closely related species occupy the same niches (Eiserhardt et al. 2013). Although there is some evidence for phenotypic convergence in Pomacentrid evolution (Frédérich et al. 2013), this seems not to be noticeable within Atlantic species in particular. However, further studies should better explore reef fish niche evolution in the Atlantic Ocean.

The reason why environmental variables explained less of pomacentrid functional betadiversity in the WA is likely due to their diets. Pomacentrids are more generalistic and they are probably more plastic, hence more resilient to environmental variation (Bernhardt and Leslie 2013). On the other hand, although high specialization allows assemblages of Labriidae to be more homogenous as to functional traits, due to niche partitioning, it also makes them more susceptible to environmental constraints. This may be the reason why functional beta diversity of labriids was largely explained by environmental variables. But, again, to confirm these hypotheses a study on the patterns of alfa and gama diversity is needed.

Effectiveness of environmental predictors

With regard to the best environmental predictor of reef fish diversity variation, patterns varied markedly between scales and biogeographical regions. However, there were also differences between families and, in the Western Atlantic, between biodiversity modes.

It is worth noting that, in the WA, coral richness proved to be important in determining the variation of fish composition between reefs. This suggests that reef fish diversity distribution in the

WA may be more sensitive to environmental changes driven by climatic variations and anthropic activity that leads to coral bleaching.

In the Brazilian province, although the combination of all environmental variables failed to explain functional beta diversity between reefs, it was significantly explained by each variable alone. Coral richness, reef area or SST alone explained labrid functional beta diversity, whereas coral richness or SST alone explained pomacentrid functional beta diversity.

There was no substantial Turnover component in the Caribbean, whereas the full Jaccard index was only explained by area. Since reef fish species richness is highly dependent on reef area (Hachich et al. in press), it is quite likely that the strong area component of reef fish taxonomic diversity variation in this region is mainly due to variation of species richness between these reefs. Moreover, the complexity of habitats added by area probably supports the maintenance of more functional traits in larger reefs.

In summary, the particular processes that determine reef fish composition in the Caribbean lead to a more homogenous distribution of species, functional groups and phylogenetic lineages than in the Brazilian region. Therefore reef fish compositional variation in the Caribbean is probably due to marked differences in richness driven by variation of reef size, while in the Brazilian province reef fish composition varies independently of richness and is driven by differences in coral richness, SST and also reef area.

CONCLUSION

In this study we showed that, although reef fish taxonomic diversity varies greatly between assemblages, phylogenetic lineages and especially functional groups, tend to be much more constant among reefs.

Much of the beta diversity between reefs is due to variation in species richness. Except for such differences in species richness, Caribbean reefs are more homogenous in species, functional groups and lineages. Conversely, the large-scale Western Atlantic and the Brazilian region show more variation in species composition among reefs, which can be ascribed to environmental variation. The environmental aspect that best explains the diversity variation between reefs is coral richness in the Western Atlantic, and coral richness again, in addition to reef area and SST, in Brazil.

We also showed that, in general, the variation of reef fish composition in reefs in the western region of the Atlantic Ocean is mainly driven by environmental filters and weakly influenced by processes that cause spatial autocorrelation of species distributions. Nonetheless, to a large extent, diversity variation was driven by a combination of environmental and spatially related processes.

The environmental variables that best explained reef fish beta diversity between assemblages were manifestly distinct, especially between scales and biogeographical regions. We therefore suggest that the configuration of each reef system is crucial to produce reef fish distribution patterns. Thus, beyond the important role of environmental filters that proved to be general, those environmental variables that lead to compositional dissimilarity between reefs are idiosyncratic to each reef and region.

ACKNOWLEDGEMENTS

We are grateful for the help of Luiz Rocha with the construction of phylogenetic composite trees, Mariana Bender with the organization of species functional traits and island environmental variables, Leonardo Jorge and Thiago Gonçalves-Souza with R programming and statistical analyses, and to Renato Morais and Alexandre Siqueira for discussions about reef fish ecology. We also thank FAPESP and CAPES for financial support.

REFERENCES

Alfaro, M. E. et al. 2009. Does evolutionary innovation in pharyngeal jaws lead to rapid lineage diversification in labrid fishes? - BMC Evol. Biol. 9: 255.

Barton, P. S. et al. 2013. The spatial scaling of beta diversity. - Glob. Ecol. Biogeogr. 22: 639–647.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. - Glob. Ecol. Biogeogr. 19: 134–143.

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

Bernhardt, J. R. and Leslie, H. M. 2013. Resilience to climate change in coastal marine ecosystems. - Ann. Rev. Mar. Sci. 5: 371–92.

Briggs, J. C. 1974. Marine Zoogeography. - McGraw-Hill.

Brokovich, E. et al. 2008. Descending to the twilight-zone⍰: changes in coral reef fish assemblages along a depth gradient down to 65 m. - Mar. Ecol. Prog. Ser. 371: 253–262.

Cavender-Bares, J. et al. 2009. The merging of community ecology and phylogenetic biology. - Ecol. Lett. 12: 693–715.

Eiserhardt, W. L. et al. 2013. Dispersal and niche evolution jointly shape the geographic turnover of phylogenetic clades across continents. - Sci. Rep. 3: 1164.

Floeter, S. R. et al. 2008. Atlantic reef fish biogeography and evolution. - J. Biogeogr. 35: 22–47.

Frédérich, B. et al. 2013. Iterative ecological radiation and convergence during the evolutionary history of damselfishes (Pomacentridae). - Am. Nat. 181: 94–113.

Gower, J. C. and Legendre, P. 1986. Metric and Euclidean properties of dissimilarity coefficients. - J. Classif. 3: 5–48.

Hachich, N. F. et al. Island biogeography: patterns of marine shallow-water organisms in the Atlantic Ocean.

Halpern, B. and Floeter, S. 2008. Functional diversity responses to changing species richness in reef fish communities. - Mar. Ecol. Prog. Ser. 364: 147–156.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography.

Jombart, T. et al. 2009. Finding essential scales of spatial variation in ecological data: a multivariate approach. - Ecography (Cop.). 32: 161–168.

Keddy, P. a. 1992. Assembly and response rules: two goals for predictive community ecology. - J. Veg. Sci. 3: 157–164.

Kinlan, B. P. and Gaines, S. D. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. - Ecology 84: 2007–2020.

Lalli, C. M. and Parsons, T. R. 1997. Biological Oceanography an Introduction. - Elsevier.

Leduc, D. et al. 2012. Nematode beta diversity on the continental slope of New Zealand: spatial patterns and environmental drivers. - Mar. Ecol. Prog. Ser. 454: 37–52.

Legendre, P. and Anderson, M. J. 1999. Distance-based Redundancy Analysis: testing multispecies responses in multifactorial ecological experiments. - Ecol. Monogr. 69: 1–24.

Legendre, P. and Legendre, L. 2012. Numerical ecology. - Elsevier.

Leprieur, F. et al. 2012. Quantifying phylogenetic beta diversity: Distinguishing between “true” turnover of lineages and phylogenetic diversity gradients. - PLoS One in press.

Lin, G. et al. 2013. Separating the Effects of Environment and Space on Tree Species Distribution: From Population to Community. - PLoS One in press.

Lindo, Z. and Winchester, N. N. 2009. Spatial and environmental factors contributing to patterns in arboreal and terrestrial oribatid mite diversity across spatial scales. - Oecologia 160: 817–825.

Longenecker, K. 2007. Devil in the Details: High-resolution Dietary Analysis Contradicts a Basic Assumption of Reef-Fish Diversity Models. Copeia 3: 543 – 555.

Luiz, O. J. et al. 2013. Adult and larval traits as determinants of geographic range size among tropical reef fishes. - Proc. Natl. Acad. Sci. U. S. A. 110: 16498–16502.

MacArthur, R. H. 1957. On the relative abundance of bird species. - Proc. Natl. Acad. Sci. U. S. A. 43: 293–295.

Mouillot, D. et al. 2014. Functional over-redundancy and high functional vulnerability in global fish faunas of tropical reefs. - Proc. Natl. Acad. Sci. in press.

Munday, P. L. and Jones, G. P. 1998. The Ecological Implications of Small Body Size Among Coral-reef Fishes. - Oceanogr. Mar. Biol. an Annu. Rev. 36: 373–411.

Pavoine, S. and Bonsall, M. B. 2011. Measuring biodiversity to explain community assembly: a unified approach. - Biol. Rev. Camb. Philos. Soc. 86: 792–812.

Pavoine, S. et al. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. - Oikos 118: 391–402.

Peres-Neto, P. R. et al. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. - Ecology 87: 2614–2625.

Peters, R. H. 1983. The ecological implications of body size.

Sale, P. F. 2006. The science we need to develop for more effective management. - In: Sale, P. F. (ed), Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. Academic Press, pp. 549.

Sattler, T. et al. 2010. Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. - Ecology 91: 3343–3353.

Swenson, N. G. 2011. Phylogenetic beta diversity metrics, trait evolution and inferring the functional beta diversity of communities. - PLoS One 6: e21264.

Wainwright, P. C. and Bellwood, D. R. 2002. Ecomorphology of Feeding in Coral Reef Fishes. - Mar. Biol. in press.

Webb, C. O. et al. 2002. Phylogenies and Community Ecology. - Annu. Rev. Ecol. Syst. 33: 475–505.

3.1. APPENDIX S1. CONSTRUCTION OF LABRIDAE AND POMACENTRIDAE PHYLOGENETIC COMPOSITE TREES

We constructed one phylogenetic composite tree for each family. The phylogenetic composite trees first included as tips all the species of that family that were presented in at least one phylogeny. Nodes with known age were dated. When there was a range of possible ages for a node (e.g. sepation between *Clepticus* species, Beldade et al., 2009) the middle age was used. The remaining nodes were than dated by age interpolation, using the Bladj (Branch Lenth Adjuster) algorithm of Phylocom (Webb et al. 2008). Finaly, we removed from the composite trees those species that were not present on at least one of the studied reefs.

Labridae phylogenetic composite tree (Fig 1) first incorporated all species of Cowman *et al.* (2009) phylogeny, which was used to arrange the position of the main tribes. Phylogenies of subgroups were then added to this structure, following: 1) Hanel *et al.* (2002) for species of the tribe Labrini; Bernardi *et al.* (2004) for those of genus *Thalassoma* and *Gomphosus*, Beldade *et al.* (2009) for *Clepticus*, Gomon (2006) for *Bodianus*, Robertson *et al.* (2006) for Sparisoma, Barber & Bellwood (2005), Rocha *et al.* (2010) and Luiz-Jr *et al.*(2009) for *Halichoeres* and, finally, Smith *et al.* (2008) and Choat *et al.* (2012) for parrotfish.

In cases in which there was more than a single phylogeny of the same group, we first incorporated in the composite tree those phylogenies containing more taxa and for which more genes were used in its construction. The same priority order was used when solving conflicts between different phylogenies.

We dated the phylogenetic composite tree using ages of compatible nodes showed on Cowman *et al.* (2009) and Smith *et al.* (2008). Moreover, minor datings were made according to

Beldade *et al.*, (2009; for *Clepticus*) and Aurelle *et al.* (2003); for separation between *Coris julis* and *C. atlantica*).

Pomacentridae phylogenetic composite tree (Fig 2) construction and dating were based on Frédérich *et al.* (2013), to which were added taxa of phylogenies provided by Luiz Rocha (*pers. comm.*).

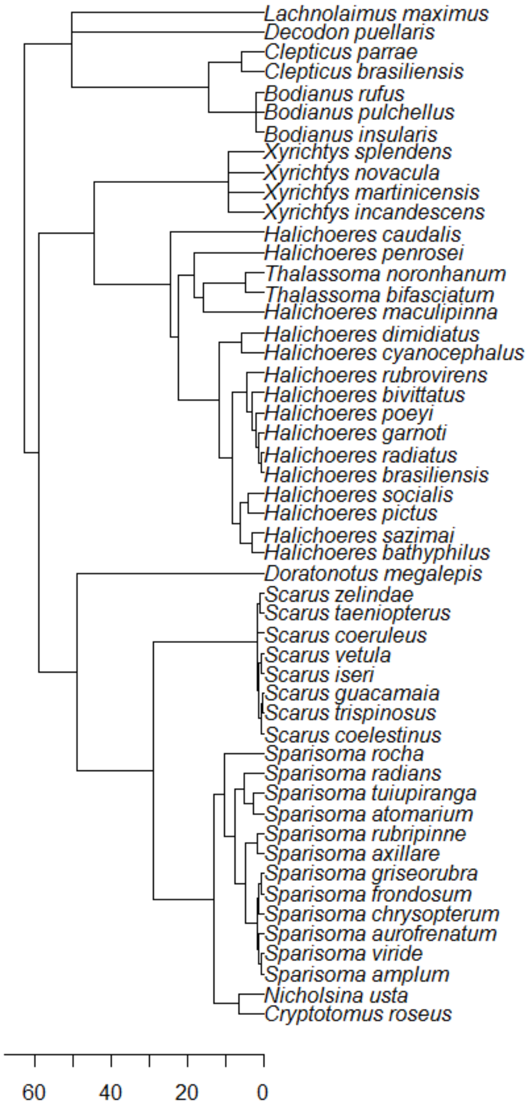


Figure 1. Labridae phylogenetic composite tree with ages.

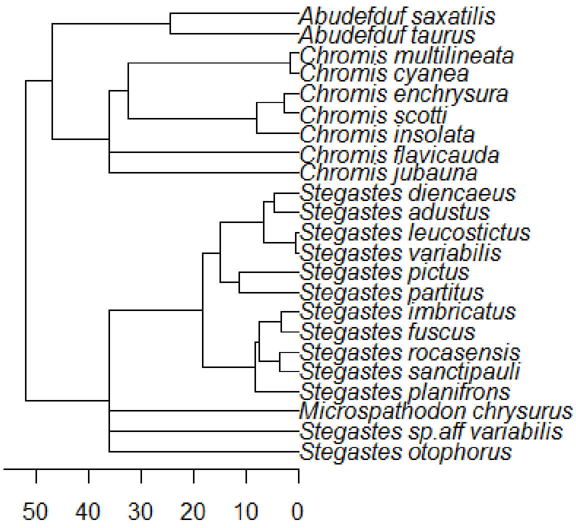


Figure 2. Pomacentridae phylogenetic composite tree with ages.

REFERENCES

Aurelle, D. 2003. Genetic study of Coris julis (Osteichtyes, Perciformes, Labridae) evolutionary history and dispersal abilities. - C. R. Biol. 326: 771–785.

Barber, P. H. and Bellwood, D. R. 2005. Biodiversity hotspots: evolutionary origins of biodiversity in wrasses (Halichoeres: Labridae) in the Indo-Pacific and new world tropics. - Mol. Phylogenet. Evol. 35: 235–53.

Beldade, R. et al. 2009. Historical biogeography and speciation in the Creole wrasses (Labridae, Clepticus). - Mar. Biol. 156: 679–687.

Bernardi, G. et al. 2004. Evolution of coral reef fish Thalassoma spp. (Labridae). 1. Molecular phylogeny and biogeography. - Mar. Biol. 144: 369–375.

Choat, J. H. et al. 2012. Patterns and processes in the evolutionary history of parrotfishes (Family Labridae). - Biol. J. Linn. Soc. 107: 529–557.

Cowman, P. F. et al. 2009. Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs. - Mol. Phylogenet. Evol. 52: 621–631.

Frédérich, B. et al. 2013. Iterative ecological radiation and convergence during the evolutionary history of damselfishes (Pomacentridae). - Am. Nat. 181: 94–113.

Gomon, M. F. 2006. A revision of the labrid fish genus Bodianus with descriptions of seven new species. - Rec. Aust. Museum, Suppl. 30: 1–133.

Hanel, R. et al. 2002. Phylogenetic relationships, evolution of broodcare behavior, and geographic speciation in the wrasse tribe Labrini. - J. Mol. Evol. 55: 776–89.

Luiz-Júnior, O. J. et al. 2009. Halichoeres sazimai, a new species of wrasse (Perciformes: Labridae) from the Western South Atlantic. - Zootaxa: 37–46.

Robertson, D. R. et al. 2006. Mechanisms of speciation and faunal enrichment in Atlantic parrotfishes. - Mol. Phylogenet. Evol. 40: 795–807.

Rocha, L. A. et al. 2010. Description of Halichoeres rubrovirens, a new species of wrasse (Labridae: Perciformes) from the Trindade and Martin Vaz Island group, southeastern Brazil, with preliminary mtDNA molecular phylogeny of New World Halichoeres. - Zootaxa 2422: 22 – 30.

Smith, L. L. et al. 2008. Phylogenetic relationships and the evolution of regulatory gene sequences in the parrotfishes. - Mol. Phylogenet. Evol. 49: 136–152.

Webb, C. O. et al. 2008. Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. - Bioinformatics 24: 2098–2100.

3.2. APPENDIX S2. VARIATION PARTITIONING COMPONENTS AND COEFICIENT OF SIGNIFICANCE VALUES

The values of spatial and environment components of Labridae reef fish diversity variation are shown in Table 1, those of Pomacentridae are show in Table 2.

Tabela 1. Labridae diversity variation partitioning into Spatial (S) and Environmental (E) components at the Western Atlantic (WA), South-Western Atlantic (referred herein as Brazilian Province - BRA) and Caribbean (CAR). Uppercases represent the total variation explained by a variable. Lowercases indicate the pure effects, i.e. the variation explained by the variable alone, controling for the interaction between environment and space (S*E). Residuals (res) and coefficients of significance values (p) are shown. Significant values are in bold letters.

	Beta	S	p(S)	s	p(s)	E	p(E)	e	p(e)	S*E	res
WA	**T**	**0.36**	**0.005**	**0.06**	**0.022**	**0.58**	**0.005**	**0.28**	**0.005**	0.29	0.36
	F	**0.41**	**0.005**	**0.23**	**0.005**	**0.58**	**0.005**	**0.40**	**0.005**	0.18	0.19
	P	**0.26**	**0.010**	0.02	0.250	**0.52**	**0.005**	**0.28**	**0.005**	0.24	0.46
BRA	**T**	**0.28**	**0.005**	**0.11**	**0.031**	**0.30**	**0.005**	**0.13**	**0.026**	0.17	0.59
	F	**0.41**	**0.043**	0.14	0.080	**0.43**	**0.015**	0.17	0.078	0.26	0.43
	P	**0.20**	**0.013**	0.03	0.330	**0.21**	**0.015**	0.04	0.260	0.16	0.76
CAR	**T**	-0.03	0.460	0.04	0.200	**0.40**	**0.026**	**0.47**	**0.015**	-0.07	0.56
	F	-0.10	0.640	-0.04	0.550	**0.54**	**0.005**	**0.60**	**0.005**	-0.06	0.50
	P	0.00	0.320	**0.11**	**0.036**	**0.56**	**0.015**	**0.67**	**0.010**	-0.12	0.33

Tabela 2. Pomacentridae diversity variation partitioning into Spatial (S) and Environmental (E) components at the Western Atlantic (WA), South-Western Atlantic (referred herein as Brazilian Province - BRA) and Caribbean (CAR). Uppercases represent the total variation explained by a variable. Lowercases indicate the pure effects, i.e. the variation explained by the variable alone, controling for the interaction between environment and space (S*E). Residuals (res) and coefficients of significance values (p) are shown. Significant values are in bold letters.

	Beta	**S**	**p(S)**	**s**	**p(s)**	**E**	**p(E)**	**e**	**p(e)**	**S*E**	**res**
WA	**T**	**0.35**	**0.005**	0.05	0.053	**0.52**	**0.005**	**0.23**	**0.005**	0.29	0.42
	F	0.10	0.072	0.05	0.200	0.13	0.070	0.08	0.240	0.05	0.82
	P	**0.32**	**0.005**	**0.08**	**0.046**	**0.46**	**0.005**	**0.22**	**0.005**	0.24	0.46
BRA	**T**	**0.25**	**0.005**	0.07	0.097	**0.37**	**0.005**	**0.19**	**0.020**	0.18	0.56
	F	-0.04	0.670	0.00	0.450	0.14	0.085	0.19	0.084	-0.05	0.86
	P	0.13	0.063	-0.02	0.600	**0.34**	**0.005**	**0.19**	**0.043**	0.15	0.68
CAR	**T**	-0.01	0.360	0.03	0.250	**0.26**	**0.042**	**0.31**	**0.049**	-0.04	0.70
	F	-0.09	0.820	-0.07	0.560	0.26	0.115	0.28	0.130	-0.02	0.81
	P	-0.08	0.710	-0.08	0.700	0.16	0.150	0.16	0.260	0.00	0.91

4. CONCLUSÕES

A escala e conformação de cada região de estudo se mostraram muito importantes na formação de padrões espaciais de biodiversidade recifal, tanto em relação à riqueza quanto à identidade das espécies. Essa falta de generalidade nos padrões indica que processos atuam em diferentes intensidades, de maneira que estratégias de conservação serão mais eficazes se levarem em conta as peculiaridades de cada região de estudo. Por conseguinte, estudos que explorem mais as particualridades das províncias caribenha e brasileira serão de grande importância para a compreensão dos processos estruturadores das comunidades recifais, visto que essas províncias são importantes componentes da biodiversidade total de organismos recifais do Atlântico.

Organismos recifais têm diferentes respostas a variáveis puramente espaciais. Grupos com dispersão mais restrita, como as algas, são mais sensíveis ao isolamento de recifes. Já para grupos com grande capacidade de dispersão, como os peixes recifais, variáveis puramente espaciais tiveram pouca influência na composição das espécies nos recifes, e nenhuma influência na sua riqueza de espécies.

Embora a distribuição de organismos recifais no oceano Atlântico seja afetada pelas características dos recifes, a maneira como cada grupo responde a essas características varia muito entre os táxons. Isso vale tanto para a comparação de táxons mais elevados (entre peixes, gastrópodes e algas) quanto de táxons mais baixos (entre famílias, Labridae e Pomacentridae). Por exemplo, os gastrópodes parecem não ser influenciados pela idade geológica de ilhas oceânicas, enquanto peixes e algas são. Também a diversidade funcional de labrídeos responde mais a características ambientais do que a diversidade funcional de pomacentrídeos.

Esse estudo mostrou evidências da ação simultânea de processos histórico-evolutivos, ecológicos e neutros em diferentes componentes (i.e. quantitativo e qualitativo) e dimensões (i.e. taxonômica, funcional e filogenética) da biodiversidade de organismos recifais no oceano Atlântico. Algumas evidências de processos histórico-evolutivos na distribuição de organismos recifais no oceano Atlântico são:

(1) a forte diferenciação na composição de linhagens filogenéticas de peixes recifais conforme as características ambientais dos recifes, o que sugere que a evolução de nichos é limitada;

(2) a variação na riqueza de peixes e algas com a idade geológica das ilhas. Isso sugere que haja influência da história de desenvolvimento das ilhas oceânicas nos processos de incorporação e perda de espécies;

(3) a variação no grau de endemismo de peixes recifais com o isolamento das ilhas. Isso aponta para o papel do reduzido fluxo gênico nos processos de especiação, e, portanto, na importância da especiação alopátrica para a diversidade de organismos recifais no oceano Atlântico.

Já as evidências de processos ecológicos na distribuição de organismos recifais no oceano Atlântico são:

(1) a distribuição de espécies e grupos funcionais de peixes recifais no Oceano Atlântico está muito vinculada às características ambientais dos recifes. Isso sugere que haja uma ação de filtros ambientais estruturando essas comunidades;

(2) ilhas maiores, por apresentarem maior diversidade de habitats – e, portanto, de nichos ecológicos – comportam uma maior riqueza de organismos recifais.

Os resíduos nos ajustes das curvas de riqueza ou endemismo com área, idade ou isolamento das ilhas, assim como a porção de variação de diversidade de Labridae e Pomacentridae não explicada por espaço e/ou ambiente podem representar um componente randômico na distribuição de espécies recifais no oceano Atlântico. Entretanto, erros inerentes dos métodos de coleta de dados (seja imagens de satélites, variações em esforço amostral de espécies, etc), assim como a não inclusão de variáveis preditoras importantes também podem produzir esses resíduos.

Por fim, esse estudo, a partir da identificação de padrões espaciais de biodiversidade, contribuiu para uma melhor compreensão dos processos, passados ou presentes, que contribuem para a organização das comunidades recifais do Oceano Atlântico, e poderá contribuir para o embasamento de decisões acerca da conservação da biodiversidade recifal.