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ESTRUTURAÇÃO DE ASSEMBLEIAS DE PEIXES RECIFAIS EM MÚLTIPLAS ESCALAS: TAXONOMIA E FUNÇÃO.

Tese apresentada ao Programa de Pós-Graduação em Ecologia e Conservação do Setor de Ciências Biológicas da Universidade Federal do Paraná, como requisito parcial para obtenção do título de Doutora em Ecologia e Conservação.
Área de concentração: Ecologia e Conservação.

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PARECER

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Secretaria do Programa de Pós-Graduação em Ecologia e Conservação.

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RESUMO

Os mecanismos por trás da estruturação de comunidades constituem uma questão central em ecologia e biogeografia. Identificar estes mecanismos é fundamental para prever as implicações da perda da biodiversidade no futuro. Uma gama de processos atuam em diferentes escalas temporais e espaciais interagem para produzir comunidades ecológicas. Além disso, tais processos podem influenciar de maneira distinta os componentes taxonômico, funcional e filogenético das comunidades. Neste estudo investigou-se os padrões e processos de estruturação de comunidades de peixes recifais, que constituem o mais diverso grupo de vertebrados do mundo. Comunidades de peixes recifais foram avaliadas ao longo de diferentes escalas espaciais, sob uma perspectiva taxonômica e funcional. Nossos principais objetivos foram: (i) identificar os processos/ fatores que determinam a estrutura de comunidades na escala regional e local; (ii) avaliar se os processos por trás da estruturação de comunidades são consistentes para os grupos taxonômicos e funcionais; e (iii) compreender os padrões de raridade funcional de peixes recifais em escala global. Duas bases de dados foram utilizadas: (1) uma extensa base de dados contendo características funcionais e as distribuições de mais de 6000 espécies de peixes recifais em seis regiões biogeográficas marinhas; e (2) um conjunto de dados que inclui as ocorrências de 1474 espécies em 9681 transectos visuais ($40m^2$) distribuídos em 252 locais, também ao longo das principais regiões biogeográficas. No Oceano Atlântico, as estruturas taxonômica e funcional das comunidades têm influência da biogeografia, com uma evidente divisão entre recifes biogênicos (localizados principalmente no Caribe e habitados por grandes proporções de espécies pequenas) e regiões periféricas, onde espécies de maior porte predominam. Nesta escala, tanto processos histórico-evolutivos, que estabeleceram a biogeografia de peixes de recifais no Atlântico, quanto fatores ambientais (recifes de coral vs. ambientes periféricos) moldaram a estruturação de ambos os componentes das comunidades. Esta importância de fatores ambientais também é válida para a estrutura de comunidades em outras regiões (Indo-Pacífico e Pacífico Oriental Tropical). Enquanto a composição taxonômica está relacionada ao isolamento, a estrutura funcional é influenciada pela disponibilidade de habitat na escala local. Espécies pequenas predominam na maioria dos locais com maior riqueza de espécies, e espécies de grande porte prevalecem em locais isolados ou depauperados, um padrão relacionado à capacidade de colonização das espécies. Na maioria das regiões biogeográficas as comunidades apresentaram uma estrutura funcional significativamente aninhada, e um número menor de regiões foram aninhadas taxonomicamente. Além disso, o aninhamento funcional foi detectado entre locais com médias e altas variações de isolamento, fato atribuído à redundância funcional – diferentes espécies são reunidas em grupos funcionais. Este padrão aninhado resulta da interação entre a capacidade de dispersão e/ou colonização de espécies com gradientes de isolamento e área. Apesar da existência de grupos funcionais chave e da redundância funcional ao longo de comunidades, na escala local a maioria das espécies são raras (com pequena abundância ou ocupação). Além disso, espécies raras muitas vezes desempenham papéis únicos. A perda de espécies raras (8 a >200 espécies raras/média: 78,2 ± 62) pode comprometer a diversidade funcional na maioria das comunidades de peixes recifais avaliadas, reduzindo até 80% da diversidade funcional em um único local. Entretanto, a grau em que estes grupos funcionais contribuem para o funcionamento do ecossistema é desconhecido. Nossos resultados revelam que processos histórico-evolutivos são responsáveis por padrões de estruturação das comunidades que diferem entre as regiões. Além disso, o papel fundamental da capacidade de colonização das espécies destaca a importância da conectividade para a estrutura funcional das comunidades de peixes recifais. Finalmente, a contribuição de espécies raras para a diversidade funcional indica que estas espécies devem ser protegidas para que o conjunto de funções e serviços ecossistêmicos destas comunidades sejam mantidos.

Palavras-chave: Peixes recifais. Grupos funcionais. Regiões biogeográficas.
Isolamento. Aninhamento. Raridade.

ABSTRACT

Understanding the mechanisms of community assembly patterns is one of the main questions in ecology and biogeography, and is also essential for predicting the implications of future biodiversity loss. It is known that an array of processes operating at different spatial and temporal scales interact to produce ecological communities. These processes may affect differently the multiple components of communities: the taxonomic, functional and phylogenetic components. Here we investigate the patterns and processes structuring one of the most diverse vertebrate assemblages of Earth: reef fishes. Reef fish assemblages were assessed across multiple spatial scales, under a taxonomic and functional perspective. Our main objectives included: (i) the identification of determinants of structure in reef fish assemblages across scales (regional to local); (ii) assessing to which extent the processes behind assemblage structures are consistent for taxonomic and functional groups; (iii) understanding the patterns of functional rarity in reef fish assemblages at a global scale. Two databases were utilized to achieve these goals: (1) an extensive database on the functional traits and the global distributions of over 6,000 reef fish species across six marine biogeographic regions; (2) a dataset comprising the occurrences of 1,474 fish species over 9,681 underwater visual transects of 40m^2 across 252 sites, also throughout the major biogeographic regions. Within the Atlantic Ocean, the taxonomic and functional structure of reef fish assemblages exhibit a biogeographic fingerprint, with a marked discrimination between species rich biogenic reefs – primarily in the Caribbean, where communities were dominated by small invertebrate feeders – and poorer peripheral regions dominated by larger species with more diverse diets. At the regional scale, both historical events, that have shaped the biogeography of reef fishes, and environmental characteristics (coral reefs vs. periphery) have played a role in structuring both components of assemblages. The role of environment features (coral reef vs. periphery) also holds for the structure of assemblages in other biogeographic realms (*i.e.* Indo-Pacific and Tropical Eastern Pacific). While the taxonomic composition of assemblages is mainly related to reef isolation, the functional structure is influenced by local habitat availability. Again, there is a greater contribution of small-bodied species in the most species-rich locations; and large-bodied species prevailing in peripheral or depauperate assemblages, a pattern related to species' colonization capacity. Reef fish assemblages across most biogeographic regions depicted significantly functional nested structures, but fewer were taxonomically nested. Functional nestedness was found both under intermediate and high isolation gradients attributed to functional redundancy – different species across sites are gathered into a number of key functional entities. The nested structure of assemblages results from the interaction between fish species' dispersal capabilities/ colonization capacity and/or resource requirements, and gradients of isolation and area. Despite the existence of key functional groups and redundancy across fish assemblages, at local scales the majority of species in communities are rare (low abundance or occupancy). Also, rare species fulfil much of the range of functional traits within reef fish communities and often perform unique roles. Under scenarios of rare species loss (from 8 to over 200 rare species/ mean: 78.2±62) there would be high functional diversity erosion in the majority of reef fish communities, this level reaching up to 80% of functional diversity in one location. However the extent to which these functional groups actually contribute to ecosystem functioning is relatively unknown. Overall our results reveal that within-realm processes, such as evolutionary histories, are responsible for patterns of taxonomic and functional structure of assemblages in each realm. Moreover, the key role of species' colonization capacity highlights the importance of connectivity to the maintenance of the functional structure across reef fish communities. Finally, the contribution of rare species to the functional diversity indicates that these taxa must be protected in order to maintain the whole set of functions and ecosystem services in reef fish communities.

Keywords: Reef fish. Functional entities. Biogeographical regions. Isolation. Nestedness. Rarity.

SUMÁRIO

INTRODUÇÃO

INTRODUÇÃO

O estudo da estruturação de comunidades de peixes recifais

> "Assembly is the processes of nature through which a diverse range of entities – individuals, phenotypes or traits, species, guilds – interact at many temporal and spatial scales to produce ecological communities (Drake *et al*., 1999)."

Identificar padrões de estruturação de comunidades bem como os processos/ mecanismos por trás destes padrões constituem uma questão central em ecologia e biogeografia (M'Closkey *et al*., 1997; Ricklefs, 1987; Keddy & Weiher, 1999). Numa ampla escala espacial e temporal, tanto a história evolutiva quanto a biogeografia atuam através de uma série de processos – especiação, colonização, imigração e extinção – (Ricklefs, 1987; Hortal *et al*., 2012), os quais têm papel fundamental na estruturação de *pool*s regionais de espécies (Bellwood & Wainwright, 2002; Whittaker *et al*., 2001; Scheiner *et al*., 2011). Também existem fatores e/ou processos que influenciam a estruturação de comunidades em menores escalas espaciais (Hortal *et al.,* 2012). Além destas diferenças relacionadas à escala, estes processos podem afetar de maneira diferente (Meynard *et al*., 2011) cada componente das comunidades ecológicas – o componente taxonômico, funcional ou filogenético (DeVictor *et al*., 2010; Mouillot *et al*., 2011). Portanto, é fundamental distinguir e avaliar a influência relativa destes diferentes processos em cada componente das comunidades, e através de escalas. Um dos desafios para avaliar esta questão reside na existência de um grupo de organismos modelo com resolução taxonômica adequada e informação suficiente em termos de atributos biológicos e distribuição ao longo de escalas espaciais.

A fauna de peixes recifais constitui o grupo mais diverso de vertebrados na Terra (Bellwood & Wainwright, 2002; Parravicini *et al*., 2013), com mais de seis mil espécies distribuídas ao londo de províncias biogeográficas tropicais e subtropicais (Briggs, 1974; Bellwood & Wainwright, 2002; Floeter *et al*., 2008; Parravicini *et al.*, 2013). Além disso, os peixes recifais são encontrados ao longo de amplos gradientes de latitude, isolamento e diversidade; e dados de ocorrência bem como de atributos biológicos estão disponíveis para a maioria das espécies (Parravicini *et* *al.*, 2013; Mouillot *et al.*, 2014). Dessa forma, os peixes recifais constituem um modelo ideal para explorar a questão dos padrões de estruturação de comunidades em múltiplas escalas espaciais. Muitos avanços foram feitos no que tange aos padrões e processos que influenciam a estruturação das comunidades de peixes recifais, tanto sob uma perspectiva taxonômica (Bellwood & Hughes, 2001), quanto funcional (Bellwood *et al.*, 2002; Bender *et al.*, 2013) e filogenética (Hubert *et al.*, 2011). No Indo-Pacífico, por exemplo, as comunidades recifais são estruturadas em proporções constantes de espécies nas principais famílias de peixes recifais e corais, sendo que as comunidades com menor riqueza de espécies representam subconjuntos daquelas mais ricas (Bellwood & Hughes, 2001). Sob esta regra de estruturação (*assembly rule*), a proporção de espécies das famílias Labridae, Pomacentridae e Serranidae é restrita a um intervalo de valores em todas as comunidades, apesar do amplo gradiente de riqueza. Na escala local, e sob uma perspectiva filogenética, Hubert *et al.* (2001) mostram que a estrutura de comunidades de peixes recifais no Indo-Pacífico segue um modelo neutro. Além disso, comunidades de diferentes regiões (da Grande Barreira de Corais, na Austrália, Polinésia Francesa e do Caribe) apresentam regras comuns de estruturação de atributos funcionais de peixes recifais, apesar de diferenças marcantes na riqueza e composição de espécies entre estas regiões (Bellwood *et al.*, 2002). Entretanto, os diferentes componentes das comunidades de peixes recifais – taxonômico e funcional – e os processos subjacentes aos padrões de estruturação raramente são investigadas conjuntamente. Quando avaliados sob a mesma perspectiva, é possível que os diferentes processos/ mecanismos que moldam a estrutura funcional e taxonômica das comunidades sejam identificados e distinguidos.

Aninhamento e grupos funcionais

O aninhamento – uma métrica amplamente estudada em ecologia – descreve padrões de composição de espécies em comunidades (Patterson & Atmar, 1986, Patterson, 1987; Ulrich & Gotelli, 2007; Almeida-Neto & Ulrich, 2011) e também de redes de interação de espécies (Bascompte *et al.*, 2003). Sob uma estrutura aninhada, a composição daqueles locais com menor riqueza de espécies representam subconjuntos de locais com maior riqueza de espécies (Patterson & Atmar, 1986; Almeida-Neto & Ulrich, 2011). Uma gama de processos, determinísticos ou estocásticos, podem gerar um padrão ou estrutura aninhada (Ulrich *et al.*, 2009), como diferentes taxas de colonização e extinção em faunas insulares (Patterson & Atmar, 1986) ou habitats fragmentados (Patterson & Atmar, 2000); a capacidade suporte de um local associada ao potencial de dispersão de espécies (Ulrich & Zalewski, 2007); bem como a heterogeneidade de habitats associada aos diferentes graus de especialização de espécies (Wright & Reeves, 1992). O grau de aninhamento também pode representar o quanto que grandes áreas contêm a diversidade de espécies e de atributos biológicos e/ou funcionais existente em áreas menores, sendo relevante para estratégias de conservação (Semmens *et al.*, 2010; Wang *et al.*, 2013).

Dessa forma, um padrão aninhado contém informações importantes relacionadas à estrutura de grupos funcionais – e outros componentes das comunidades ecológicas – ao longo de um conjunto de locais e gradientes de riqueza de espécies. Grupos funcionais podem ser definidos como conjuntos de espécies que compartilham atributos de relevância ecológica (see Violle *et al.,* 2007), respondendo de maneira semelhante ao ambiente e/ou tendo efeitos similares sobre processos ecossistêmicos (Hooper *et al.,* 2002). O grau de redundância funcional – quando diferentes espécies possuem funções equivalents (Lawton & Brown, 1994; Naeem, 1998) – em determinado grupo funcional pode garantir a manutenção de um processo no ecossistema, uma vez que a perda de uma espécie poderia ser compensada por outra(s) espécie(s) com determinada função (Hooper *et al.*, 2002; Bellwood *et al.*, 2004; Halpern & Floeter, 2008). Dessa forma, a redundância funcional confere maior resistência e resiliência às comunidades de peixes recifais contra possíveis alterações ambientais (Bellwood *et al.*, 2004, 2012). Sob um padrão aninhado, aquelas funções mais redundantes em locais com maior riqueza de espécies são também redundantes em locais com menor riqueza de espécies; e funções com menor redundância podem estar restritas àqueles locais mais ricos. Entretanto, uma estrutura não-aninhada implica em composições taxonômicas e/ou funcionais divergentes ou homogêneas através das comunidades (Almeida-Neto & Ulrich, 2011). Portanto, é fundamental avaliar padrões de estruturação de comunidades marinhas sob a perspectiva das funções ecológicas de espécies (Michelli & Halpern, 2005; Halpern & Floeter, 2008). Além disso, abordagens baseadas em atributos biológicos podem contribuir para a compreensão dos processos que estruturam as características funcionais de comunidades diversas (McGill *et al.*, 2006; Weiher *et al.*, 2011).

Existem diferenças na dinâmica e resiliência de ecossistemas recifais de diferentes regiões atribuídas às variações regionais na composição funcional e riqueza de espécies de comunidades (Bellwood *et al.*, 2004). Os recifes do Caribe e da Grande Barreira de Corais da Austrália, por exemplo, compartilham grupos funcionais de peixes recifais semelhantes, contudo, a composição taxonômica e a riqueza de espécies (redundância) dentro dos grupos diferem entre estas regiões. Devido essas diferenças, é provável que os recifes da GBR apresentem maior resistência às perturbações quando comparados aos ecossistemas recifais do Caribe (Bellwood *et al.*, 2004).

Em comunidades de peixes recifais do Oceano Atlântico o número de grupos funcionais não é proporcional à riqueza de espécies nas comunidades (Halpern & Floeter, 2008). Sob as previsões de um modelo nulo, as comunidades poderiam ter maior diversidade funcional, no entanto, o aumento da riqueza conduz à adição de espécies em poucos grupos funcionais, enão grupos funcionais novos. Padrões similares são encontrados em comunidades de peixes recifais da Nova Caledônia, no Oceano Pacífico (Guillemot *et al.*, 2011). Em escala global, a fauna de peixes recifais de diferentes regiões biogeográficas é caracterizada pela elevada redundância funcional (*functional over-redundancy*, *sensu* Mouillot et al., 2014), onde o grau de redundância é desproporcionalmente maior em poucos grupos funcionais; por exemplo, no Indo-Pacífico Central um único grupo funcional é representado por 222 espécies enquanto que 38% das funções são representadas por apenas uma espécie (Mouillot *et al.*, 2014). Portanto, a riqueza de espécies não está distribuída de maneira uniforme entre os grupos, sendo que algumas funções são redundantes enquanto outras são tidas como vulneráveis – representadas por uma ou poucas espécies (Bellwood *et al.*, 2004; Halpern & Floeter, 2008; Guillemot *et al.*, 2011; Mouillot *et al.*, 2014). Este padrão de *over-redundancy* de grupos funcionais foi encontrado para as seis regiões biogeográficas que compõem a fauna global de peixes recifais (Kulbicki *et al.*, 2013). No entanto, não se sabe como se comporta a relação entre a riqueza de espécies e a redundância funcional em comunidades dentro de cada região, e se este padrão se repete quando comparamos comunidades com maior riqueza de espécies com aquelas de menor riqueza e isoladas dos centros de diversidade (Figura 1). Entretanto, os padrões de estruturação – sob uma perspectiva taxonômica e funcional – de assembléias de peixes recifais ao longo de diferentes regiões biogeográficas são desconhecidos. Além disso, não sabemos se aquelas funções presentes em um dado local estão presentes em outros locais dentro da mesma região. Dentro deste contexto, análises de aninhamento constituem uma ferramenta analítica apropriada para explorar o grau de redundância funcional em assembléias/ comunidades ao longo de diferentes regiões biogeográficas (Kulbicki *et al*., 2013).

Raridade funcional em comunidades de peixes recifais

Intensos impactos antrópicos sobre os ecossistemas recifais ameaçam espécies que apresentam diferentes atributos biológicos (Hawkins *et al*., 2000; Jackson *et al*, 2001; Dulvy *et al*., 2003; Reynolds *et al*., 2005, Bender *et al*., 2013), comprometendo a diversidade funcional e os processos e serviços ecossistêmicos (Bellwood *et al*., 2012; Naeem *et al*., 2012). Todavia, espécies raras estão entre as mais afetadas devido um conjunto de características que aumentam o risco de extinção de espécies (Rabinowitz, 1981; Gaston, 1994): distribuição restrita, tamanho populacional e/ou especificidade de habitat (grau de especialização). A perda de espécies raras pode não só diminuir a riqueza de comunidades locais, mas também comprometer a gama de funções das mesmas (Lyons & Schwartz, 2001; Lyons *et al*., 2005; Bracken & Low, 2012, Mouillot *et al*., 2013; Pendleton *et al*., 2014). Descobertas recentes mostram que a perda de espécies raras pode comprometer vários níveis tróficos das comunidades (Bracken & Low, 2012; Pendleton *et al*., 2014), e que as funções associadas à espécies raras são, muitas vezes, insubstituíveis (Mouillot *et al*., 2013a).

A redundância funcional tem o potencial de prevenir contra impactos no funcionamento do ecossistema decorrentes da perda de biodiversidade (Bellwood *et al*., 2004). Contudo, o grau de redundância de entidades funcionais determina o impacto da perda de espécies sobre funções do ecossistema (Halpern & Floeter, 2008). Dessa forma, é importante avaliar o grau de sobreposição nas funções associadas a espécies raras e espécies comuns, *i.e.* abundantes, nos ecossistemas (Mouillot *et al*., 2013a). Espécies raras poderiam tanto compartilhar sua combinação de características funcionais com espécies comuns, ou apresentar combinações de atributos funcionais únicas. Neste caso, espécies raras teriam funções vulneráveis, onde um pequeno número de espécies e indivíduos apresenta aquela combinação única de características funcionais (Mouillot *et al*., 2013a).

Os padrões de raridade em comunidades são pouco explorados (Kunin & Gaston, 1993), especialmente no ambiente marinho (Gaston, 1994; Jones *et al*., 2002). Entretanto, existem alguns avanços recentes associados ao entendimento da raridade em comunidades de peixes recifais (Hawkins *et al*., 2000; Morris *et al*., 2000; Jones *et al*., 2002), e às funções desempenhadas por espécies de peixes raras em ecossistemas recifais (Mouillot *et al*., 2013a). Muitas espécies raras representam entidades funcionais únicas em comunidades de peixes recifais do Pacífico Sul (Mouillot *et al*., 2013a). Por outro lado, os padrões de raridade, bem como as funções de espécies raras, devem ser explorados em ecossistemas recifais de outras regiões biogeográficas. Além disso, não temos conhecimento sobre os impactos da perda de espécies raras na diversidade funcional de comunidades. Avaliar os padrões de raridade – e funções de espécies raras – através de múltiplas escalas espaciais pode fornecer informações relevantes para a conservação e funcionamento dos recifes em tempos de mudanças ambientais.

Objetivos

O objetivo principal desta tese foi investigar os padrões e processos de estruturação de comunidades de peixes recifais através de múltiplas escalas espaciais, avaliando grupos funcionais e taxonômicos de maneira complementar. Este objetivo principal pode ser entendido a partir das seguintes partes:

- Identificar os determinantes da estrutura de comunidades de peixes recifais através de múltiplas escalas (do local ao regional);
- Avaliar o quanto os processos de estruturação são consistentes para o componente taxonômico e funcional das comunidades;

- Compreender os padrões de raridade em comunidades de peixes recifais em escala global.

Os objetivos específicos incluem:

- Avaliar os fatores que influenciam a estrutura das comunidades de peixes recifais dentro e entre regiões biogeográficas distintas;
- Investigar se comunidades de peixes recifais são taxonomicamente e funcionalmente aninhadas através de escalas espaciais;
- Investigar se a estrutura aninhada de um componente (funcional ou taxonômico) é determinado pelo padrão aninhado do outro componente;
- Identificar diferenças na diversidade funcional de espécies raras e comuns em assembléias de peixes recifais em escala global;
- Investigar se existem grupos funcionais únicos entre as espécies raras;
- Medir o grau de perda funcional em comunidades de peixes recifais após a remoção de espécies raras.

ARTIGO I

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Biogeographic, historical and environmental influences on the taxonomic and functional structure of Atlantic reef fish assemblages

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ABSTRACT

Aim To disentangle how historic, biogeographic and environmental factors have shaped the composition of different reef fish assemblages, we analyzed assemblage structure from a taxonomic (family proportions) and functional perspective (diet and body size).

Methods The distributions of 1,629 fish species were compiled for 31 locations across the Atlantic Ocean (39°66' N; 27°50' S). These locations provide a richness gradient ranging from 54 species in St. Paul's Rocks to 474 in Cuba. We used cluster analyses to assess how historical and biogeographical factors have shaped the taxonomic and functional structure (*i.e.*, the distribution of species within families, diet and body size groups) of assemblages. We then employed a Constrained Analysis of Principal Coordinates (CAP) to test the relative influence of the distance from the biodiversity center in the Atlantic, sea surface temperature, isolation, coral species richness and area, and coastal length on the observed patterns of assemblage structure.

Results The taxonomic and functional structure of reef fish assemblages across the Atlantic exhibit a biogeographic fingerprint, with a marked discrimination between species rich biogenic reefs (concentrated primarily in the Caribbean and composed of small invertebrate feeders) and poorer peripheral regions dominated by larger species with more diverse diets. The first CAP axis explains 87% of body size distribution in assemblages showing that the effects of sea surface temperature and coral richness and those of isolation are antagonistic and can be embedded into a single dimension. Environmental factors, such as temperature and habitat complexity, explain the disproportionate number of small species in the Caribbean, whereas in the remaining regions the predominance of large-bodied fish increases with isolation due to high dispersal ability.

Conclusions We found that both historical events, that have shaped the biogeography of reef fishes, and environmental characteristics (coral reefs vs. periphery) have played a role in structuring the taxonomic and functional components of Atlantic fish assemblages.

INTRODUCTION

Evolutionary history and biogeography have an essential role in the assembly of regional species pools (Bellwood & Wainwright, 2002; Whittaker *et al.*, 2001; Scheiner *et al.*, 2011). While a number of historical processes – speciation, colonization, immigration, extinction – are known to shape regional species pools (Ricklefs, 1987; Hortal *et al.*, 2012), there is major interest in understanding which factors are structuring the species assemblages at finer scales (Hortal *et al.*, 2012). Ultimately, understanding the different processes underpinning the structure of species assemblages can improve the predictions of their trajectories under global change scenarios (Cavender-Bares *et al.*, 2009; Götzenberger *et al.*, 2012). Thus, the question is no longer to determine which process shapes the structure of species assemblages but to disentangle and assess the relative influence of these different processes at any given scale.

This question is even more challenging because the structure of species assemblages encompasses multiple components (taxonomic, functional, phylogenetic) (Devictor *et al.*, 2010; Mouillot *et al.*, 2011) that may respond differently to each process (Meynard *et al.,* 2011). Most of the research on the structure of marine assemblages has focused on species richness patterns (e.g. Bellwood & Hughes, 2001), yet there is evidence that the structure of functional traits within assemblages determines ecosystem functioning (Fisher *et al.*, 2010). For instance, body size distribution within fish assemblages drives the structure of trophic interactions (Jennings *et al.*, 2001) and fish responses to exploitation (Reynolds *et al.*, 2005). Thus, assessing the functional component of species assemblages and identifying the processes underlying their structure can improve our knowledge of ecosystem functioning under ever increasing multiple threats (Halpern *et al.*, 2008). The integration of this component into the comprehension of biodiversity patterns has been a major step forward in biogeography (Stevens *et al.*, 2003; Safi *et al.*, 2011; Münkemüller *et al.*, 2012) but with still few applications to marine assemblages over large scales (but see Bellwood *et al.*, 2002; Halpern & Floeter, 2008).

The reef fish fauna is recognized as one of the most diverse vertebrate assemblages on Earth (Bellwood & Wainwright, 2002), encompassing over six thousand species that occur in all tropical and subtropical biogeographic provinces (Briggs, 1974; Bellwood & Wainwright, 2002; Floeter *et al.*, 2008; Parravicini *et al.*, 2013). This diversity of species and ecological attributes provides ecosystem services to millions of people (Sadovy, 2005). It is thus important to understand the structure of reef fish assemblages, not only taxonomically but also in terms of the functional characteristics that govern ecosystem functioning (Fisher *et al.*, 2010; Mora *et al.*, 2011). Bellwood & Hughes (2001) already identified remarkably consistent proportions in the taxonomic composition of reef fish and coral assemblages across a richness gradient in the Indo-Pacific Ocean. Furthermore, reef fish traits (e.g. fin shape of Labridae species) showed common assembly rules among regions (the Great Barrier Reef, French Polynesia and the Caribbean) despite differences in species composition (Bellwood *et al.*, 2002). However, relatively little is known about the extent to which these patterns hold in other oceans or with other traits such as diet or body size. More specifically, to the best of our knowledge, no study to date has carried out a comprehensive comparison of the functional structure of reef fish assemblages across a large set of conditions (biogeographical, environmental and historical).

The well-established biogeography and evolutionary history of reef fishes in the Atlantic (Briggs, 1974; Floeter *et al.*, 2008) provides a relevant context for addressing three possible scenarios shaping reef fish assemblages (Fig. 1). Our main goal was to understand the role of historical, biogeographic and environmental factors on the assembly patterns of three biodiversity components of reef fishes: families, trophic groups and body-size categories. We propose three scenarios (Fig. 1) in which history, biogeography and environment may have shaped the distribution of species richness within a given group (taxonomic, trophic, or size-based). First, the structure of fish assemblages (proportions of species within a group) differs between regions, reflecting a large influence of evolutionary history and biogeography (Fig. 1a). Second, structures are remarkably similar across fish assemblages of different regions, despite various histories and environments (Fig.1b). This scenario follows the pattern described by Bellwood & Hughes (2001) for both coral and reef fish families across the Indo-Pacific. Under the third scenario, habitat affinity (coral reef vs. periphery) dictates the structure of fish assemblages, despite different evolutionary histories across biogeographic regions (Fig. 1c). Fish assemblages differ substantially across Atlantic locations ranging from poor assemblages in isolated rocky reefs to species rich assemblages in coral reefs located in the Caribbean. Coral reefs offer a range of habitats in warm tropical shallow-waters that have remained stable over geological time; hence they are considered the main drivers of diversification in reef fishes (Cowman & Bellwood, 2011).

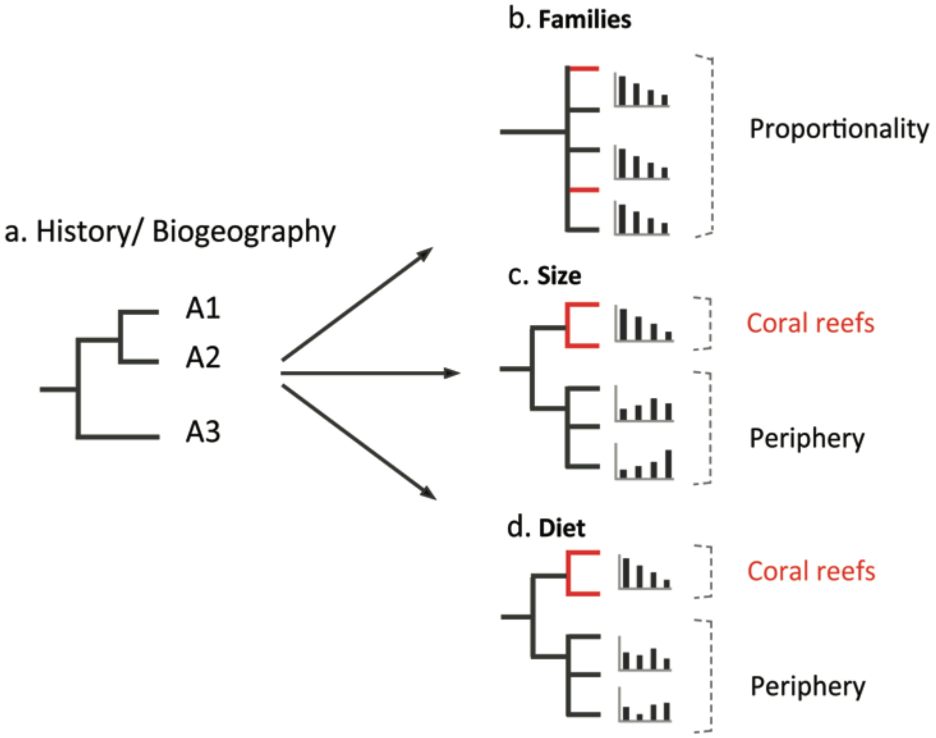

Figure 1. Scenarios about the role of history, biogeography and environment factors in the distribution of fish richness within groups (taxonomic-, trophic-, or size-based) across the Atlantic Ocean. In scenario (a), history and biogeography shape the proportion of fish richness within groups. The structure of assemblages is similar within regions independently of habitat (coral reefs or periphery habitats). Under scenario (b), proportions of fish richness within groups are remarkably similar across regions and habitats. In scenario (c), habitat affinity (coral reef vs. periphery) shapes the distribution of fish richness within groups independently of regions (see the introduction for a complete explanation of the hypotheses). Red branches represent biogenic reefs and black ones, peripheral reefs.

The shift from coral reefs to non-coral peripheral environments may thus deeply influence the structure of reef fish assemblages with the prevalence of certain families and functional groups. For instance, differences in the body-size structure of assemblages can be related to size-dependent dispersal or ecological filtering as resources decrease towards poor environments; whereas increased richness of fish species feeding on relatively low-quality food in the tropics (Harmelin-Vivien, 2002; Floeter *et al*., 2004) could lead to differences in the trophic structure of assemblages. We tested these different scenarios by compiling the distribution of fish species within families, body size categories and trophic groups across the Atlantic and by examining the potential role of historical, biogeographic and environmental factors on these structures, if any.

METHODS

Dataset

We analyzed the most comprehensive dataset on the distribution of Atlantic reef fishes to date (Floeter *et al*., 2008; Halpern & Floeter, 2008), which was based on the occurrence records from species checklists of 31 locations throughout the Atlantic Ocean (Fig. 2). Selected locations refer to the best checklists available for well-documented reefs. The entire dataset includes records of 1629 species from 465 genera and 69 families. ‘Reef fishes’ were defined as a group that includes any shallow (< 100 m) tropical or subtropical benthic or benthopelagic fish species that consistently associates with hard substrates of coral, algal, or rocky ‘reefs’ or occupies adjacent sand substrate (Floeter *et al.*, 2008). Biogenic reefs, here referred to as coral reefs for simplicity, are those constructed by large, heavily calcified organisms, mainly corals and coralline algae (Wood, 1999).

We applied species categorization into trophic groups based mainly on Ferreira *et al.* (2004), resulting in seven groups as follows: herbivores, macrocarnivores, mobile invertebrate feeders, omnivores, piscivores, planktivores and sessile invertebrate feeders. The herbivores are those species that feed on macroalgae, seagrass, filamentous algae and associated detritus, *i.e.* undefined organic material. Piscivores feed primarily on fish. Macrocarnivores eat a variety of large mobile organisms, including crustaceans and fishes. The diet of mobile invertebrate feeders consists primarily of small benthic invertebrates (*e.g.* small crustaceans, mollusks, worms, etc.) while sessile invertebrate feeders consume cnidarians, hidrozoans, bryozoans, ascidians and sponges. The omnivores eat both animal and plant material in various proportions. Finally, planktivores feed primarily on macro- and microzooplankton.

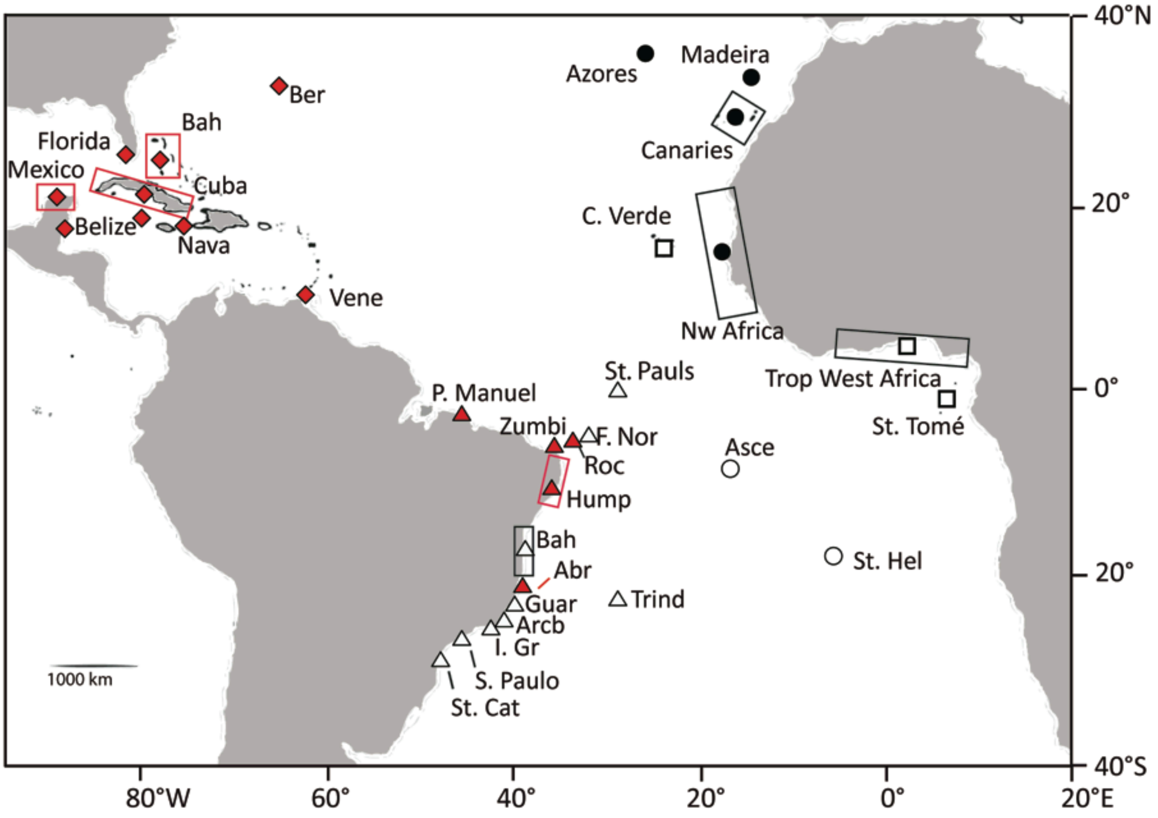

Figure 2. Thirty-one Atlantic locations where fish species presence-absence data were collected. Symbols indicate regions within the Atlantic province (*sensu* Floeter *et al.*, 2008): ♦ = Northwestern Atlantic; **Δ**= Southwestern Atlantic; ○ = Ascension and St. Helena; I = Northeastern Atlantic; □ = Tropical Eastern Atlantic. Red symbols represent locations of biogenic reefs.

Reef fish species were also classified into body size categories since this trait is a surrogate for many others (Dumay *et al.,* 2004) and underlies many ecosystems processes (Fisher *et al.*, 2010). We defined four maximum body size categories, based on total length, as follows: small, medium-small, medium and large (<10, 10-25, 25-50, >50 cm, respectively, see Halpern & Floeter, 2008 for details).

Data analyses

To understand how historical, biogeographic and environmental factors have shaped the structure of reef fish assemblages across the Atlantic, we focused on taxonomic (family), trophic and body size structures (see our three hypotheses in Figure 1). We first assessed the distribution of species within families, body size categories and trophic groups for each of the 31 reef fish assemblages. We then performed cluster analyses to classify the 31 locations based on the proportion of fish species within 69 families, four body size categories and seven trophic groups using the Bray-Curtis dissimilarity index and a complete linkage method (Borcard *et al*., 2011). *P*-values for cluster nodes (AU – **A**pproximately **U**nbiased) were calculated using bootstrap resampling (1000 replicates) (PVCLUST package in R software) to assess their reliability.

Since the taxonomic structure of assemblages, based on species membership to a given family, may influence the functional structure thanks to phylogenetic conservatism of traits (Mouquet *et al*., 2012), we tested whether closely related fish assemblages, on the basis of their taxonomic structure, were also functionally more similar. To this aim, we implemented Mantel tests between pairs of dissimilarity matrices: family vs. trophic categories, family vs. body size categories and trophic vs. body size categories.

Second**,** we performed a Constrained Analysis of Principal Coordinates (CAP) (Anderson & Willis, 2003) on species proportional data to assess the relative influence of environmental and biogeographical factors on the structure of reef fish assemblages, using the Bray-Curtis distance between pairs of locations (Legendre & Legendre, 1998). Assemblage data were previously transformed using the Hellinger transformation (Legendre & Gallagher, 2001). Variations between locations in the observed proportions of species richness within families, trophic groups and body size categories were contrasted with the following explanatory variables: the distance from the diversity center, sea surface temperature (SST), isolation (distance from the mainland in kilometers), coral species richness, coral area (km^2) and coastal length (km). The distance from the reef fish diversity center in the Atlantic Ocean, which corresponds to the Caribbean (474 species recorded in Cuba, 22°N 77°W) (Claro & Parenti, 2001; Briggs, 2003; Floeter *et al.*, 2008), was measured in degrees. Average SST for each location was obtained from BIO-oracle (Tyberghein *et al.*, 2012). For each checklist we defined, according to maps and descriptions in the original publications, the area to which the species list pertains, thereby allowing the computation of the coral reef surface and the coastline to which each checklist was referred. Coral reef area derives from the coral reef Millennium census (UNEP-WCMC, 2012). All this information has been converted to a Behrmann equal-area projection before analyses. All data analyses were performed using the software R 2.14.2 (R Core Team, 2012), and packages VEGAN version 2.0-2 (Oksanen et al., 2011) and PVCLUST version 1.2-2 (Suzuki 2011).

RESULTS

The relationships between locations based on the proportions of species within 69 families reveal the influence of species geographical distributions: Eastern and Western Atlantic are separated and, in the western portion, the Caribbean and the Brazilian coast with its oceanic islands form two distinct branches, the Northwestern and Southwestern Atlantic, respectively (Fig. 3). The only exception to that global pattern is the Brazilian oceanic island of St Pauls' Rocks, which is grouped with the islands of St. Helena and Ascension. The proportions of the ten most speciose families highly differ between assemblages: Serranidae, Labrisomidae and Gobiidae species dominate in Caribbean assemblages while the Carangidae family has the highest proportion of species in St Pauls' Rocks, St. Helena and Ascension islands. In the Eastern Atlantic, the proportions of Bleniidae, Sparidae and Scorpaenidae species are higher when compared to those of the Western Atlantic (Fig. 3, see histograms).

The relationships among locations based on the proportions of species within body size categories reveal a different pattern than that found for the taxonomic composition (Fig. 3) with a weaker influence of biogeography since locations that belong to different biogeographic regions can be in the same clusters, e.g. the Canaries (Northeastern Atlantic) along with São Paulo and Bahia (Southwestern Atlantic); Bermuda (Northwestern Atlantic) grouped with Espirito Santo (Southwestern Atlantic) and Azores (Northeastern Atlantic) with St. Helena (Mid Atlantic Ridge). Overall there is discrimination between most of Caribbean locations at the top of the cluster, forming one group, and a second group gathering the remaining 24 locations. Histograms (Fig. 3; body size categories) show that in Caribbean assemblages there is a large proportion of small-bodied species, an opposite pattern to that exhibited by São Tome, Cape Verde, Ascension and St. Pauls' Rocks.

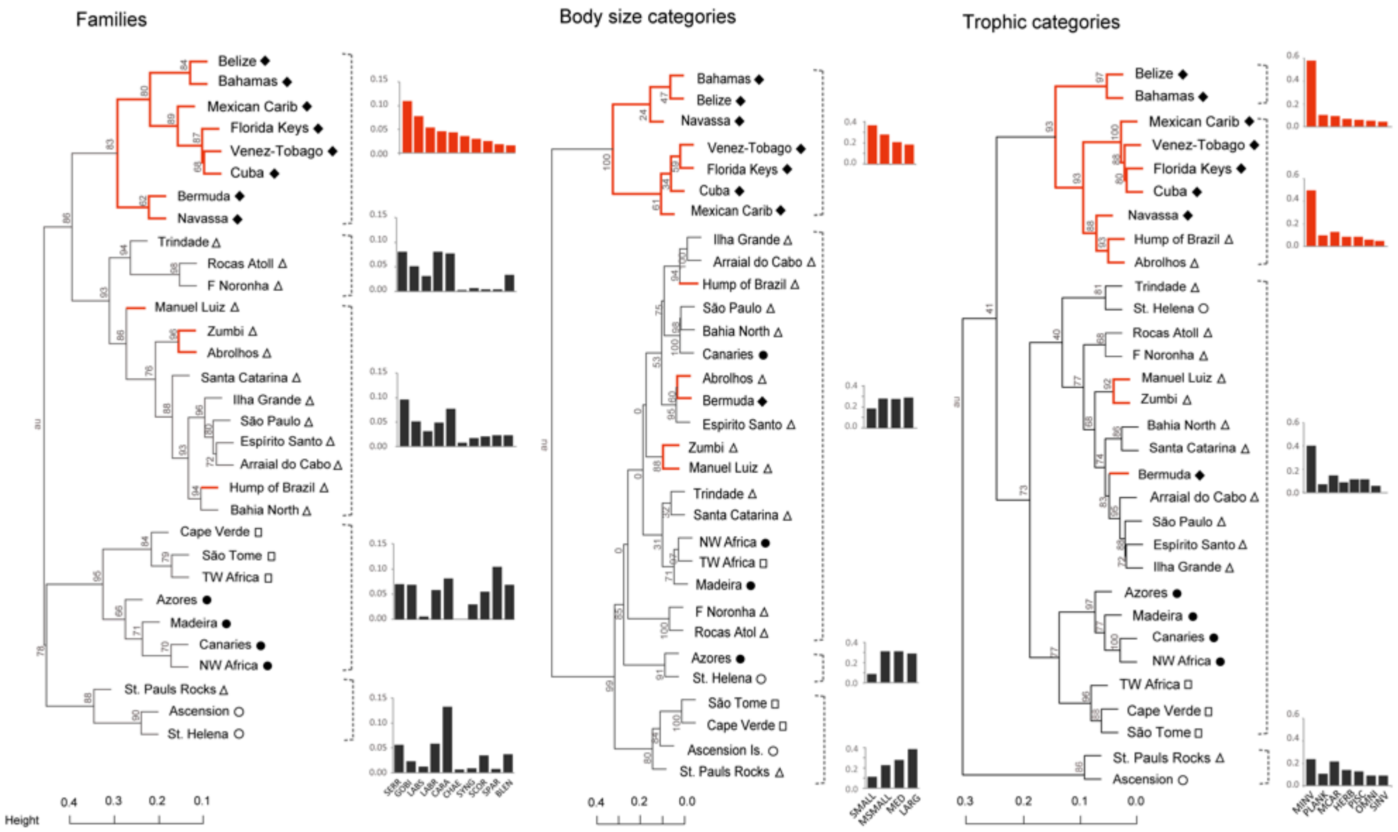

Figure 3. Cluster analyses (Bray-Curtis; complete linkage) summarize the relationship among Atlantic reef fish assemblages based on (from left to right) the taxonomic, the body size and the trophic group structure. Histograms represent the proportion of species in: (i) the ten most speciose Atlantic reef fish families; (ii) the four maximum body-size categories and (iii) the seven diet categories. Values at cluster nodes correspond to AU *p*-values (%) supported by bootstrap (1000 replicates). For the sake of simplicity, histograms grouped locations within cluster nodes exhibiting AU values> 70. Elements colored in red/ grey refer to locations of biogenic reefs. Symbols indicate regions within the Atlantic province (*sensu* Floeter *et al.*, 2008): ◆ = Northwestern Atlantic; **Δ**= Southwestern Atlantic; ○ = Ascension and St. Helena; I = Northeastern Atlantic; □ = Tropical Eastern Atlantic. Families: SERR – Serranidae, GOBI – Gobiidae, LABS – Labrisomidae, LABR – Labridae, CARA – Carangidae, CHAE – Chaenopsidae, SYNG – Syngnathidae, SCOR – Scorpaenidae, SPAR – Sparidae, BLEN – Bleniidae. Trophic groups: MINV – mobile invertebrate feeders, PLANK – planktivores, MCAR – macrocarnivores, HERB – herbivores, PISC – piscivores, OMNI – omnivores, SINV – sessile invertebrate feeders. Body size categories: SMALL, MSMALL – medium-small, MED – medium, LARG – large (<10, 10-25, 25-50, >50 cm, respectively).

For trophic categories, the cluster reveals that most locations of biogenic reef formation are grouped, including Abrolhos reefs and the Hump of Brazil, in the Southwestern Atlantic (Fig. 3). In those assemblages, there is a large proportion of mobile invertebrate feeder species compared to other trophic categories (see histograms). The islands of Ascension and St. Pauls' Rocks form a clearly separated group, possibly an outcome of the equitable distribution of species within trophic categories and the increased proportion of macrocarnivores species, compared to other assemblages. Tropical Eastern Atlantic and Northeastern Atlantic locations form one separate group, where the proportion of omnivorous species is greater compared to other locations. Bermuda, a site of coral reef formation, is grouped with sites of the Brazilian coast (Southwestern Atlantic).

The taxonomic dissimilarity between pairs of reef fish assemblages was positively correlated to both the trophic dissimilarity (Mantel test r = 0.73) and the body size dissimilarity (Mantel test r = 0.58), indicating a strong influence of phylogeny for these ecological traits. Moreover, trophic and body-size dissimilarities between reef fish assemblages are also positively correlated (Mantel test r = 0.61).

Among the examined variables that may explain the patterns of dissimilarity among reef fish assemblages, sea surface temperature and coral species richness play an important role, be it on taxonomic, trophic and body size structure (Fig. 4). Since coral richness and coral reef area were positively correlated (Appendix S1), relationships between these variables and the structure of reef fish assemblages can be an outcome of any of these variables, or its combination. Coral richness was negatively correlated to the distance from the diversity center, thus these variables have antagonistic effects on the structure of certain components of reef fish assemblages. The distance from the diversity center and isolation are also significant terms in the CAP analysis explaining variation of trophic and taxonomic structure among fish assemblages. Isolation influences the taxonomic structure of fish assemblages with high proportions of Muraenidae and Carangidae species in the oceanic islands of St. Helena and Ascension, in the Mid-Atlantic Ridge; whereas coral species richness was related to higher proportions of Chaenopsidae and Labrisomidae like in Northwestern Atlantic locations (Fig. 4).

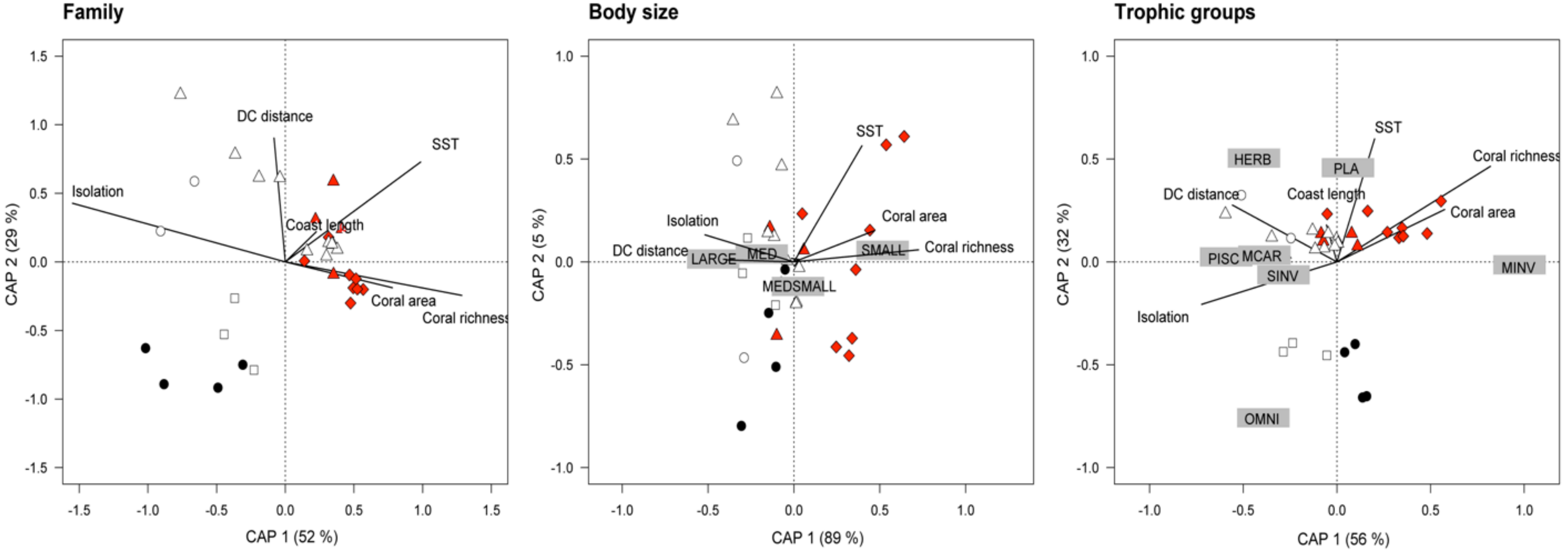

Figure 4. Biplots of Constrained Analyses of Principal Coordinates (CAP) explaining the proportions of species within (a) families, (b) body size categories and (c) trophic groups in thirty-one Atlantic reef fish assemblages as a function of biogeographic and environmental factors. Symbols indicate regions within the Atlantic province (*sensu* Floeter *et al.*, 2008): ♦ = Northwestern Atlantic; **Δ**= Southwestern Atlantic; ○ = Ascension and St. Helena; I = Northeastern Atlantic; □ = Tropical Eastern Atlantic. Red symbols represent locations of biogenic reefs. DC distance = Distance from the diversity center; SST = Sea surface temperature. Acronyms for body size and trophic groups correspond to those in figure 3 caption.

For trophic groups and body size categories, results are very consistent with the taxonomic analysis. In all cases, the first coordinate discriminates the antagonistic effects of sea surface temperature, coral reef area and richness on one hand, and isolation and distance from the diversity center on the other. This coordinate alone explains more than 50% of the variation in all analyses, and accounts for 89% of all the variation in body size structure observed across assemblages (Fig. 4). Consequently, for body size these antagonistic effects can be embedded into a single dimension that clearly discriminates rocky from biogenic reefs (Figs. 3 and 4). For trophic categories the pattern is qualitatively similar, but in this case the variation across assemblages could not be embedded into a single dimension as with body size (Fig. 4). Nonetheless, the first coordinate, explaining 56% of the total variation, discriminates those assemblages in which mobile invertebrate feeders prevail and those in which the contribution of piscivores, herbivores or omnivores is proportionally higher. The second coordinate accounting for 32% of the variation in trophic structure unravels the overall contribution of herbivores to assemblages (Fig. 4).

DISCUSSION

Our results indicate that the taxonomic structure of Atlantic reef fish assemblages varies among locations, reflecting both historic and biogeographic influences (Floeter *et al.*, 2008). This heterogeneous pattern is not concordant with the scenario based on assembly rules identified for reef fish families in the Indo-Pacific (Bellwood & Hughes, 2001) (Fig. 1b). In fish assemblages of the Indo-Pacific, Bellwood & Hughes (2001) identified a relatively constant taxonomic membership and highly correlated family species richness (mean of r = 0.83). In the Atlantic, similar analysis revealed considerably lower correlation values between family richness across assemblages (r = 0.43±0.3), which means that the patterns of taxonomic composition are not homogeneous (Appendix S2). The absence of generality in this pattern between oceans may be explained by: (i) the independent evolutionary history of the Atlantic compared to the Indo-Pacific (Floeter *et al.*, 2008; Renema *et al.*, 2008; Cowman & Bellwood, 2013), (ii) the different habitat availability through time (Bellwood & Wainwright, 2002; Cowman & Bellwood, 2013), (iii) the differences between coral and rocky reefs, and (iv) the influence of strong biogeographic barriers in the Atlantic (Floeter *et al.*, 2008; Luiz *et al.*, 2012). The Indo-Pacific is characterized by an extensive shallow-water geological complexity (Bellwood & Wainwright, 2002) that promoted species survival, origination and range extension, enhancing diversification (Cowman & Bellwood, 2013). Moreover, this diversity has remained connected over time due to increased shallow-water area availability and the existence of fewer barriers in the Indo-Pacific, compared to the Atlantic Ocean (Floeter *et al.*, 2008; Bellwood *et al.*, 2012; Mora *et al.*, 2012).

By contrast, a number of historical events have deeply influenced the Atlantic reef fish fauna in the last fifty million years (Eocene) (Budd, 2000; Floeter *et al.*, 2008), including extinctions, the Panama Isthmus closure (Bermingham *et al.*, 1997; Floeter *et al.*, 2008), and Pleistocene glaciations; the latter caused severe reductions in the shallow-water habitat available for the reef biota (Bellwood & Wainwright, 2002). The greater shallow-water habitat availability in the Caribbean compared to other areas in the Atlantic made this region the center of fish and coral diversity in the Atlantic Ocean (Briggs, 2003; Floeter *et al.*, 2008). The shared history of the coral and fish faunas might explain the role of reef isolation and coral species richness as filters to fish richness for some families of Atlantic reef fishes. Gobiidae, Labrisomidae and Chaenopsidae families with small cryptobenthic fishes, have far more species in the Caribbean region than elsewhere in the Atlantic (Floeter *et al.*, 2008). This may be attributed to limited dispersal abilities, leading to high diversification rates within those families (Munday & Jones, 1998). Isolation, on the other hand, might have favored higher proportions of Carangidae and Muraenidae species in Mid-Atlantic Ridge assemblages (Ascension and St. Helena Islands). Muraenidae species are pelagic spawners with long pelagic larval durations (Victor, 1991), while Carangidae species are rafters – raft with floating debris in the open sea – (Luiz *et al.*, 2012). These traits improve species dispersal potential across long distances (Thiel & Gutow, 2005; Luiz *et al.*, 2012). Although the Caribbean is the region of the Atlantic Ocean that most resembles the Indo-Pacific with respect to shallow biogenic habitats and connectivity, evolutionary history and diversity patterns are different between these regions, explaining the differences in family proportions.

The effects of biogeography are also reflected in the body size structure of fish assemblages, with cluster analyses and CAP discriminating the Caribbean from any other location (Fig. 3). This pattern is mainly due to the large proportions of small-bodied species in the Caribbean, which reaches up to 42% in the Bahamas and 45% in Belize. The structural complexity and niche availability of coral reef habitats combined with the short life cycles of small-bodied fish species have facilitated the diversification of Gobiidae, Labrisomidae and Chaenopsidae families in the Caribbean (Munday & Jones, 1998; Floeter *et al*., 2008). On the other hand, large-bodied species have not only higher potential to colonize new habitats, but also to expand their ranges across dispersal barriers (Luiz *et al*., 2012). This seems a plausible explanation for the high proportions of large-bodied species (>50 cm) – reaching up to 40% – in isolated locations such as St. Pauls' Rocks, São Tomé and Cape Verde. It is also possible that small migrants that eventually reach these locations cannot sustain viable populations in such poor environments and environmental filtering is taking place, as suggested by the patterns found for trophic groups.

Reef type has a high influence on the trophic structure of Atlantic reef fish assemblages, as demonstrated by the close relationship among locations of biogenic reef formation and the non-biogenic ones (see Fig. 3). This assembly pattern is in accordance with the habitat affinity scenario (Fig. 1c). The distinction of locations characterized by biogenic reefs is partly driven by the high proportion of mobile invertebrate feeders, encapsulated in the first coordinate of the CAP analysis (Fig. 4). The diversity and abundance of mobile invertebrates in reef ecosystems is favored by the complexity and productivity of coral reefs, sustaining a high diversity of fish feeding on such prey, as in the Indo-Pacific (Bellwood *et al.*, 2006). Such richness of mobile invertebrate feeders is logically related to the high proportion of small-bodied species, and the richness of Gobiidae and Chaenopsidae families in the Caribbean (Floeter *et al.,* 2008).

The second CAP coordinate discriminates trophic groups across the Eastern and Western Atlantic (Fig. 4), with omnivores prevailing in the former while herbivores and planktivores dominated in the latter. CAP analyses suggest that differences in sea surface temperature might partly explain this pattern, which is supported by previous evidence (Floeter *et al*. 2004, 2005) and illustrates why the latitudinal and thermal range of the Atlantic makes this biogeographic province truly unique as a system to study the impact of environmental conditions on the functional structure of marine communities. The adaptation of herbivores to the use of relatively low-energy food resources (*e.g.* algae, detritus, coral) combined with their high availability in the tropics (lower latitudes and warm waters) has boosted speciation rates of this trophic group (Harmelin-Vivien, 2002). By contrast, in colder peripheral locations, fishes need to exploit higher-energy resources associated to animal protein; in order to fulfill their metabolic needs to inhabit those environments (Floeter *et al.*, 2004). This metabolic constraint associated with historical environmental disturbances of these locations has favored the diversification of omnivores given its plasticity (Ferreira *et al.*, 2004). Omnivores in the Eastern Atlantic belong mainly to the Sparidae and Blenniidae families, which are particularly diverse in that region (Floeter *et al.*, 2008).

We find that, overall, biogeographical and environmental variables exert combined high influences on the taxonomic and functional structure components of Atlantic reef fish assemblages. Small invertebrate feeders prevail in the warm waters of the Caribbean, whereas larger species consuming other trophic items dominate elsewhere. This footprint of biogeography in the structure of assemblages has also been shown through the importance of large-scale processes on boreal lake fish assemblages (Van Zyll de Jong & Cowx, 2005), the geographic patterns of habitat-use in emydid turtles communities (Stephens & Wiens, 2009) and the phylogenetic structure of palm species assemblages (Kissling *et al*., 2012). Identifying different levels of influence in those components enable a better understanding of the forces determining assemblage structures, and how they may vary along richness gradients. This is especially important given the rapid changes that marine ecosystems are experiencing, such as biodiversity erosion (Jackson *et al.*, 2001; Bellwood *et al.*, 2004; Worm *et al.*, 2006). The subsequent loss of key reef fish functional groups and trait diversity in assemblages might seriously compromise reef ecosystem functioning and the provision of services.

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Appendix S1 Correlations between environmental variables

Table S1. Pair-wise correlation values between environmental variables considered in our Constrained Analyses of Principal Coordinates.

	DC distance	SST	Coral spp	Isolation	Coral area	Coastal length
DC distance		-0.26	-0.57***	0.13	-0.41*	0.26
SST			0.54 **	-0.35*	0.27	-0.02
Coral spp				-0.44*	0.59***	-0.11
Isolation					-0.20	-0.07
Coral area						-0.05
Coastal length						

DC distance = Distance from the diversity center; SST = Sea surface temperature. * $p < 0.05$; ** $p < 0.01$; ***$p < 0.001$

Appendix S2 Correlations between family species richness

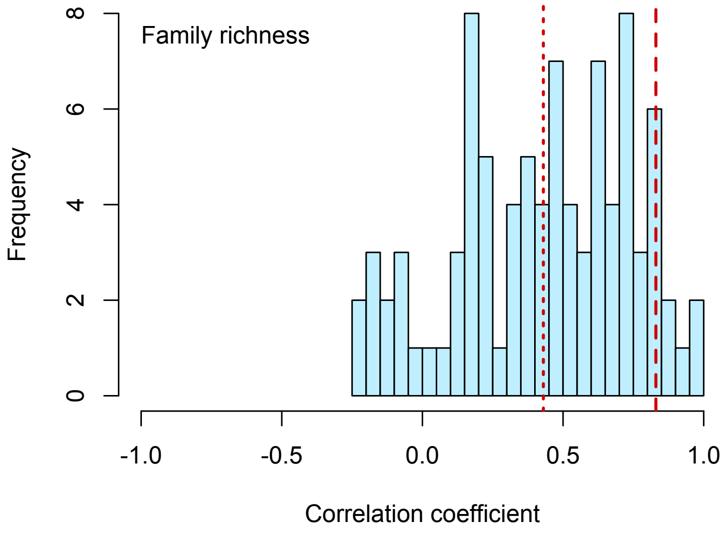

Figure S2. Pair-wise correlation coefficients between family richness across reef fish assemblages of the Atlantic Ocean. Here we considered only the 13 most speciose reef fish families in order to enable direct comparison to the study of Bellwood & Hughes (2001). The dotted line indicates the mean correlation value (*r* = 0.43±0.3) for the Atlantic while the dashed line indicates the mean correlation value for the Indo-Pacific (mean r = 0.83; Bellwood & Hughes, 2001). Many correlations obtained for the Atlantic reef fish assemblages are lower than 0.70, which is the minimum reported by Bellwood & Hughes (2001).

ARTIGO II

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Historical contingencies and coral reef determine the functional structure of global tropical fish assemblages

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Globally natural systems are experiencing biodiversity declines, with significant consequences for ecosystem functioning and the provision of services to humans. However, an understanding of the factors shaping the functional structure of species assemblages is till lacking while it is pivotal for predicting the implications of ongoing global changes. In the marine realm, coral reefs are one of the most diverse and threatened systems that support million of people worldwide. Using a global distributional database for 6,226 coral reef fishes and the analysis of two major functional traits (i.e. body size and trophic status), we show that biogeographical history is responsible for major taxonomic and functional divergence across three distinct realms (i.e. Indo-Pacific, Eastern Tropical Pacific, Atlantic). Within these realms the taxonomic structure of species assemblages often represents a random subset of the species pool. Functional structure, instead, strongly deviates from the random expectation. Species with small body size dominate locations with high richness while larger species predominate peripheral or depauperate assemblages. This difference in functional structure along the steep biodiversity gradient is largely explained by the availability of coral reef habitat. Our results reveal a central role of evolutionary history and habitat availability in shaping reef fish communities and highlight the risk of functional re-organization if ongoing coral reef fragmentation is not halted by appropriate conservation actions.

Around the world, both terrestrial and marine systems are experiencing unprecedented population and biodiversity declines [1,2,8], which may markedly alter functioning and the provision of services to humans [3–5]. Beyond species richness, the breath of functions played by species and the distribution of species among those functions drive the long term functioning of ecosystems. Surprisingly, despite the emergence of functional biogeography [9], whether the functional structure of species assemblages depends on deterministic rules, historical contingencies or random processes is still unknown, especially in the marine realm [10–14].

Coral reefs are one of the most diverse marine ecosystems and show steep biodiversity gradients in numerous taxa which support a multitude of functions [15–19]. However, concern has globally emerged about their future as they are threatened by the combination of multiple human pressures and climatic changes [7]. Although several studies have highlighted that coral reef biodiversity is shaped by evolutionary [20–22], environmental [16,18,23] and geographic factors [19,24], our understanding of the mechanisms structuring reef assemblages remains elusive, especially at the global scale where a large amount of information is required to undertake any evaluation. Using a recently compiled global database on the distribution of 6,226 coral reef fish species, at a resolution of 5°×5°, and the compilation of two major life-history traits that determine fish functional roles (i.e. species trophic status and maximum body size), we are now in the position to (*i*) assess global patterns in reef fish taxonomic and functional structure and (*ii*) test for the potential influence of biogeographica history and environmental gradients on such structures.

Here we show that at the global scale the relative proportion of fish families, trophic guilds and body size classes is primarily influenced by the different evolutionary history of three oceanic realms (i.e. Atlantic, Indo-Pacific, and Eastern Tropical Pacific). Once this effect is accounted for, the local taxonomic composition of communities is not different from a random assignment of species among families. On the contrary, the functional structure of fish assemblages deviates strongly from random expectations and these differences are mainly explained by coral reef availability.

Globally, reef fish assemblages show marked differences in their taxonomic structure (i.e. in the relative contribution of fish families to total species richness; Fig. 1). Of the 169 reef fish families examined, 69 are found only in the Indo-Pacific, while 15 families are restricted to the Atlantic. There is also considerable variation in the contribution of families to the species richness of assemblages within each realm. For example, the proportion of Pomacentridae varies from less than 1% in the Atlantic up to 9% in the Indo-Pacific, while the Serranidae show the opposite pattern (e.g. 1% of richness in Hawaii and 14% in the Caribbean). These large-scale biogeographical divergence across realms involves also the functional structure of fish assemblages with even more marked differences for size classes than for trophic guilds (Fig. 1). For instance, piscivores may represent up to 20% of the species richness in the Tropical Eastern Pacific, while they do not exceed 12% in the Indo- Pacific (in the richest areas of the Indo-Australian Archipelago). Similarly, large species (>80cm) constitute up to 40% of the total species richness in the Eastern Atlantic but only 6% in the Indo- Pacific.

We first tested for a potential role of biogeographical history in explaining the observed variation in the taxonomic and functional structure of communities. Each realm having a markedly different evolutionary history[25], we compared the observed structure of assemblages within each realm with those built by randomly sampling species from the global species pool while keeping species richness constant. Significant departures from the null expectation (no role of evolutionary history) were detected among the three realms in the proportion of species within families (Table S1), trophic categories (Table S2) and in body size classes (Table S3). These differences suggest that the different evolutionary histories of these realms are likely to have yielded distinct taxonomic and functional structures within regional assemblages.

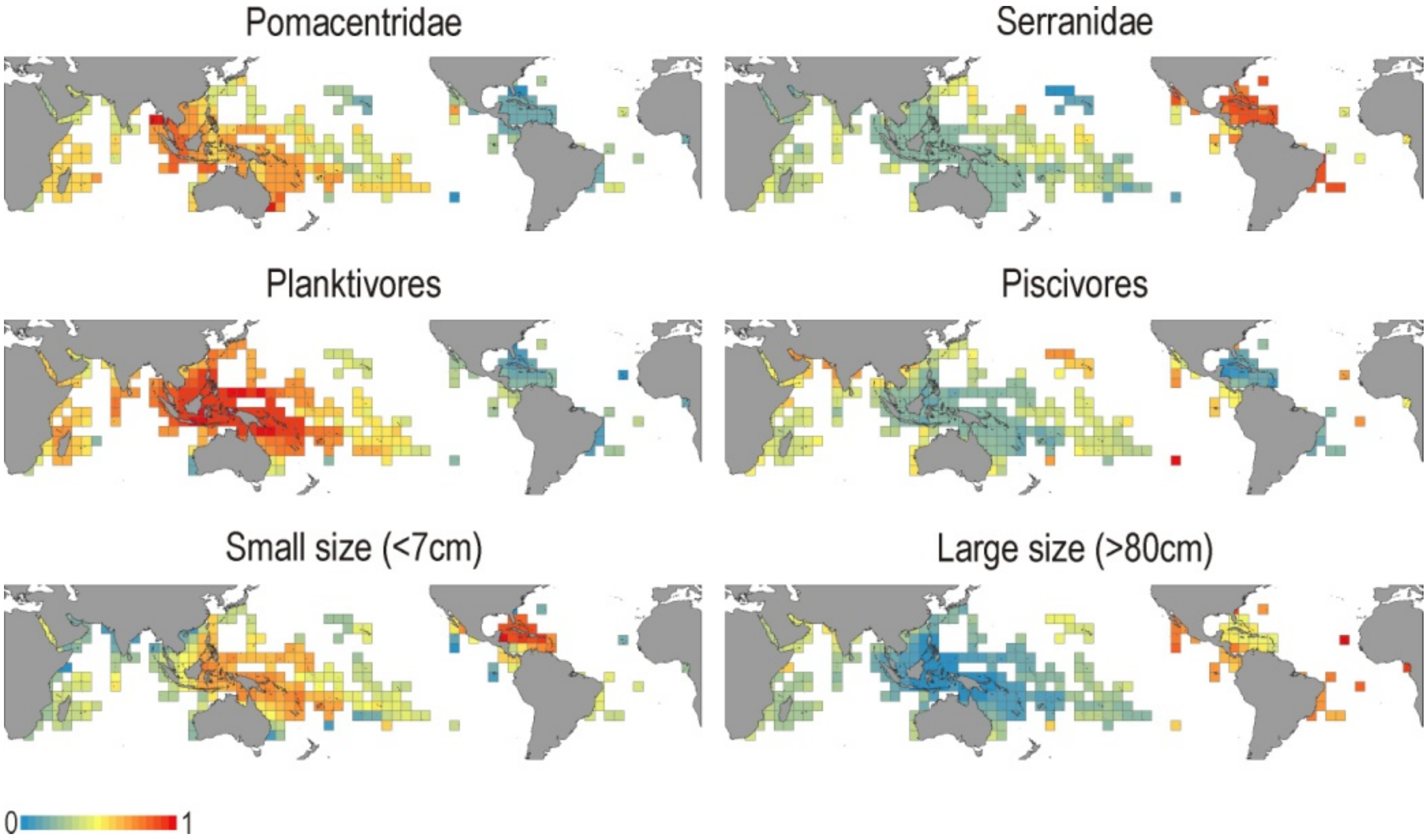

Figure 1. Spatial gradients in the proportion of two families, two diet groups and two size groups within reef fish assemblages across the globe. Color scale symbolizing proportion is different for each map. I will put a color scale legend on each map with actual min and max percentage.

Once these historical contingencies are taken into account, i.e. regional fish assemblages are randomly build using the realm species pools while keeping species richness constant, we observed strikingly different deviation patterns between taxonomic and functional structures. Despite the steep gradient in species richness within each realm, the taxonomic structure of fish assemblages remains remarkably constant (Fig. 2). Indeed, for most families their relative contribution to the biodiversity of assemblages generally lies within the range of values predicted by random draws (Fig. S1). Exceptions to this general pattern were mainly in found in species poor assemblages which host fewer Gobiidae but more Mureniade than expected. Contrary to the taxonomic pattern, large deviations were observed along the biodiversity gradients for both trophic guild (Fig. S2) and body size structure (Fig. S3). For instance, in the Indo-Pacific the relative contribution of planktivores was consistently lower than expected by chance (Fig. 2). By contrast piscivores were significantly more frequent than expected, regardless to the realm considered. Smaller deviations were observed for invertebrate feeders, while the proportions of other trophic guilds were close to random expectations. The largest departures were recorded for species body size. The proportion of small fishes (<7cm) was always significantly lower than expected by chance, while the opposite pattern was found for large species (>80cm), which always contributed more than expected, especially in species-poor assemblages (Fig. 2). More generally, strong deviations were observed in at least 5 of the 6 body size classes considered in the present study (Fig. S3).

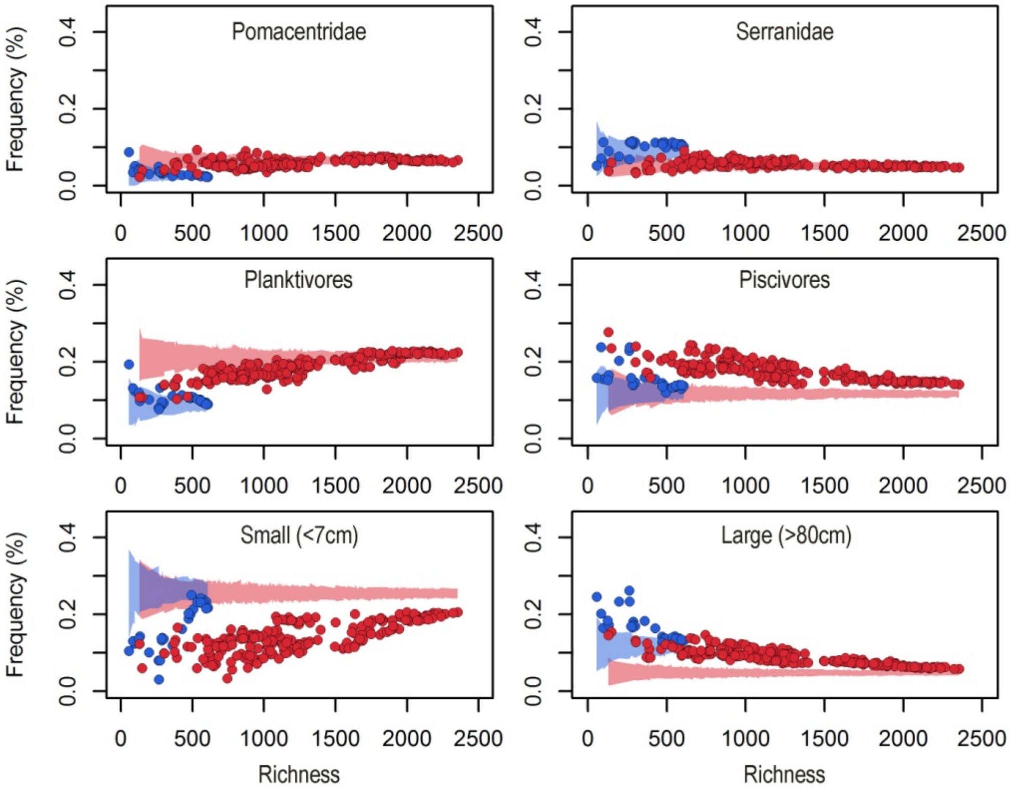

Figure 2. Variation in the contribution of two families, trophic guilds and size classes to assemblage species richness within two realms, *i.e.* the Atlantic (blue) and the Indo-Pacific (red). Colored areas represent 95% confidence intervals of the proportion from null models simulating for each level of species richness a random sampling of species from the species pool of each realm.

Using multivariate regression trees[26], we then assessed the relative contribution of biogeographical history and environmental variables in explaining the observed variation in the functional structure of assemblages. Specifically, we quantified the relative importance of biogeographical realm, geographical isolation, coral reef area and SST in explaining the reef fish structure in terms of trophic guilds and species size classes. Despite the steep gradients observed, the functional structure of fish assemblages was highly predictable (Fig. 3). Indeed, the consideration of few biogeographical and environmental variables explained 57% and 65% of the variation in size class and trophic structure, respectively. Surprisingly, at the global scale this high predictability is reached by the delineation of a remarkably low number of functionally homogeneous spatial units (4 for trophic guilds and 6 for species body size; Fig. 3). These analyses confirmed the importance of realm history in shaping the functional structure of assemblages. In terms of trophic organization, 53% of reef fish assemblage variation is explained by the realm identity. Biogeographical history have a comparatively lower role for shaping body size structure (29%) which is also explained by environmental variables, and especially coral reef area (Fig. 3).

Overall, our results support the view that the taxonomic structure and, more importantly, the functional structure of reef fish communities is primarily shaped by the combined effects of the biogeographical history and the availability of coral reefs. The historical biogeography of reef fishes[27] suggests that from the Oligocene onward, the Indo-Pacific experienced a history of connectivity, while the Eastern Pacific and the Atlantic were subjected to a history of isolation. The connectivity of the Indo-Pacific culminates during the Pliocene. In this favorable period coral reefs were expanding[20], and species originated in the IAA with subsequent movement toward the Central Pacific and the Indian Ocean. By contrast, during this period, the Tropical Eastern Pacific and the Atlantic Oceans were experiencing a contraction of their species pool probably due to extinction and increased isolation of their coral reefs[21]. In this context, our results support the hypothesis that large species, with high colonization capacities and post-dispersal persistence abilities[28,29], had greater chances of survival or recolonization in the Atlantic and Tropical Eastern Pacific than smaller species.

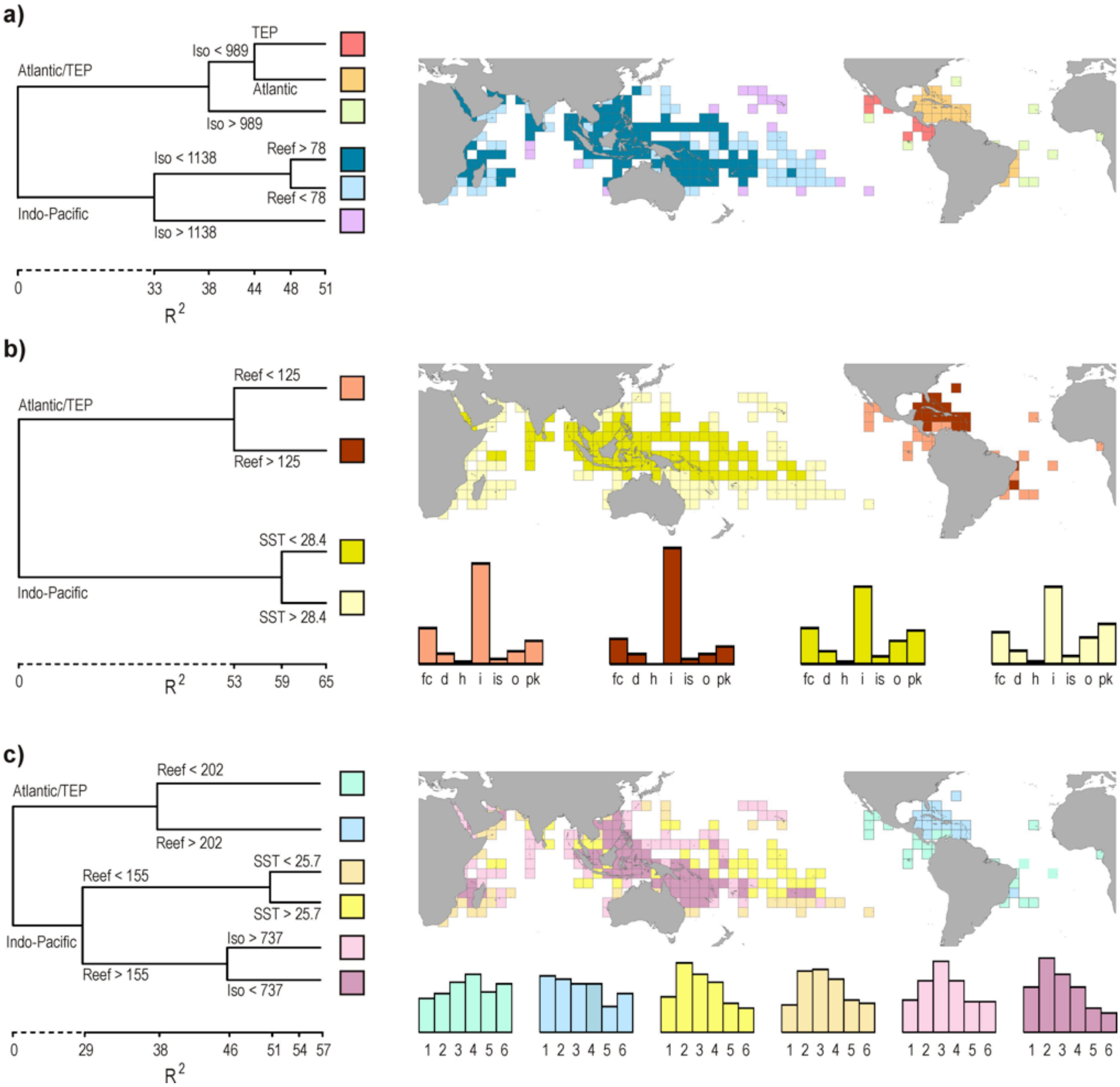

Figure 3. Biogeographic and ecological determinants of the functional structure of reef fish assemblages. **a)** Regression tree analysis and related map exploring the relationship between trophic guilds proportions and the explanatory variables. **b)** Regression tree analysis and related map exploring the relationship between the proportion of body size classes and the explanatory variables. TEP: Tropical Eastern Pacific, Iso: Isolation (km), Reef: coral reef area (km^2), SST: Sea Surface Temperature (°C). Barplots are referred to the mean proportion of each trophic guild or body size class considering the final group identified by the regression trees. fc: piscivore, d: herbivore-detritivore, h: herbivore targeting macroalgae, i: invertebrate feeders targeting mobile preys; is: invertebrate feeders targeting sessile preys; o: omnivores, pk: planktivores. 1: (<7cm), 2: (7-15cm), 3: (15-30cm), 4: (30-50cm), 5: (50-80cm), 6: (>80cm).

Once the effect of among-realm historical contingencies are taken out, the contribution of families to species richness of local assemblages is remarkably constant within the three realms. This was previously observed in the Indo-Pacific [30], and our work extends these findings to the Atlantic. The major within-realm variation is observed in terms of the functional organization of assemblages, i.e. the trophic structure, but especially the body size structure which is best explained by coral reef availability. The processes that account for functional divergence among realms also appear to apply within realms with large fishes characterizing locations with a limited coral reef area, or that are isolated from rich reef areas by barriers[27] or geographic distance [16,18,19]. Large species, showing high colonization capacity[29,31], may therefore have been favored in species-poor locations, presumably because of their ability to persist when facing unfavorable conditions or to better colonize after regional extinctions. By contrast, small species appear to have persisted better in locations with a high coral reef area, such as the IAA and the Caribbean.

Our interpretation is corroborated by the analysis of the conservatism of trophic status and species body size across families. On average, within a family, 88% of species belong to the same trophic group while only 66% of species were in the same body size class. This discrepancy in size vs. diet conservatism within families coupled to the stability of the taxonomic structure explain the comparatively higher stability of trophic organization. This pattern is also confirmed by the analysis of taxonomic composition since the few families deviating from the random expectations consistently have small (e.g. Gobiidae) or large (e.g. Carangidae) body size, while families with comparatively higher variation in body size (e.g. Serranidae) fit to the random pattern.

Our results highlight two aspects of major concern when considering the present threats on coral reefs[7]. First, we detected a marked realm-specificity in terms of functional structure. Biogeographical history is the major driver of both realm-specific taxonomic and functional structure of assemblages. This point may also be exemplified by the realm-specificity of variables determining the trophic structure of assemblages in each realm, SST in the Indo-Pacific and coral reef area in the Atlantic. Second, although taxonomic structure is mainly a legacy of biogeographical history, the functional structure of fish assemblages is strongly correlated to coral reef availability and water temperature, which are both being affected by global changes[7].

Our work calls for regional management strategies that must be tailored to the realm-specific taxonomic and functional structure of reef fish assemblages. Of course, conservation actions cannot address the inherent vulnerability of assemblages inherited from the past. However, our results support the view that evolutionary history structured fish assemblages by shaping connectivity among reefs, thereby filtering species according to their colonization and survival capacity[29]. This raises concerns given the ongoing fragmentation of coral reefs as a result of local human impact and global climatic changes. However, it emphasizes the importance of conservation efforts in sustaining coral reef connectivity. Connectivity can maintain populations and species, but it also prevents functional alteration as a result of the loss of species with limited colonization ability.

Methods summary

Distributional data

Presence-absence data on reef fish was obtained at 169 locations worldwide by 455 published references[18]. From these we obtained range maps, which were individually verified by experts. Species composition was extracted to a 5°×5° grid and further analyses were limited to coral reef assemblages (see Supplemetary methods).

Species functional traits

Fish body size was coded using 6 categories: 0-7cm, 7.1-15cm, 15.1-30cm, 30.1-50cm, 50.1-80cm, >80cm. Trophic strategy was defined according to 7 trophic guilds: herbivorous-detritivourous (i.e. fish feeding on turf and/or undefined organic material), macro-algal herbivorous (i.e. fish eating large fleshy algae and seagrass), invertivorous targeting sessile invertebrates (i.e. corals, sponges, ascidians), invertivorous targeting mobile invertebrate (i.e. benthic species such as crustaceans), planktivours (i.e. fish eating small organisms in the water column), piscivorous (including fish and cephalopods) and omnivorous, or fish for which both plant and animal material are important.

Null models

Two types of null models were conducted following a hierarchical approach. First, we tested for a potential influence of evolutionary history on the proportion of reef fish families, trophic guild and body size in the three biogeographic realms. For each realm we thus simulated 9999 assemblages of the same species richness by randomly sampling species in the global species pool. The observed proportions of each family, size class and trophic guild in the focal realm were then compared to the corresponding values in the simulated assemblages.

Second, we tested whether the taxonomic and functional structure at grid cell level was a random subset of the realm species pool using a similar approach, i.e. random sampling of species in the pool of species present in the realm to which the grid cells belongs

Multivariate regression trees

The effect of biogeographical realm, coral reef availability, Sea Surface Temperature and geographical isolation on the functional structure of fish assemblages were assessed using multivariate regression tree. Trees were calculated on multivariate matrices of the proportion of trophic guild and side classes with splitting based on information gain and were then pruned based on 100 cross-validations using the packages "mvpart" and "MVPARTwrap" within the R programming environment.

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Table S1. Results of null models comparing the proportions of different species body size classes in the three different realms (i.e. Atlantic, Indo-Pacific and TEP). Obs: observed proportion in each realm and lower and upper limits of the 95% confidence interval obtained with the null model. S1: size class 1 (<7cm), S2: size class 2 (7-15cm), S3: size class 3 (15-30cm), S4: size class 4 (30-50cm), S5: size class 5 (50-80cm), S6: size class 6 (>80cm).

Atlantic	**Obs**	**Lower**	**Upper**
S1	0.260642919	0.238922676	0.283231972
S2	0.191138141	0.250217202	0.297132928
S3	0.172893136	0.170286707	0.211989574
S4	0.166811468	0.120764553	0.157254561
S5	0.094700261	0.06342311	0.091225022
S6	0.113814075	0.046046916	0.070373588
Indo-Pacific	**Obs**	**Lower**	**Upper**
S1	0.254951011	0.255159475	0.267250365
S2	0.298311445	0.268084219	0.280175109
S3	0.196998124	0.185741088	0.196581197
S4	0.129872837	0.133625182	0.143214509
S5	0.072128414	0.073170732	0.080675422
S6	0.04773817	0.054617469	0.061079842
TEP	**Obs**	**Lower**	**Upper**
S1	0.224222586	0.22913257	0.294599018
S2	0.168576105	0.240589198	0.307692308
S3	0.173486088	0.16202946	0.222585925
S4	0.186579378	0.112929624	0.165302782
S5	0.117839607	0.057283142	0.096563011
S6	0.129296236	0.04091653	0.075286416

Table S2. Results of null models comparing the proportions of different species trophic categories in the three different realms (i.e. Atlantic, Indo-Pacific and TEP). Obs: observed proportion in each realm and lower and upper limits of the 95% confidence interval obtained with the null model. FC: Piscivores; HD: Herbivores-Detritivores; HM: Macroalgae feeders; IM: Mobile invertebrate feeders; IS: Sessile invertebrate feeders; OM: Omnivores; PK: Planktivores.

Atlantic	**Obs**	**Lower**	**Upper**
FC	0.118158123	0.09730669	0.13032146
HD	0.055603823	0.049522155	0.073848827
HM	0.005212858	0.003475239	0.011294526
IM	0.663770634	0.463944396	0.51694179
IS	0.015638575	0.013900956	0.028670721
OM	0.057341442	0.105125977	0.139009557
PK	0.084274544	0.164205039	0.205039096
Indo-Pacific	**Obs**	**Lower**	**Upper**
FC	0.116531165	0.109443402	0.118198874
HD	0.066499896	0.058161351	0.064623723
HM	0.0068793	0.006045445	0.008338545
IM	0.436939754	0.483010215	0.496977277
IS	0.023764853	0.01897019	0.022930999
OM	0.138836773	0.117573483	0.126537419
PK	0.210548259	0.179070252	0.190118824
TEP	**Obs**	**Lower**	**Upper**
S1	0.224222586	0.22913257	0.294599018
S2	0.168576105	0.240589198	0.307692308
S3	0.173486088	0.16202946	0.222585925
S4	0.186579378	0.112929624	0.165302782
S5	0.117839607	0.057283142	0.096563011
S6	0.129296236	0.04091653	0.075286416

Table S3. Results of null models comparing the proportions of the richest 100 families in the three different realms (i.e. Atlantic, Indo-Pacific and TEP). Obs: observed proportion in each realm and lower and upper limits of the 95% confidence interval obtained with the null model

	Atlantic			**Indo-Pacific**			**TEP**		
Family	**Obs**	**Lower**	**Upper**	**Obs**	**Lower**	**Upper**	**Obs**	**Lower**	**Upper**
Acanthuridae	0.1060	0.0999	0.1338	0.1222	0.1124	0.1211	0.1222	0.1124	0.1211
Acropomatidae	0.0834	0.0634	0.0877	0.0834	0.0707	0.0780	0.0834	0.0707	0.0780
Albulidae	0.0452	0.0556	0.0721	0.0659	0.0580	0.0636	0.0659	0.0580	0.0636
Ambassidae	0.0443	0.0504	0.0652	0.0590	0.0555	0.0611	0.0590	0.0555	0.0611
Ammodytidae	0.0391	0.0452	0.0599	0.0571	0.0507	0.0567	0.0571	0.0507	0.0567
Anomalopidae	0.0391	0.0374	0.0547	0.0513	0.0452	0.0511	0.0513	0.0452	0.0511
Antennariidae	0.0339	0.0243	0.0356	0.0284	0.0248	0.0281	0.0284	0.0248	0.0281
Apistidae	0.0304	0.0226	0.0313	0.0277	0.0238	0.0267	0.0277	0.0238	0.0267
Aploactinidae	0.0295	0.0209	0.0287	0.0254	0.0225	0.0254	0.0254	0.0225	0.0254
Aplodactylidae	0.0287	0.0200	0.0261	0.0236	0.0213	0.0242	0.0236	0.0213	0.0242
Apogonidae	0.0287	0.0182	0.0243	0.0231	0.0202	0.0229	0.0231	0.0202	0.0229
Aracanidae	0.0278	0.0174	0.0235	0.0227	0.0192	0.0219	0.0227	0.0192	0.0219
Ariidae	0.0269	0.0165	0.0217	0.0223	0.0179	0.0211	0.0223	0.0179	0.0211
Arripidae	0.0252	0.0156	0.0209	0.0156	0.0154	0.0177	0.0156	0.0154	0.0177
Atherinidae	0.0226	0.0148	0.0191	0.0152	0.0150	0.0169	0.0152	0.0150	0.0169
Atherinopsidae	0.0217	0.0148	0.0182	0.0152	0.0146	0.0163	0.0152	0.0146	0.0163
Aulopidae	0.0191	0.0139	0.0174	0.0150	0.0144	0.0158	0.0150	0.0144	0.0158
Aulostomidae	0.0165	0.0130	0.0174	0.0146	0.0140	0.0154	0.0146	0.0140	0.0154
Balistidae	0.0156	0.0122	0.0165	0.0138	0.0136	0.0152	0.0138	0.0136	0.0152
Batrachoididae	0.0148	0.0122	0.0156	0.0119	0.0131	0.0148	0.0119	0.0131	0.0148
Belonidae	0.0139	0.0113	0.0148	0.0115	0.0127	0.0144	0.0115	0.0127	0.0144
Blenniidae	0.0122	0.0113	0.0148	0.0108	0.0123	0.0140	0.0108	0.0123	0.0140
Bothidae	0.0113	0.0104	0.0139	0.0100	0.0119	0.0136	0.0100	0.0119	0.0136
Bregmacerotidae	0.0113	0.0096	0.0130	0.0098	0.0115	0.0131	0.0098	0.0115	0.0131
Bythitidae	0.0113	0.0096	0.0130	0.0094	0.0110	0.0127	0.0094	0.0110	0.0127
Caesionidae	0.0104	0.0087	0.0122	0.0092	0.0104	0.0123	0.0092	0.0104	0.0123
Callanthiidae	0.0104	0.0078	0.0113	0.0088	0.0096	0.0117	0.0088	0.0096	0.0117

Callionymidae	0.0104	0.0078	0.0113	0.0085	0.0077	0.0094	0.0085	0.0077	0.0094
Caproidae	0.0096	0.0070	0.0104	0.0083	0.0073	0.0088	0.0083	0.0073	0.0088
Caracanthidae	0.0096	0.0070	0.0096	0.0075	0.0071	0.0081	0.0075	0.0071	0.0081
Carangidae	0.0087	0.0070	0.0096	0.0069	0.0067	0.0079	0.0069	0.0067	0.0079
Carapidae	0.0087	0.0061	0.0087	0.0069	0.0065	0.0075	0.0069	0.0065	0.0075
Centracanthidae	0.0087	0.0061	0.0087	0.0067	0.0063	0.0073	0.0067	0.0063	0.0073
Centriscidae	0.0087	0.0061	0.0078	0.0065	0.0060	0.0071	0.0065	0.0060	0.0071
Centrogenyidae	0.0078	0.0052	0.0078	0.0065	0.0058	0.0069	0.0065	0.0058	0.0069
Centropomidae	0.0078	0.0052	0.0070	0.0060	0.0056	0.0067	0.0060	0.0056	0.0067
Chaenopsidae	0.0078	0.0052	0.0070	0.0060	0.0054	0.0065	0.0060	0.0054	0.0065
Chaetodontidae	0.0078	0.0052	0.0070	0.0058	0.0052	0.0063	0.0058	0.0052	0.0063
Cheilodactylidae	0.0070	0.0043	0.0070	0.0054	0.0050	0.0060	0.0054	0.0050	0.0060
Chirocentridae	0.0070	0.0043	0.0061	0.0054	0.0048	0.0058	0.0054	0.0048	0.0058
Chironemidae	0.0061	0.0043	0.0061	0.0052	0.0046	0.0054	0.0052	0.0046	0.0054
Chlopsidae	0.0061	0.0043	0.0061	0.0048	0.0044	0.0052	0.0048	0.0044	0.0052
Cirrhitidae	0.0061	0.0043	0.0052	0.0046	0.0042	0.0050	0.0046	0.0042	0.0050
Clinidae	0.0052	0.0043	0.0052	0.0046	0.0040	0.0048	0.0046	0.0040	0.0048
Clupeidae	0.0052	0.0035	0.0052	0.0044	0.0040	0.0046	0.0044	0.0040	0.0046
Congiopodidae	0.0052	0.0035	0.0052	0.0044	0.0038	0.0046	0.0044	0.0038	0.0046
Congridae	0.0043	0.0035	0.0052	0.0042	0.0038	0.0044	0.0042	0.0038	0.0044
Creediidae	0.0043	0.0035	0.0043	0.0040	0.0035	0.0042	0.0040	0.0035	0.0042
Cynoglossidae	0.0035	0.0035	0.0043	0.0040	0.0035	0.0042	0.0040	0.0035	0.0042
Cyprinidae	0.0035	0.0035	0.0043	0.0033	0.0033	0.0040	0.0033	0.0033	0.0040
Dactylopteridae	0.0026	0.0035	0.0043	0.0031	0.0033	0.0038	0.0031	0.0033	0.0038
Dactyloscopidae	0.0026	0.0026	0.0043	0.0029	0.0031	0.0038	0.0029	0.0031	0.0038
Dentatherinidae	0.0026	0.0026	0.0043	0.0029	0.0031	0.0038	0.0029	0.0031	0.0038
Dichistiidae	0.0026	0.0026	0.0043	0.0027	0.0031	0.0035	0.0027	0.0031	0.0035
Dinopercidae	0.0026	0.0026	0.0035	0.0027	0.0029	0.0035	0.0027	0.0029	0.0035
Diodontidae	0.0026	0.0026	0.0035	0.0025	0.0029	0.0033	0.0025	0.0029	0.0033
Drepaneidae	0.0026	0.0026	0.0035	0.0025	0.0029	0.0033	0.0025	0.0029	0.0033
Echeneidae	0.0026	0.0026	0.0035	0.0025	0.0027	0.0033	0.0025	0.0027	0.0033

Eleotridae	0.0017	0.0026	0.0035	0.0023	0.0027	0.0031	0.0023	0.0027	0.0031
Elopidae	0.0017	0.0026	0.0035	0.0023	0.0027	0.0031	0.0023	0.0027	0.0031
Embiotocidae	0.0017	0.0017	0.0035	0.0023	0.0025	0.0029	0.0023	0.0025	0.0029
Engraulidae	0.0017	0.0017	0.0026	0.0021	0.0025	0.0029	0.0021	0.0025	0.0029
Enoplosidae	0.0017	0.0017	0.0026	0.0021	0.0023	0.0029	0.0021	0.0023	0.0029
Ephippidae	0.0017	0.0017	0.0026	0.0021	0.0023	0.0027	0.0021	0.0023	0.0027
Epigonidae	0.0017	0.0017	0.0026	0.0021	0.0023	0.0027	0.0021	0.0023	0.0027
Eschmeyeridae	0.0017	0.0017	0.0026	0.0019	0.0021	0.0027	0.0019	0.0021	0.0027
Exocoetidae	0.0017	0.0017	0.0026	0.0019	0.0021	0.0025	0.0019	0.0021	0.0025
Fistulariidae	0.0017	0.0017	0.0026	0.0019	0.0019	0.0025	0.0019	0.0019	0.0025
Gerreidae	0.0017	0.0017	0.0026	0.0019	0.0019	0.0023	0.0019	0.0019	0.0023
Glaucosomatidae	0.0009	0.0017	0.0026	0.0017	0.0019	0.0023	0.0017	0.0019	0.0023
Gnathanacanthidae	0.0009	0.0017	0.0026	0.0017	0.0017	0.0021	0.0017	0.0017	0.0021
Gobiesocidae	0.0009	0.0017	0.0017	0.0015	0.0017	0.0021	0.0015	0.0017	0.0021
Gobiidae	0.0009	0.0017	0.0017	0.0013	0.0017	0.0021	0.0013	0.0017	0.0021
Grammatidae	0.0009	0.0009	0.0017	0.0013	0.0015	0.0019	0.0013	0.0015	0.0019
Haemulidae	0.0009	0.0009	0.0017	0.0010	0.0015	0.0019	0.0010	0.0015	0.0019
Hapalogenyidae	0.0009	0.0009	0.0017	0.0010	0.0015	0.0019	0.0010	0.0015	0.0019
Hemiramphidae	0.0009	0.0009	0.0017	0.0010	0.0013	0.0017	0.0010	0.0013	0.0017
Hexagrammidae	0.0009	0.0009	0.0017	0.0010	0.0013	0.0017	0.0010	0.0013	0.0017
Holocentridae	0.0009	0.0009	0.0017	0.0008	0.0010	0.0015	0.0008	0.0010	0.0015
Inermiidae	0.0009	0.0009	0.0017	0.0008	0.0010	0.0015	0.0008	0.0010	0.0015
Kraemeriidae	0.0009	0.0009	0.0017	0.0008	0.0010	0.0013	0.0008	0.0010	0.0013
Kuhliidae	0.0009	0.0009	0.0017	0.0008	0.0010	0.0013	0.0008	0.0010	0.0013
Kyphosidae	0.0009	0.0009	0.0017	0.0008	0.0008	0.0013	0.0008	0.0008	0.0013
Labridae	0.0009	0.0009	0.0017	0.0008	0.0008	0.0013	0.0008	0.0008	0.0013
Labrisomidae	0.0009	0.0009	0.0017	0.0008	0.0008	0.0010	0.0008	0.0008	0.0010
Lateolabracidae	0.0009	0.0009	0.0009	0.0008	0.0008	0.0010	0.0008	0.0008	0.0010
Latidae	0.0009	0.0009	0.0009	0.0008	0.0008	0.0010	0.0008	0.0008	0.0010
Latridae	0.0009	0.0009	0.0009	0.0006	0.0008	0.0008	0.0006	0.0008	0.0008
Leiognathidae	0.0009	0.0009	0.0009	0.0006	0.0006	0.0008	0.0006	0.0006	0.0008

Lethrinidae	0.0009	0.0009	0.0009	0.0006	0.0006	0.0008	0.0006	0.0006	0.0008
Lobotidae	0.0009	0.0009	0.0009	0.0006	0.0006	0.0008	0.0006	0.0006	0.0008
Lophiidae	0.0009	0.0009	0.0009	0.0006	0.0006	0.0008	0.0006	0.0006	0.0008
Lutjanidae	0.0009	0.0009	0.0009	0.0006	0.0006	0.0008	0.0006	0.0006	0.0008
Malacanthidae	0.0009	0.0009	0.0009	0.0006	0.0006	0.0008	0.0006	0.0006	0.0008
Megalopidae	0.0000	0.0009	0.0009	0.0006	0.0006	0.0008	0.0006	0.0006	0.0008
Menidae	0.0000	0.0009	0.0009	0.0006	0.0006	0.0006	0.0006	0.0006	0.0006
Merlucciidae	0.0000	0.0009	0.0009	0.0006	0.0006	0.0006	0.0006	0.0006	0.0006
Microdesmidae	0.0000	0.0009	0.0009	0.0006	0.0006	0.0006	0.0006	0.0006	0.0006
Monacanthidae	0.0000	0.0009	0.0009	0.0006	0.0006	0.0006	0.0006	0.0006	0.0006
Monocentridae	0.0000	0.0026	0.0174	0.0163	0.0169	0.0208	0.0163	0.0169	0.0208

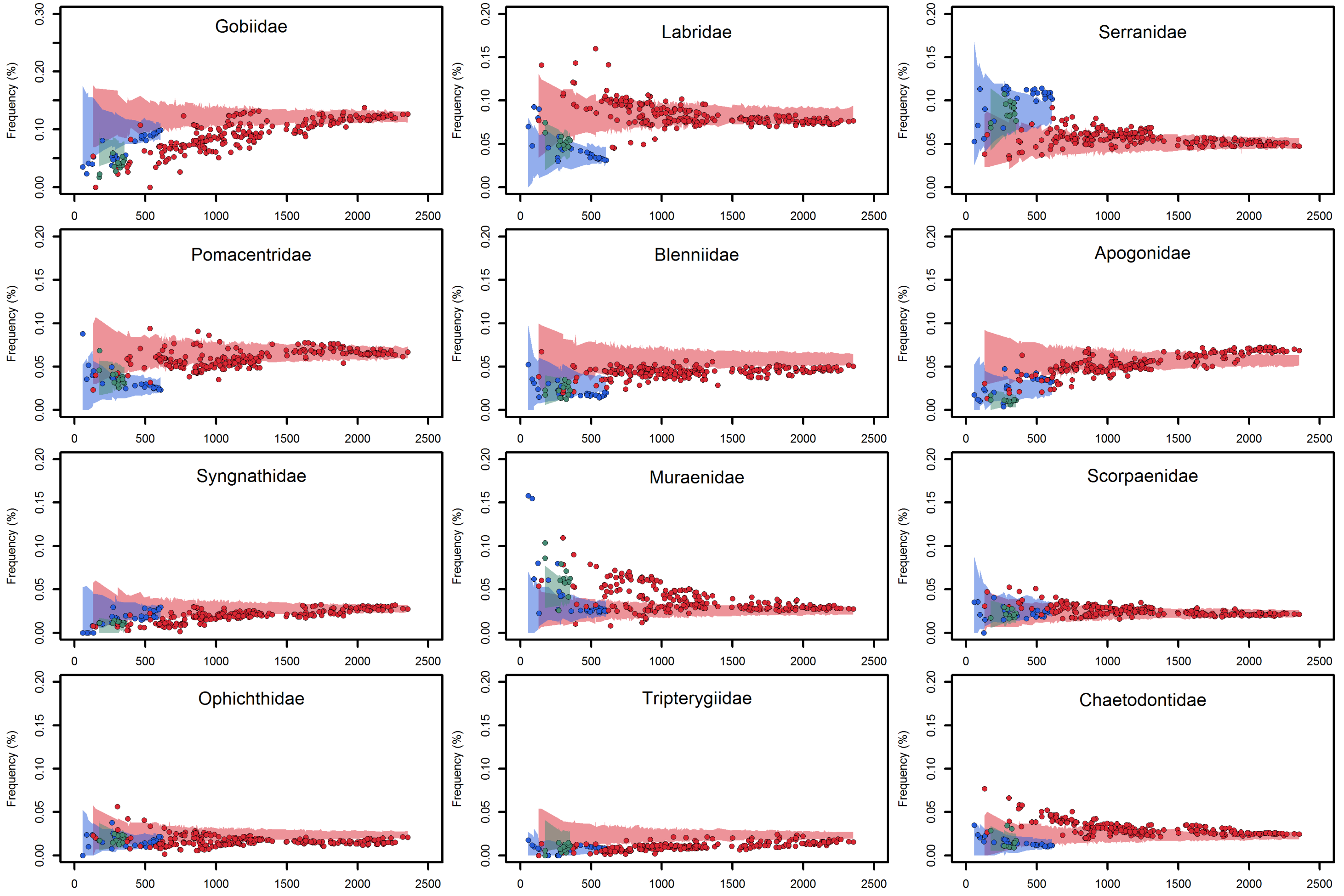

Fig. S1. Variation in the contribution to the total species richness by the 12 richest families (56% of the global species richness) within the three realms, i.e. the Atlantic (blue) and the Indo-Pacific (red) and Eastern Tropical Pacific (green). Polygons represent 95% confidence intervals by null models based on the random sampling of species from the pool of each realm maintaining fixed the species richness at each location.

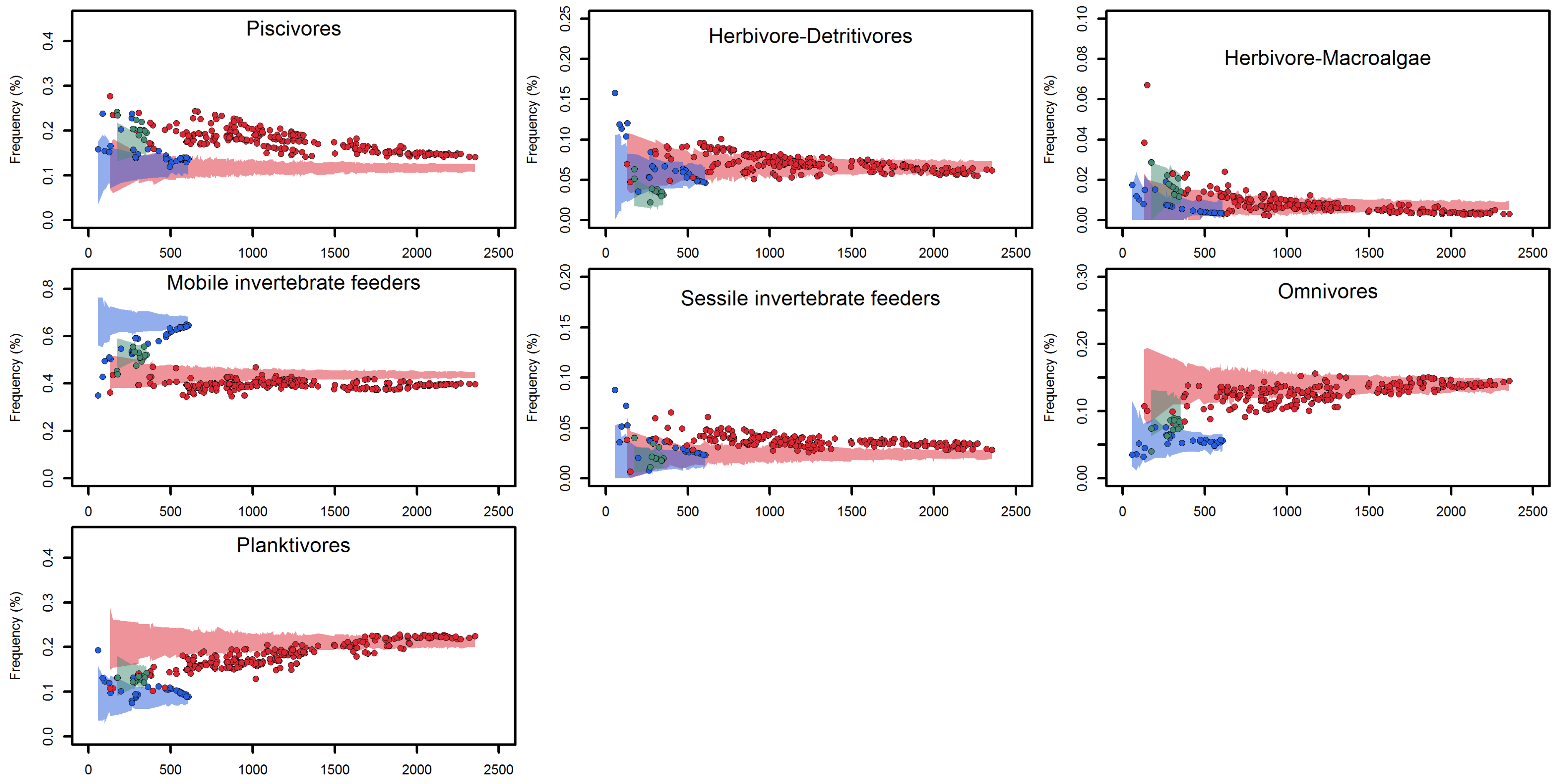

Fig. S2. Variation in the contribution to the total species richness by 7 trophic categories within the three realms, i.e. the Atlantic (blue) and the Indo-Pacific (red) and Eastern Tropical Pacific (green). Polygons represent 95% confidence intervals by null models based on the random sampling of species from the pool of each realm maintaining fixed the species richness at each location.

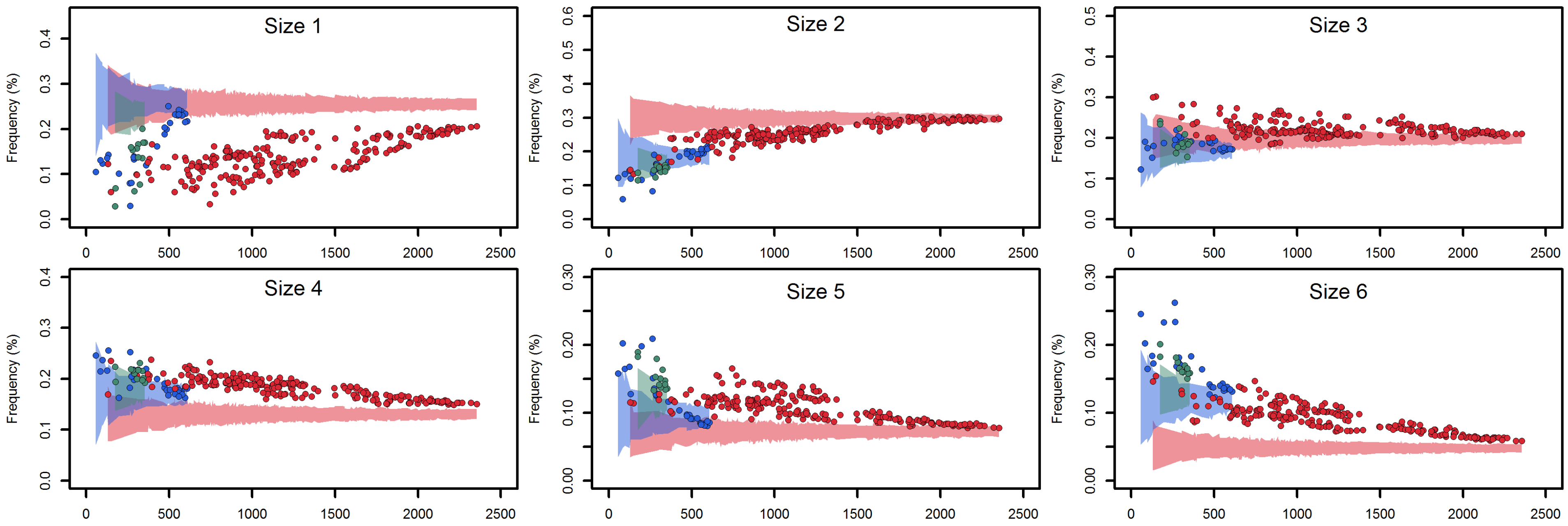

Fig. S3. Variation in the contribution to the total species richness by 6 body size classes within the three realms, i.e. the Atlantic (blue) and the Indo-Pacific (red) and Eastern Tropical Pacific (green). Polygons represent 95% confidence intervals by null models based on the random sampling of species from the pool of each realm maintaining fixed the species richness at each location.

ARTIGO III

Formatado segundo instruções aos autores para a revista *Ecography*

Contrasting patterns of taxonomic and functional nestedness among tropical reef fish assemblages

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ABSTRACT

Taxonomic nestedness, the degree to which the taxonomic composition of species-poor assemblages represents a subset of richer sites, generally occurs in habitat fragments and islands differing in size and isolation from a source pool. However, species are not ecologically equivalent and the extent to which nestedness is observed also in terms of functional trait composition of assemblages still remains poorly know. Here, using an extensive database on the functional traits and the distributions of 6,316 tropical reef fish species across 169 sites, we assessed the levels of nestedness of reef fish assemblages at the global scale, contrasting patterns of taxonomical vs. functional composition of assemblages. Most reef fish assemblages showed nested functional structures, but not taxonomical. Functional nestedness was generally associated to sites of small area with high levels of geographical isolation. Because a nested pattern in the functional composition implies that certain traits may be represented by few species, we identified these groups of low redundancy that include large herbivore-detritivores and omnivores, small piscivores, and macro-algal herbivores. The identified patterns of nestedness may be an outcome of the interaction between species' dispersal capabilities and/or resource requirements, and gradients of isolation and habitat area. The importance of reef area and isolation in generating the observed pattern of functional nestedness may indicate that habitat loss in depauperate and isolated sites can have disproportionate effects on the functional structure of their reef fish assemblages.

INTRODUCTION

Species assemblages are nested when species-poor sites are subsets of species-rich sites (Patterson and Atmar 1986, Almeida-Neto and Ulrich 2011), a pattern commonly observed at large spatial scales (Simberloff and Martin 1991, Lomolino 1996). A variety of processes, deterministic or stochastic, have been proposed to cause nested patterns of species assemblages (Ulrich et al. 2009). These processes include differential colonization and extinction driven by species-specific traits, such as dispersal ability (Patterson and Atmar 1986, 2000; Srinivasan et al. 2013) and habitat heterogeneity or quality associated with species with varying degrees of specialization (Wright and Reeves 1992). The level of nestedness modulates the extent to which large areas contain the diversity of species and traits hosted in smaller areas (Patterson and Atmar 1986, 2000; Ulrich et al. 2009).

The breadth of functions performed by species is a biodiversity facet that is worth preserving within the context of an impeding mass extinction (Naeem et al. 2012). Indeed, functional diversity (FD), i.e. the diversity of functional traits within a species assemblage, sustains core ecosystem functions such as productivity (Mouillot et al. 2011) and resilience under multiple stressors (Bellwood et al. 2004). Functional redundancy, where different species perform similar functions (Lawton and Brown 1994; Naeem 1998), is thus key to ensure ecosystem functioning since it buffers the loss of functions against the loss of species (Hooper et al. 2002, Bellwood et al. 2004). The level of functional redundancy within assemblages has been widely investigated but the level of spatial insurance among assemblages, i.e. the extent to which different assemblages host species supporting the same functional roles, is still unknown at large scales and in the marine realm. Given the potential erosion of FD following the loss of species (Flynn et al. 2009, Mouillot et al. 2013a), the level of functional nestedness among assemblages would modulate the resilience of FD. Thus, the patterns and processes underlying functional nestedness need further investigations.

Taxonomic nestedness tends to emerge in archipelagos or habitat patches through a combination of differences in island (or patch) sizes and degrees of isolation from a source pool (Lomolino 1996, 1999) (Fig. 1A). However, we still lack predictions about the influence of such biogeographic factors on the functional nestedness among assemblages. The identification of associations between nestedness and habitat variables (e.g. area, isolation, habitat type) can offer relevant perspectives on the interaction between traits and the environment, which in turn are important to conservation strategies and management efforts (Fleishman et al. 2002, Semmens et al. 2010, Novak et al. 2011, Wang et al. 2013). Here, we estimated the degree of nestedness among reef fish assemblages across the world's oceans to assess whether the taxonomic and functional structures of depauperate assemblages represent subsets of richer ones.

We hypothesize that the degree of nestedness among reef fish assemblages is determined by biogeographical gradients of reef area and isolation (Fig. 1). The highest degree of nestedness is expected under large differences in area and an intermediate level of isolation among sites (Fig. 1A) since differences in area and isolation generate gradients in species richness according to the Theory of Island Biogeography, a key element to cause a nested pattern (Patterson and Atmar 1986, Almeida-Neto and Ulrich 2011). For taxonomic nestedness, a low gradient of isolation among sites should generate non-nested homogeneous patterns, regardless the area size, since high connectivity among sites should maintain similarity among assemblages (Azeria 2004). At an intermediate isolation gradient we expect a more pronounced nested pattern for larger area gradients, since differences in area among sites would favour species richness gradients, and poor sites would be subsets of rich sites (Patterson and Atmar 1986, Almeida-Neto and Ulrich 2011). At the other extreme, a strong isolation gradient would shape a non-nested subset pattern of species composition regardless the gradient in area (Fig. 1C) because isolated sites would tend to have dissimilar species compositions due to high speciation and extinction rates (Budd and Pandolfi 2010). For functional nestedness, these effects are predicted under a wider gradient of isolation, given that functional entities (FEs), i.e. unique combinations of species traits, may be represented by different species along biogeographical gradients. Two alternative hypotheses can thus be made about the effects of area and isolation on the functional nestedness of assemblages. First, functional nestedness patterns may follow those of taxonomic nestedness where species tend to occupy different FEs. In this case taxonomic nestedness would imply functional nestedness (Fig. 1D). However, several species could be gathered into a small number of highly redundant

FEs (see Fig. 1B). In that case, functional nestedness may occur at both intermediate and high degrees of isolation. This is expected since taxonomic dissimilarity among sites does not necessarily imply functional dissimilarity even under high degrees of isolation (Fig. 1E). Thus the level of functional redundancy among species modulates the patterns of functional nestedness that is not totally driven by taxonomic nestedness.

Here, we aim to investigate whether (i) reef fish assemblages are functionally or taxonomically nested across scales; (ii) the nested structure of the functional component is driven by taxonomic patterns; (iii) the degree of nestedness are correlated with biogeographical factors, habitat area and isolation.

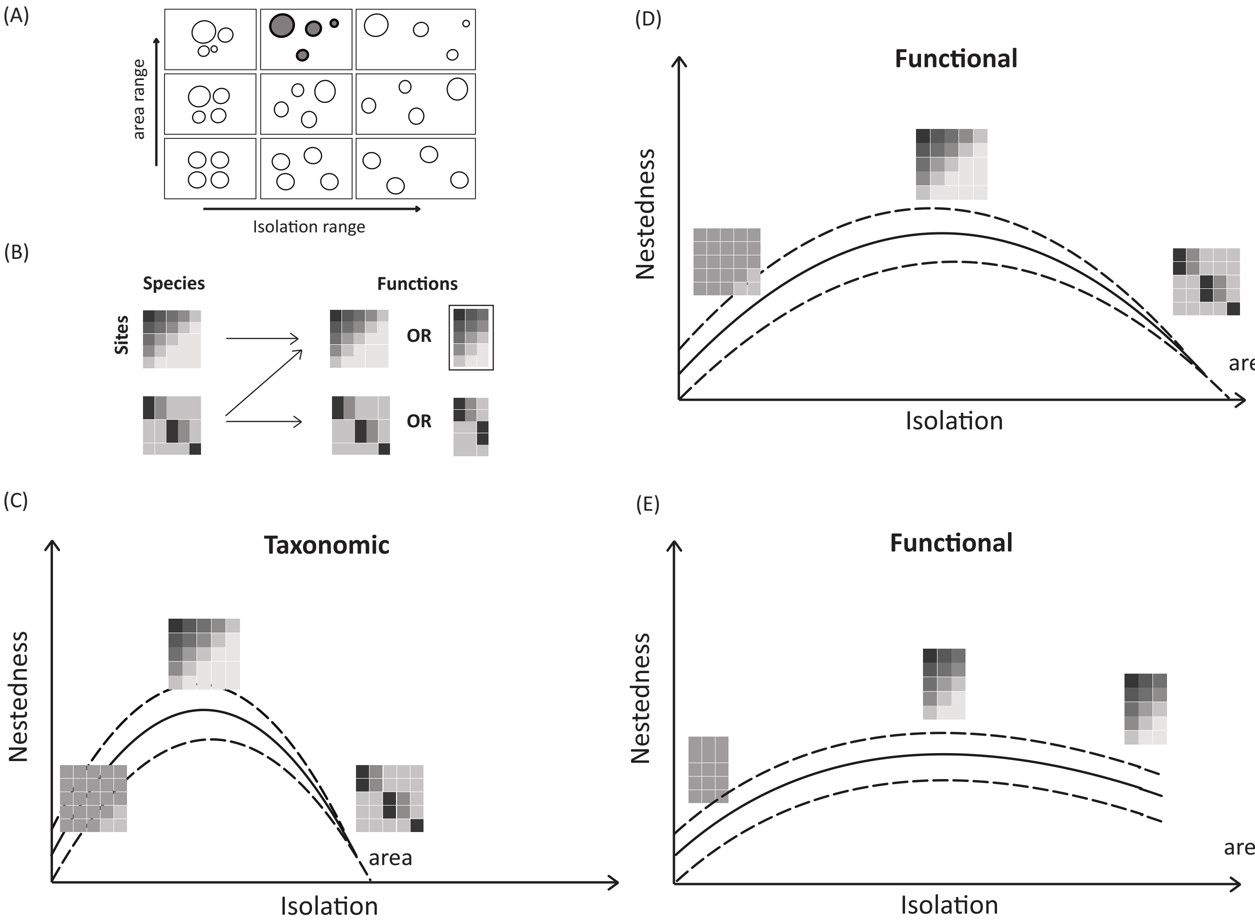

Figure 1. The expected trend of taxonomic and functional nestedness among sites along gradients of area and isolation. (A) Diagram showing nine configurations mixing gradients of area and isolation for a set of four sites. Circle sizes are proportional to site areas while the spread among circles depicts isolation. The highest degree of nestedness is expected under a large gradient of areas and an intermediate degree of isolation (filled circles). (B) The transition from the taxonomic to the functional structure of assemblages. Taxonomic nestedness can generate functional nestedness when each species represents a functional entity (FE) or when several species are gathered into one FE (functional redundancy, highlighted box) (top). A dissimilar taxonomic composition among assemblages can generate either functional nestedness or functional dissimilarity among assemblages. (C) For taxonomic nestedness, a low gradient of isolation among sites tends to generate non-nested homogeneous patterns (left matrix) regardless the area gradient. Intermediate isolation among sites might cause a nested pattern (central matrix) that should be more pronounced for larger area gradients. In contrast, more isolated sites should exhibit non-nested taxonomic patterns whatever the area gradient. Dashed lines denote the effects of area gradients – increase and decrease – in nestedness. (D) For functional nestedness, these effects are predicted under a wider gradient of isolation, given that functional entities may be represented by different species along biogeographical gradients. (E) Under this scenario, species are concentrated into a smaller number of FEs, and functional nestedness occurs at both an intermediate and high degree of isolation. This is expected because the taxonomic turnover does not necessarily result in functional turnover under high degrees of isolation.

METHODS

The database

Our database comprises estimates of reef fish species richness at 169 sites distributed across six marine biogeographic regions (Kulbicki et al. 2013) (Fig. 2). Employing a cut-off at 17°C of minimum Sea Surface Temperature, we limited our study to tropical reefs including both coral and rocky formations (Parravicini et al. 2013). In addition to reef fish species distributions, compiled information includes detailed biological attributes for reef fish species, as well as environmental and geographic data for each site (Parravicini et al. 2013, Kulbicki et al. 2013).

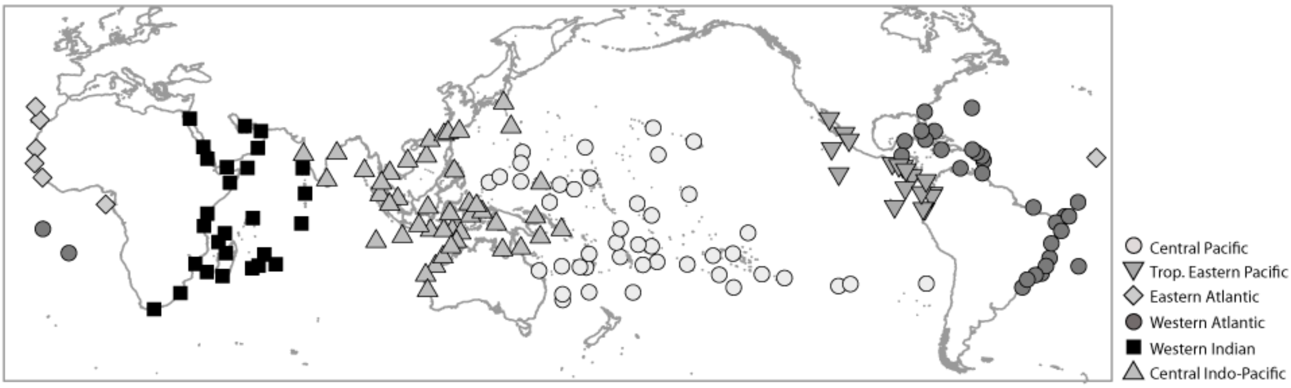

Figure 2. Map of 169 sites, which correspond to reef fish assemblages, distributed across six biogeographic regions. From left to right: Eastern Atlantic (grey diamonds), Western Indian (black squares), Central Indo-Pacific (grey triangle), Central Pacific (light-grey circles), Tropical Eastern Pacific (inverted triangles), Western Atlantic (dark-grey circles). For a map of provinces embedded in regions see Appendix S4.

Reef fish functional entities

Reef fish species were classified into one of the maximum body size categories: 0-7 cm, 7.1-15 cm, 15.1-30 cm, 30.1-50 cm, 50.1-80 cm and >80 cm. Species were also classified according to their diet based on the main items consumed by each species, which led to the following categories: herbivore-detritivores (i.e. fish feeding on turf or filamentous algae and/or undefined organic material), macro-algal herbivores (i.e. fish eating large fleshy algae and/or seagrass), invertivores targeting sessile invertebrates (i.e. corals, sponges, ascidians), invertivores targeting mobile invertebrate (i.e. benthic species such as crustaceans), planktivores (i.e. fish eating small organisms in the water column), piscivores (including fish and cephalopods) and omnivores, i.e. fish for which both vegetal and animal material are important in their diet.

The functional entity of each reef fish species was described as a combination of maximum body size and diet categorical traits. Such combinations of attributes have been previously employed to describe FEs of reef fish species (Halpern and Floeter 2008; Mouillot et al. 2013a). Fish species body size, for instance, is a proxy to other related traits, including species' geographic range size and pelagic larval duration (Luiz et al. 2012, 2013), reproductive output and growth rate (Munday and Jones 1998; Wong et al. 2007). A species' trophic level is determined by the type and variety of food items it consumes, which can provide information on specific habitat requirements (Berumen and Pratchett 2008; Burkepile and Hay 2008), dependence on other trophic levels and home range (see Supplemental material Appendix 1 for a complete justification of the chosen life history traits). We counted the number of species in each FE across all sites contained in provinces and biogeographic regions. Data was arranged into matrices with FEs as rows and sites as columns.

We also employed a second functional entity scheme to assess the sensitivity of nestedness to more refined trait combinations. In addition to body size and diet categories, mobility and schooling behavior were included in order to describe reef fish FE.

Reef fish taxonomic groups

The taxonomic units considered in our analysis were reef fish families. The use of this taxonomic level is appropriate because it enables comparisons among reef fish assemblages across large biogeographic regions, since families tend to be more conservative (i.e. similar) across such regions when compared to reef fish genera for instance (Bellwood and Wainwright 2002; Floeter et al. 2008). The reef fish families considered herein comprise those referred to by Bellwood & Wainwright (2002) and Floeter et al. (2008), including the typical reef fish families Acanthuridae, Apogonidae, Blennidae, Carangidae, Chaetodontidae, Holocentridae, Labridae, Mullidae, Pomacentridae and Scaridae (Bellwood 1996), as well as other typical reef taxa that occur in certain areas (Chaenopsidae, Labrisomidae, Siganidae, etc.). We counted the number of species in a given family occurring across all sites of provinces and biogeographic regions as defined by Kulbicki et al. (2013). Again, data was organized in matrices where rows denote taxonomic groups, i.e. families, and columns represent sites.

Site attributes

For each site we defined, according to maps and descriptions in the original publications, the area to which the site's species list pertains, thereby allowing the computation of environmental variables around each site (see Parravicini et al. 2013). All information was converted to a global equal-area Behrmann projection before analyses. In studies of nestedness, isolation has been traditionally quantified as the distance from a source pool; yet it is also important to consider the influence of connectivity among sites, which can also operate as a source of species. Here we made use of two complementary measures of isolation: the distance from the biodiversity centre, and the distances of each site to the 10 nearest reef habitat patches, a measure of connectivity (Parravicini *et al.*, 2013). The distance from the diversity center for each biogeographical realm was measured in degrees, and it corresponded to the Caribbean (474 species recorded in Cuba) (Briggs 2003; Floeter et al. 2008), for sites within the Atlantic, and to the Indo-Australian Archipelago (>2000 species in the Philippines) (Carpenter and Springer 2005) for sites in the Indo-Pacific. Connectivity was calculated using a nearest neighbor approach (Moilanen & Nieminen, 2002), which corresponded to the mean distance from the site to the 10 nearest patches of habitat (Parravicini et al. 2013). Coral reef area derived from the Coral Reef Millennium Census project (UNEP-WCMC 2012), while rocky reef layer derived from Halpern et al. (2008).

Data analysis

Nestedness analysis

Analyses were carried out at two spatial scales. The first and larger scale corresponded to six biogeographic regions defined for reef fish faunas (Kulbicki et al. 2013), namely: Eastern Atlantic, Western Atlantic, Tropical Eastern Pacific, Central

Pacific, Central Indo-Pacific, and Western Indo-Pacific (Fig. 2). These regions were composed of a number of provinces, which in turn were constituted by a given number of sites (Fig. 2; Appendix 2, Fig. A2). The second set of analysis was conducted at the Province scale (Kulbicki et al. 2013), encompassing 14 provinces presenting specific characteristics of its associated reef fish fauna (see Appendix 2, Table A2 for a complete list of provinces, their sites and local species richness).

We assessed the degree of nestedness of reef fish assemblages at both spatial scales to investigate whether the patterns were similar across regions and its constituent provinces. Within a region, provinces might exhibit different degrees of nestedness, which could correspond to particular processes operating and structuring their reef fish assemblages. At both scales, we examined the nestedness degree of the taxonomic and functional structure of reef fish assemblages.

There are many indices available to measure nestedness using presence-absence data (see Ulrich et al. 2009), and more recently, metrics designed to estimate nestedness for quantitative data have been developed (Galeano et al. 2009, Almeida-Neto and Ulrich 2011). Quantitative data may contain more accurate and complex information on the possible mechanisms underpinning community structure compared to binary presence-absence data (Ulrich and Gotelli 2010). Moreover, quantitative data can provide important information regarding the structure of different components of assemblages (functional and taxonomic) along large gradients of species richness. In order to estimate the nestedness degree of the taxonomic and functional structures of reef fish assemblages, we used the weighted nestedness metric based on overlap and decreasing fill (WNODF) (Almeida-Neto and Ulrich 2011), the quantitative version of NODF (Almeida-Neto et al. 2008). Under this metric, nestedness can be quantified for the whole matrix, as well as the nestedness of species and sites, *i.e.*, rows and columns. A WNODF nestedness score ranges from 0 (non-nested) to 100 (perfectly nested).

To assess the probability that functional and taxonomic nestedness could be obtained by chance, we have contrasted the empirical WNODF values with 95% confidence limits of WNODF values obtained from random matrices (1000 random matrices). Random matrices were generated through the quasiswap count algorithm (available in VEGAN R Package). In this method, a matrix is filled preserving the original row and column totals, and then the algorithm implements swaps in random 2 x 2 submatrices.

We calculated the Z-score = $(X - \mu\, simul)/\sigma\, simul$ where X is the observed WNODF, and $\mu\, simul$ and $\sigma\, simul$ are the mean and standard deviation, respectively, of 1000 simulated matrices. Positive Z-scores indicate higher X than expected by chance, whereas negative Z-scores indicate lower X than expected by chance. These steps were repeated for both the functional structure and the taxonomic structure at both spatial scales (regions and provinces).

Permutation-based gradient analysis

One of the objectives of nestedness analysis is unveiling the drivers of nested patterns in communities. To this end, nestedness analyses are coupled with gradient analyses, in which the ordering of species vs. sites maximizes nestedness and reveals the causes of extinction or colonization in assemblages (Lomolino 1996; Ulrich et al. 2009). A recently developed analytical framework, the permutation-based gradient analysis (Novak et al. 2011), is an improved version of gradient analysis and controls issues such as collinearity among predictor variables (see Novak et al. 2011). Under this framework it is possible to assess the influence of site attributes as well as species attributes on the nestedness degree of the species assemblages (Novak et al. 2011). We conducted the permutation-based gradient analysis to investigate the influence of site attributes in the nestedness degree of reef fish assemblages within biogeographic regions. The rows and columns of the matrix were randomly shuffled and the rows of the matrix containing site attributes were ordered correspondingly. After each shuffle (10.000 permutations), the analysis estimated the WNODF values ($\mathrm{WNODF_M}$= total matrix, $\mathrm{WNODF_C}$ = columns and $\mathrm{WNODF_R}$= rows) and a correlation between the rank order of each site attribute and a numbered sequence that corresponds to the number of sites arranged in descending order.

To estimate the contribution of each site attribute to the overall taxonomic and functional nestedness of reef fish assemblages we conducted a multiple regression analysis:

$$\mathrm{WNODF_M} \sim \beta_0 + \sum \beta_i \, x_i$$

where $\mathrm{WNODF_M}$ is the overall matrix nestedness degree, and $\sum \beta_i \, x_i$ is the causal correlation value for each site attribute obtained through permutation-based gradient analysis. The evaluated site attributes include the distance from the biodiversity center, isolation among sites, and reef area. To assess the determinants of nestedness across regions, contrasting to our conceptual framework, we contrasted regression models (linear and quadratic). All data analyses were conducted in the software R 2.14.2 (R Core Team 2012) using the packages VEGAN version 2.0-2 (Oksanen et al*.* 2011) and BIPARTITE version 2.01 (Dormann et al*.* 2008).

RESULTS

At the regional scale, the taxonomic structure of reef fish assemblages was significantly nested in the Tropical Eastern Pacific and the Western Atlantic regions. In the Central Pacific region, assemblages were significantly less nested than expected by chance for their taxonomic structure. On the other hand, reef fish assemblages within five out of the six regions presented higher functional nestedness than expected by chance, i.e. reef fish FEs that occurred in depauperate sites were subsets of species-rich sites (Table 1, Appendix 3). The Western Atlantic and Tropical Eastern Pacific regions exhibited significantly nested taxonomic and functional structures, whereas the Central Pacific, Central Indo-Pacific and Western Indo-Pacific were only functionally nested. At the opposite, fish assemblages of the Eastern Atlantic region were not nested for any diversity component. At the province scale, the taxonomic and functional structures were significantly nested only in three and four provinces (n = 12) respectively, but all taxonomically nested provinces were also functionally nested (Table 1): the Southwestern Atlantic, the Southwestern Pacific and Easter Island provinces.

Table 1. Quantitative nestedness (WNODF) of taxonomic and functional matrices of reef fish assemblages in six biogeographic regions and its provinces (in *italic*). Obs.: observed WNODF values; 95% CL: WNODF confidence limits from 1000 random matrices obtained from null model "quasiswap" (see methods); Z-score = $(X - \mu\, simul)/\sigma\, simul$, where X is the observed WNODF, and $\mu\, simul$ and $\sigma\, simul$ are the mean and standard deviation, respectively, of 1000 simulated matrices. Positive Z-scores indicate higher x than expected by chance, whereas negative Z-scores indicate lower x than expected by chance. All matrices were double sorted according to marginal richness and abundance totals. Regions and provinces in **bold** were significantly nested.

Matrix	Taxonomic			Functional		
Site	WNODF			WNODF		
	Obs.	Z-score	95% CL	Obs.	Z-score	95% CL
Western Atlantic	58.3	**3.25**	52.3–57.3	56.9	**5.02**	44.3–51.0
Southwestern Atlantic	55.8	**6.15**	44.6–50.4	44.2	**3.43**	31.8–41.4
Caribbean	51.6	2.07	44.3–51.5	31.7	1.71	23.3–32.6
Atlantic Islands	17.4	2.80	11.4–16.5	14.7	2.33	10.1–15.1
Eastern Atlantic	43.5	0.32	38.8–46.7	54.1	1.48	44.9–55.5
Tropical Eastern Pacific	50.9	**3.93**	43.2–48.1	54.2	**2.76**	43.7–52.8
Continental TEP	41.5	1.78	35.2–42.3	47.3	1.67	36.1–48.5
TEP Islands	43.9	**4.09**	31.6–40.2	42.2	0.01	35.4–48.3
Western Indo-Pacific	62.9	0.90	59.0–64.5	58.1	**4.87**	41.6–51.7
Somali/Arabian	51.1	1.56	44.0–52.1	44.1	1.18	32.5–43.8
Western Indo-Pacific	61.6	1.75	56.1–62.3	47.1	1.06	38.4–49.9
Central Indo-Pacific	63.2	-0.02	60.1–66.4	57.8	**5.64**	40.3–50.1
Central Pacific	64.3	**-5.98**	66.7–70.0	67.3	**8.19**	46.4–55.2
Central Pacific	58.8	-2.44	59.1–65.5	48.8	1.44	39.5–50.4
Polynesia	42.7	2.48	34.8–41.9	43.8	2.24	31.7–43.5
Easter	45.4	**3.61**	25.2–40.5	49.6	**3.72**	23.5–43.2
Southwestern Pacific	55.2	-2.34	54.9–62.1	57.1	**2.72**	40.9–56.1
Hawaii	30.5	2.09	22.6–30.6	20.4	-1.56	18.5–25.6

Area and isolation exerted important effects on the levels of nestedness of reef fish assemblages (Fig. 3, Table 2). Within regions, large gradients in reef area and narrow gradients of isolation significantly contributed to generate nested subsets of reef fish FEs (Table 2). Across regions, we found a significant quadratic relationship between taxonomic nestedness and isolation (Fig. 3, Appendix 4) ($P<0.02$, $r^2=0.49$), but not between functional nestedness and isolation (Fig. 3, $P<0.63$, $r^2=0.10$). Additionally, most set of sites with small differences in area among them, exhibited lower levels of nestedness across the isolation gradient (Fig. 3).

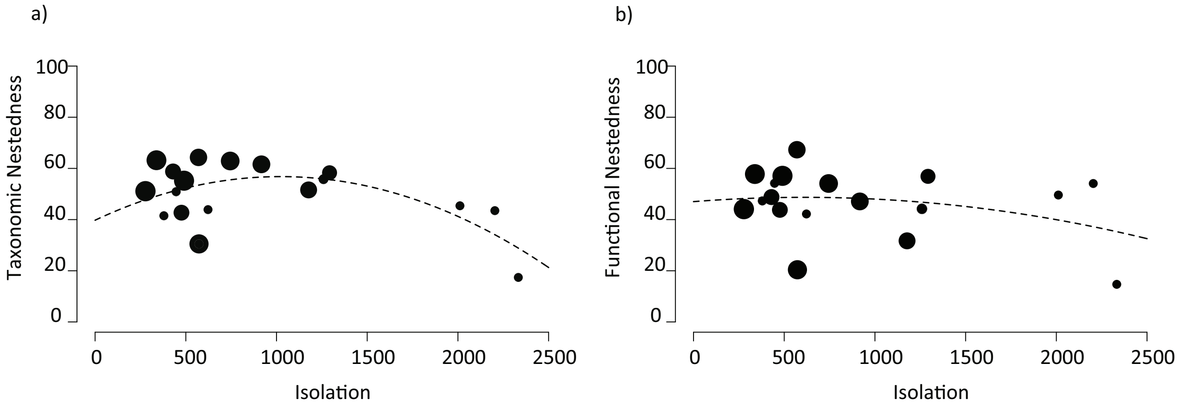

Figure 3. The observed relationship between levels of taxonomic (a) and functional nestedness (b) and gradients in isolation for global reef fish assemblages. Nestedness values were obtained for six biogeographic regions and 12 provinces, and correspond to those in table 1. Isolation expressed in km and measured as the distance from the 10 nearest reef sites. Circle size is proportional do area gradients in each region and province. Dashed line corresponds to predicted values under a quadratic regression. (Taxonomic: $P<0.02$, $r^2=0.49$; Functional: $P<0.63$, $r^2=0.10$).

Table 2. Results of multiple regression analysis to predict the effects of reef area, isolation and distance from the biodiversity center on functional nestedness of reef fish assemblages within biogeographical regions.

Region	Explanatory variables	Estimate (β)	Std. error	t-value	*p*-value	R^2
Western Atlantic	Intercept	28.56	0.09	300.28		0.22
	Area	4.13	0.66	6.191	***	
	Isolation	-1.15	0.56	-2.11	*	
	BC distance	-3.28	0.66	-4.95	***	
Eastern Atlantic	Intercept	27.06	0.15	174.76		0.01
	Area	0.85	0.44	1.94	-	
	Isolation	1.56	0.78	1.99	*	
	BC distance	-1.58	0.73	-2.15	*	
Tropical Eastern Pacific	Intercept	27.46	0.13	210.83		0.05
	Area	2.45	0.55	4.37	***	
	Isolation	-2.36	0.60	-3.88	***	
	BC distance	-1.39	0.63	-2.18	*	
Western Indo-Pacific	Intercept	28.76	0.11	253.39		0.12
	Area	3.04	0.53	5.95	***	
	Isolation	-5.80	0.59	-9.82	***	
	BC distance	3.30	0.56	5.88	***	
Central Indo-Pacific	Intercept	29.01	0.08	329.24		0.25
	Area	9.12	0.58	15.48	***	
	Isolation	-6.56	0.67	-9.70	***	
	BC distance	1.17	0.69	1.70	-	
Central Pacific	Intercept	33.69	0.08	419.92		0.37
	Area	10.14	0.54	18.78	***	
	Isolation	-2.49	0.53	-4.62	***	
	BC distance	-4.48	0.52	-10.35	***	

***$p<0.001$ ** $p<0.01$ * $p<0.0$

The reef fish FEs that occurred across most assemblages were the invertivores feeding on mobile invertebrates (Fig. 4). The top positions of a maximally nested matrix were an assembly of invertivores from all different size categories, intermediate to large bodied piscivores (piscivores > 30 cm) and planktivores (7.1-50 cm) (Fig. 4). Conversely, the least redundant FEs differed across regions. Large bodied herbivore-detritivores (>80 cm) and small piscivores (< 7 cm) had low redundancy across all biogeographic regions, but omnivores (>80 cm) and macro-algal herbivores (15.1-50 cm and >80 cm) also figured as rare FEs in certain assemblages.

In the Western Atlantic, eleven FE exhibited very low-redundancy, with only one or two species representing those entities in most cases. These were mostly small piscivores, invertivores feeding on sessile invertebrates and large bodied herbivore-detritivores. Eastern Atlantic assemblages had low-redundancy of sessile invertebrate feeders and small-bodied planktivores, the latter group being absent from most assemblages. In contrast, small planktivores (7-15 cm) were among the most redundant FEs in assemblages of the Central Pacific and Central Indo-Pacific region. Five out of ten rare FEs in such assemblages were herbivores: large-bodied (>80 cm) herbivore-detritivores and medium to large-bodied (size classes: 15.1-80 cm) macro-algal herbivores. In addition to herbivores, small (0.1-7 cm) invertivores feeding on sessile invertebrates were another FE with low redundancy. Rare FEs in Western Indo-Pacific sites were mainly invertivores feeding on sessile invertebrates (size classes: < 15 cm, 30.1-50 cm and 50.1-80 cm), as well as omnivores. Finally, in the Tropical Eastern Pacific region, rare FEs were omnivores of different size categories (size classes: < 15 cm and 30.1-50 cm) and herbivore-detritivores (size classes: < 15 cm and >80 cm).

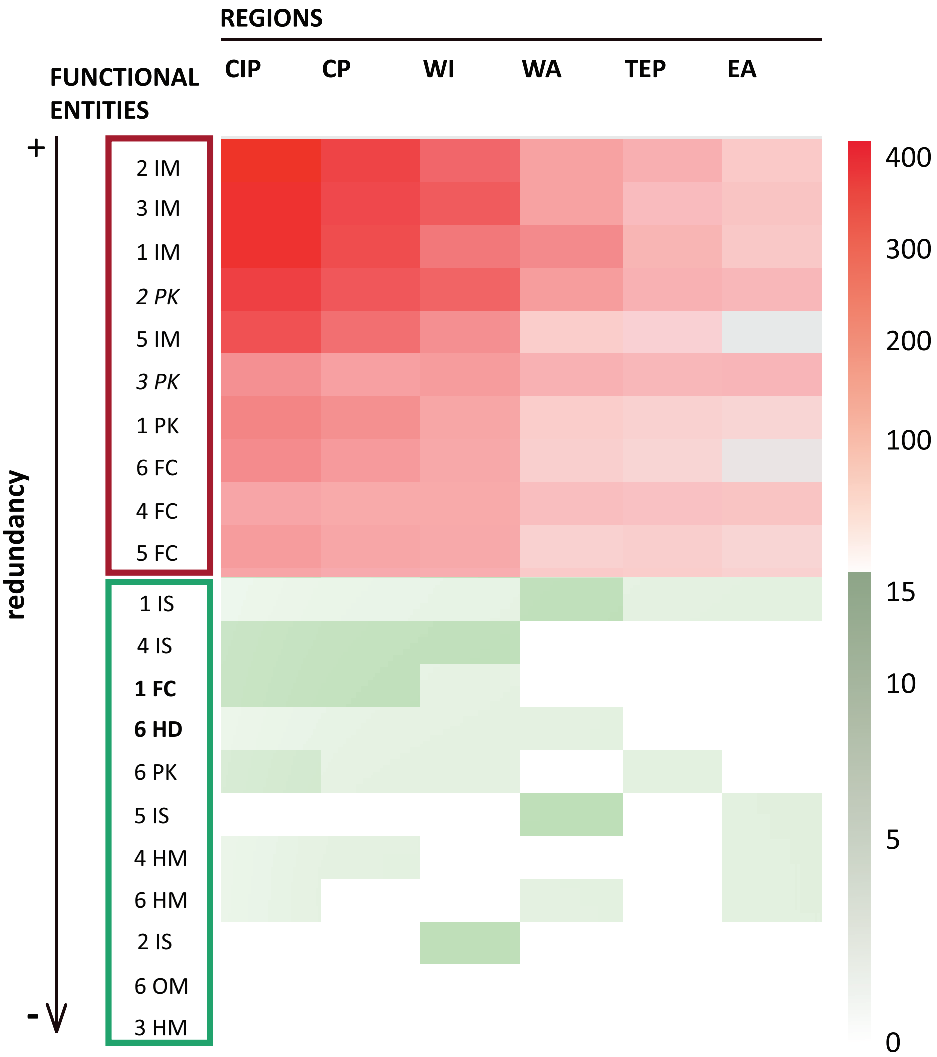

Figure 4. The nested functional structure of global reef fish assemblages. Reef fish FE that occupy the top ten positions (red portion), as well as those in the bottom ten positions (green portion/area) of a maximally nested matrix. FE in the red rectangle are the ten most widespread and redundant FE across the six biogeographical regions, whereas FE inside the green rectangle are those absent from certain sites and/or represented by a smaller number of species, *i.e.,* less-redundant FE. The gradients from dark-red/ dark-green to pale-red/ pale-green represent decreasing values in matrix cells. Inside the red rectangle, functional entities in italic (2 PK, 3 PK = planktivores <15 cm) appear as very redundant FE in assemblages of the Indo-Pacific. Inside the green rectangle, functional entities in bold (6 HD = herbivore-detritivores > 80 cm; and 1 FC = piscivores < 7 cm) are those with low redundancy across all 6 regions. CIP = Central Indo-Pacific, CP = Central Pacific, WI = Western Indian, WA = Western Atlantic, TEP = Tropical Eastern Pacific, EA = Eastern Atlantic

DISCUSSION

Our findings reveal that the functional structure – i.e., the number of species per FE – of depauperate reef fish assemblages represents a subset of the structure found in richer assemblages, and such nested pattern was found across five biogeographic regions. This functional nestedness is unrelated to taxonomic nestedness. In contrast, our results revealed a low degree of taxonomic nestedness, which can be related to the homogeneity of the taxonomic structure – for families – across sites (Bellwood and Hughes 2001). Studies have highlighted the importance of nestedness to reef fish assemblages of the Indo-Pacific (Bellwood and Hughes 2001; Mouillot et al. 2013b; Kulbicki *et al.,* 2013); yet a turnover component is also present, associated with high levels of endemism or recent cladogenesis (Mouillot et al. 2013b). Such spatial turnover in species composition was identified at the boundaries of the Indo-Pacific, and could have its origins in the higher endemism of regions such as the eastern Pacific and southern Australia (Mouillot et al*.* 2013b, Kulbicki et al. 2013). The taxonomic turnover of Central Pacific sites (Marquesas, Easter, Hawaii, Polynesia) may account for the non-nested taxonomic pattern identified for this region (here referred to as Central Pacific *sensu* Kulbicki et al*.* 2013). Turnover between assemblages could be related to the effects of dispersal limitation and environmental filtering (Svenning et al. 2011; Luiz et al. 2013). Nevertheless, filters known to limit the distribution of reef fish, such as area availability and isolation, seem to have stronger effects on the taxonomic composition than on the functional structure of assemblages. Functional nestedness could emerge as a consequence of key FEs that are essential to ecosystem functioning and would be maintained across sites (Bellwood et al*.* 2004).

While the relationship between taxonomic nestedness and isolation differed from the expected trend, that between functional nestedness and ranges in isolation is consistent with our predictions – nestedness peaks at intermediate and high isolation gradients possibly attributed to functional redundancy. The effect of area on both taxonomic and functional nestedness appears consistent to that presented in our scenarios, with most locations of small area ranges exhibiting lower levels of nestedness across the isolation gradient. We are aware, however, that our conceptual framework did not include predictions for nestedness relative to potential variations in the spatial distribution of patches relative to other patches, as well as differences in island age. The geographical position, size and age of one patch could possibly affect nestedness among species assemblages through its influence on colonization and/or extinction events. This is an interesting avenue for further research on the assembly of communities.

The roles of habitat area and isolation on the structure of assemblages are widespread in ecology and biogeography (MacArthur and Wilson, 1967; Lomolino, 1999) with smaller or isolated sites being subsets of larger and less isolated ones (Patterson & Atmar 1986; Lomolino 1999). Insular nestedness would result from processes of extinction and colonization (Patterson and Atmar 1986), mediated by species abilities to interact with isolation and area (Lomolino 1999). Thus, nested patterns are attributable to species traits (Lomolino 1999; Hu et al. 2011; Novak et al. 2011; Sasaki et al. 2012), and how these traits are related to dispersal ability and colonizing capacity (Luiz et al. 2013), vulnerability to extinction and habitat specificity. By looking at functional nestedness, we are ultimately assessing which attributes contribute to such pattern. Among species widely distributed across fish assemblages, many are large-bodied piscivores and carnivores (mobile invertebrate feeders). For reef fishes, large body size implies greater range sizes, as well as higher potential to expand their ranges across dispersal barriers and to colonize new habitats (Luiz et al. 2012; 2013). On the contrary, FEs such as small piscivores and sessile invertebrate feeders have restricted ranges and also habitat specificity (Hawkins et al. 2000). These contrasting patterns in dispersal capabilities and resource requirements – also related to species' body sizes – can generate both taxonomic and functional nested patterns (Lomolino 1999).

Functional nestedness has been identified for plant communities across land-bridge islands in China (Hu et al. 2011), where area and isolation significantly affected such pattern. In the case of reef fish assemblages, the highest level of functional nestedness is identified for the Central Pacific, which can be due to the physical geography of that region, comprising several islands and atolls of various sizes, sufficiently isolated from each other. Conversely, the lowest nestedness level is observed for the Central Indo-Pacific where historical habitat connectivity is high (Cowman and Bellwood 2013) with low isolation among sites. Also, in the Central Indo-Pacific, the higher habitat diversity and lower dispersal constraints to species compared to the Central Pacific could decrease nestedness.

Reef area emerges as one of the major causes of functionally nested subsets in fish faunas of different marine regions. Indeed, coral reefs and reef fishes are closely connected in their evolutionary history (Bellwood and Wainwright 2002; Cowman and Bellwood 2013), with reef systems acting as a center for survival, as well as diversification, of fish lineages (Cowman and Bellwood, 2013). Reef area has been identified as a key habitat attribute in structuring reef fish assemblages both at global (Parravicini et al. 2013), regional (Bellwood and Hughes 2001; Bender et al. 2013) and local scales (Hubert et al. 2011). Furthermore, reef features (*e.g.* patch size, reef type, reef habitat, coral richness) may act as filters to the functional (Bellwood et al. 2002; Bender et al. 2013) and phylogenetic structure (Hubert et al. 2011) of associated assemblages. Reef area was the main factor shaping the nested subset structure of Indo-Pacific reef fish families along the diversity gradient (Bellwood and Hughes 2001). At the local scale – Glover's Reef, Belize –, reef patch size did not cause a nested subset pattern on the structure and diversity of reef fish assemblages (Acosta and Robertson 2002) because a greater number of rare species occupied small reefs compared to larger ones. Also, members of those assemblages were capable of inter-patch dispersal reducing reef isolation. Thus, it seems that area can shape nested patterns of reef fish assemblages when considered at the large scale, as showed by the present study.

Our results reveal that redundant FEs mostly exhibit an homogeneous distribution across biogeographic regions; yet those Fes supported by few species may differ across regions. Overall, low functional redundancy in reef fish assemblages across biogeographic regions appears related to those FEs that have a close link to reef habitats: sessile invertebrate feeders (in the Indo-Pacific), macro-algal herbivores, herbivore-detritivores. In sites where these species occur, they may be the first to be impacted by reef stressors. Moreover, the importance of reef area and isolation to generate the observed nested pattern may indicate that habitat loss in depauperate and isolated sites can have disproportionate effects on the functional structure of reef fish assemblages potentially imperiling ecosystem functioning.

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Appendix 1: Justification for the choice of maximum body size and diet as reef fish functional attributes.

Body size

Size has a primary role in defining the ecological niche and ecological role of species, general reviews on this subject can be found in Wilson (1975) and LaBarbera (1986). More specifically the following aspects are important for reef fish:

- Energy needs: the amount of energy for metabolism increases with body size, but the amount of energy per unit of body mass decreases with body size (Munday & Jones, 1998).
- Prey selection or predator escape (Costa *et al.*, 2009): prey selection is linked to mouth gape size, which is itself a function of body size, larger fish being able to eat larger prey. Predators are also limited by the size of their prey. Therefore large fish tend to be less predated than smaller ones, all other factors being equal. In addition larger fish have higher swimming speed, which enables them to flee their predator more efficiently. Large fish have the capacity to swim over longer distances therefore increasing their foraging range compared to smaller species or smaller individuals.
- Reproductive capacity, sex ratio, size at maturity, sex reversal: the size of gonads and therefore the quantity of reproductive products is proportional to body weight, usually according to a power function. This means that larger species or larger fish will produce far more gametes than smaller species or smaller individuals. The sex ratio of many species is a function of body size, for instance small parrotfish are nearly always females, small anemone fish are nearly always males (Wong *et al.,* 2007). The size at maturity is proportional to body size, larger species being mature at relatively larger sizes than small ones. Similarly, sex reversal, which is a frequent process for reef fish, occurs at larger sizes in large species (Wong *et al.,* 2007).
- Diversity services in particular biomass production: fish weight is exponential to its body length, therefore assemblages with large species will tend to have larger biomasses than assemblages with small species, for a given diversity level. As the geographical distribution of species fish size is not random (Luiz *et al.*, 2013) this means that the biomass-diversity relationship for reef fish is not spatially homogeneous (Mora *et al.,* 2011). See also Ackerman et al. (2004) on the relationship between density and body size.

- Growth and production: small fish species tend to grow faster and have a higher production rate than larger species (see Paloheimo & Dickie, 1966; for general information) (there are exceptions both ways however). This means that biomass and production may not be related in the same way in reef fish assemblages dominated by small species compared to assemblages dominated by large species
- Mortality rate: small species tend to have a much higher mortality rate than larger ones (Henrique *et al.,* 2013; Munday & Jones, 1998). There are however intrinsic factor to each species. In particular mortality is linked to many other traits such as school size, mobility, level in the water column.
- PLD: large species tend to have wider geographical ranges and also longer Pelagic Larval Durations (PLD) than small species (Luiz *et al*., 2013)
- Temperature tolerance is related to body size in reef fishes (Ospina & Mora, 2004)

Diet

Diet, as size, is an essential component of reef fish ecological niche as indicated in general reviews such as Hiatt & Strasburg (1960), Hobson (1974), Sale (1977), Bellwood *et al*. (2006). In particular diet may be important for the following:

- Trophic level and trophic niche width (for general views see Araujo *et al*., 2011; Bearhop *et al*., 2004): the trophic level of a species and its trophic niche width is determined by the food type it feeds on as well as the variety of food items (Floeter *et al.,* 2004; Ferreira *et al.,* 2004; Wilson *et al*., 2008; Frederich *et al*., 2010; Curtis-Quick *et al*., 2012; Litsios *et al*., 2012) For instance a species may be specialized in coral polyps but depending on where it lives it may eat polyps from different species (Lawton & Pratchett, 2012). Within the same trophic guild other species may eat only polyps from a given species or genus of Acropora wherever it lives.
- Habitat requirements (prey need to be present): many species having a specialized diet will restrict their habitat to areas where the food they need is present is sufficient in quantity and quality. Coral feeders are typical (Berumen & Pratchett, 2008) but there are many herbivores and plankton feeders (Frederich *et al*., 2009; Burkepile & Hay, 2008) that live in specific habitats because of their diet.
- Feeding behavior: the way fish feed on a given item may have profound implication on the habitat and community. For instance, herbivorous fishes can be split according to several feeding behaviors such as grazers, browsers, scrapers

(Bellwood & Choat, 1990). Each of these behaviors will generate different consequences on the algae/coral relationship and on many other ecological processes. The same could be said of coral feeders, of mobile invertebrate feeders.

- Home range (depending on energy requirements and type of prey and prey availability, home range will be either small or wide). For instance, large carnivorous species will necessarily have a wide home range as the resources needed to sustain their metabolism cannot be found on a restricted part of the reef. On the opposite, some small plankton feeders may stay their entire adult live on the same spot as plankton drifts by.

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Appendix 2: The hierarchical spatial structure of reef fish assemblages

List of sites within provinces and regions, and map depicting marine biogeographic regions and its provinces (Fig. S1) (sensu Kulbicki *et al.*, 2013).

Table A2. List of sites embedded in provinces (scale 2) and regions (scale 1). Sites are ordered based on decreasing species richness.

Western Atlantic			**Local Richness**
	Southwestern Atlantic		
		Hump of Brazil	281
		São Paulo	257
		Espírito Santo	252
		Arraial do Cabo	247
		North Bahia	246
		Ilha Grande	233
		Abrolhos	187
		Santa Catarina	182
		Zumbi	167
		Manuel Luiz	133
		Fernando de Noronha	119
		Rocas' Atoll	103
		Trindade	97
		St. Paul's Rocks	57
	Atlantic Islands		
		Ascension	84
		St. Helena	72
	Caribbean		
		Cuba	452
		Bahamas	442
		Virgin Islands	436
		Florida Keys	419
		Venezuela – Tobago	404
		Pelican Cays, Belize	374
		Mexican Caribbean	360
		Martinique	290
		Guadeloupe	287
		Bonaire Island	273
		Bermuda	272
		Georgia	244
		Saba, Netherland Antilles	223
		Navassa	192
Eastern Atlantic			
	Eastern Atlantic		
		Cabo Verde	251
		São Tome	196
		Senegal	177
		Guinea-Sierra Leone	171
		Canaries	163
		Mauritania	134
		Madeira	121
Tropical Eastern Pacific			
	TEP Islands		
		Galapagos	282
		Cocos	232
		Malpelo	197
		Revillagigedos	165
		Clipperton	111
	Continental TEP		
		Panama	297

		Costa Rica	277
		Colombia	267
		Nicaragua	248
		Gulf of California	246
		Honduras	236
		El Salvador	235
		Ecuador	231
		Sinaloan	216
		Tresmarias	193
		Gorgona	182
		Isla la Plata	163
		Guatemala	96
Western Indian			
	Western Indo-Pacific		1617
	Red Sea		1043
	Somali/Arabian		995
	West India and South Indian Shelf		1062
	Central Indian Islands		439
	Eastern India		431
	Andaman		
	Somali/Arabian		
		Red Sea	766
		Gulf of Aqaba	681
		Gulf of Aden	629
		Oman South	527
		Gulf of Oman	441
		Arabian Gulf	319
		Erythrea-Djibouti	312
	Western Indo-Pacific		
		Seychelles	1009
		Mozambique	983
		Mauritiues	941
		Kenya	933
		Tanzania	928
		Maldives	896
		Comores	854
		Aldabra	821
		Madagascar	775
		Chagos	753
		La Reunion	709
		Somalia	699
		Rodrigues Island	451
		Laccadives	432
		Socotra	422
		Europa	360
		Carajos	312
Central Indo-Pacific			
		Philippines	1951
		China Sea	1728
		Solomon Islands	1688
		Sulawesi	1616
		Bali	1566
		Flores	1550
		Birds Head Peninsula	1538
		Great Barrier Reef North	1499
		Kalimantan	1482
		Yaeyama	1460
		Sumatra	1373
		Java	1363
		Irian Jaya	1336
		Komodo	1294
		Taiwan	1292

		Thailand	1112
		Milne Bay	1103
		Ambon Islands	1052
		Bismark Sea & Kimbey Bay	1039
		Western Australia	994
		Malay Peninsula	943
		Raja Ampat	898
		Pescadores	874
		Timor	805
		Sri Lanka	755
		Ogasawara	720
		Chuck	651
		Halmahera	617
		India – West coast	599
		Christmas	580
		Hong Kong	565
		Dampier	544
		Cocos-Keeling	538
		North Sumatra	528
		Gulf of Thailand	514
		Vietnam	505
		India – East coast	437
		Andaman-Nicobar	430
		Izu Islands	370
		Gulf of Carpentaria	356
Central Pacific			
	Easter		
		Easter Island	124
		Sala y Gomez	59
		S. Fernandez	8
	Central Pacific		
		Palau	1467
		Vanuatu	1458
		Fiji	1445
		Tonga	1061
		Samoa	1051
		Marshall Islands	964
		South Marianas	925
		Yap	816
		Ifaluk	772
		Pohnpei	744
		Wallis Island	598
		Tuvalu	589
		Phoenix	582
		Line Islands	579
		Kosrae	545
		North Marianas	491
		Kapingamagari	454
		Wake	438
		Rotuma Island	401
		Niue	366
		Baker & Howland	331
	Polynesia		
		Society Islands	708
		Tuamotu Islands	594
		Cook Islands	585
		Gambier	509
		Marquesas	485
		Rapa Island	393
		Pitcairn	379
		Australes Islands	351
	Hawaii		
		Hawaii	512

		Jonston Attol	292
		Midway and Northwestern Hawaii	293
	Southwestern Pacific		
		New Caledonia	1324
		Capricorn bunker	1017
		Chesterfield	743
		Loyalty Islands	683
		Lord Howe	427
		Middleton-Elizabeth	415
		Norfolk	255
		Kermadec	145

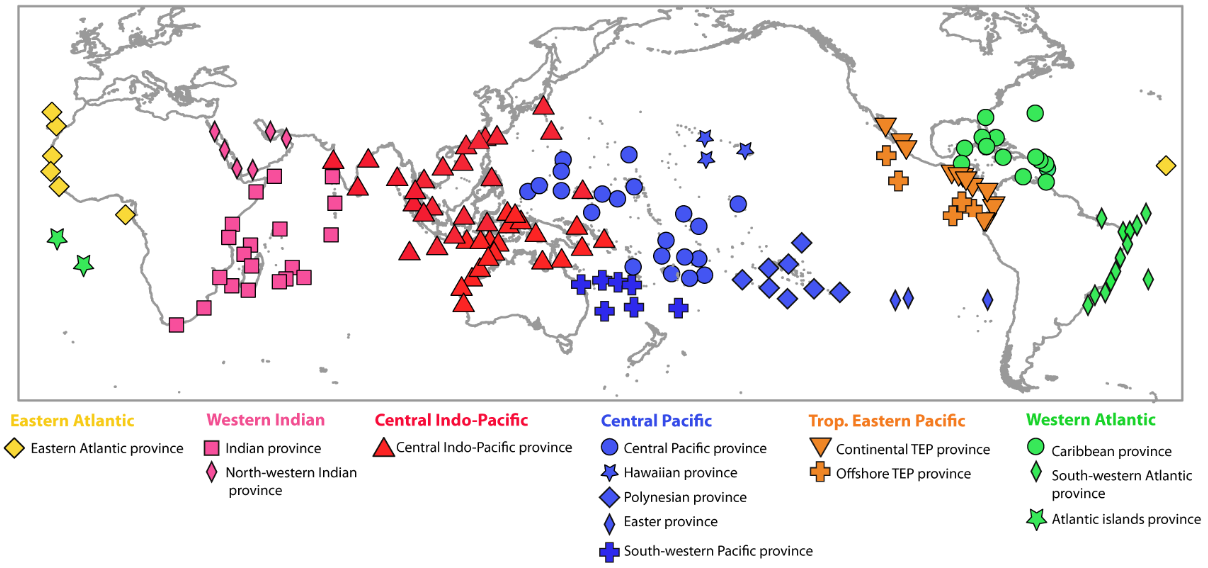

Figure A2. Map of six marine biogeographic regions and its provinces (modified from Kulbicki *et al.*, 2013). Nestedness was assessed at both scales.

Appendix 3: Sensitivity of nestedness analysis to functional group classification scheme

Table A3. Functional nestedness of reef fish assemblages across six biogeographic regions. In order to assess the sensitivity of nestedness analysis to the choice of functional group classification, two distinct functional group schemes were applied. Functional 1 corresponds to the combination of four traits (body size, trophic group, home range and schooling behaviour), while Functional 2 combines six different traits (body size, trophic group, home range, schooling behaviour, activity and level). Obs.: observed WNODF values; 95% CL: WNODF confidence limits from 1000 random matrices obtained from null model "quasiswap" (see methods); Z-score = $(X - \mu\, simul)/\sigma\, simul$, where X is the observed WNODF, and $\mu\, simul$ and $\sigma\, simul$ are the mean and standard deviation, respectively, of 1000 simulated matrices. Positive Z-scores indicate higher x than expected by chance. All matrices were double sorted according to marginal richness and abundance totals.

Matrix	Functional 1			Functional 2		
Site	WNODF			WNODF		
	Obs.	Z-score	95% CL	Obs.	Z-score	95% CL
Western Atlantic	46.9	6.72	40.4–43.7	32.2	6.62	30.9–33.1
Eastern Atlantic	37.7	3.97	30.9–35.8	29.3	4.59	23.5–27.3
Tropical Eastern Pacific	45.5	9.28	34.0–37.3	30.8	8.68	25.3–27.5
Western Indo-Pacific	57.9	18.7	47.5–49.7	44.6	22.6	36.1–37.6
Central Indo-Pacific	61.7	12.7	54.6–56.7	49.7	20.4	42.3–43.7
Central Pacific	58.4	15.7	49.9–52.0	45.5	25.8	37.0–38.4

Appendix 4: Model selection for the relation between taxonomic and functional nestedness with isolation gradients and plots of the model residuals vs. area gradients.

Table A4. Model selection through analysis of variance (ANOVA) for the relation between taxonomic and functional nestedness across reef fish assemblages with isolation gradients. Nestedness (y) was estimated for regions and provinces, and its corresponding isolation value (x) refers to the mean distance from one site to all other sites within each biogreographic regions and province.

						ANOVA (model comparison)		
			F-statistic	adj R^2	*p*-value	Sum of squares	F-value	*p*-value
Taxonomic	Model 1	$y \sim x$	3.78	0.14	0.06			
	Model 2	$y \sim x + x^2$	4.99	0.49	0.02*	534.01	5.21	0.037*
Functional	Model 1	$y \sim x$	1.60	0.03	0.22			
	Model 2	$y \sim x + x^2$	0.88	0.10	0.63	41.167	0.23	0.633

* $p<0.01$

ARTIGO IV

Formatado segundo instruções aos autores para a revista *Functional Ecology*

Global patterns of functional rarity in reef fish communities

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ABSTRACT

The loss of biodiversity caused by human-mediated impacts has reached unprecedented level across all ecosystems, with rare species being by far the most threatened. This biodiversity can in turn compromise the breath of functions performed in ecosystems but little is known about the particular functions supported of rare species or the extent to which the loss of rare species would drop the level of functional diversity within communities. Thus, assessing the spatial distribution of functional rarity may provide crucial knowledge about the functional vulnerability of communities to rare species loss. Through the use of an extensive dataset gathering information for 1,474 species, we assessed the global patterns of functional rarity and implemented scenarios of functional diversity loss across 93 reef fish communities. We found that rare species fulfil much of the range of functional traits within reef fish communities and often perform unique roles. We also showed high functional diversity erosion in a scenario of rare species loss (from 8 to over 200 rare species) in the majority of reef fish communities, this level reaching up to 80% of functional diversity in one location. This pattern is more marked in communities where rare species support the most distinct combinations of traits. Our results highlight the vulnerability of ecological roles supported by rare species, even in highly diverse reef fish communities. It also calls for new thinking and improved approaches into the preservation of rare taxa in order to maintain the extant set of functions and ecosystem services in reef fish communities.

INTRODUCTION

Ecosystems are facing an unprecedented level of human-mediated impacts (Pimm *et al*., 1995; Jackson *et al*., 2001; Dulvy *et al*., 2003) with rare species being the most affected given their restricted geographic range, population size or habitat specificity (Munday, 2004; Van Calster *et al*., 2008). This loss of rare species may not only decrease taxonomic diversity, but it may also erode the breath of functions performed by ecological communities (Lyons & Schwartz, 2001; Lyons *et al*., 2005; Bracken & Low, 2012, Mouillot *et al*., 2013a; Pendleton *et al*., 2014) potentially imperilling ecosystem functioning and associated services. Indeed, some species may play a unique role in the ecosystem while others may share their role with many species therefore being functionally redundant (Halpern & Floeter, 2008; Mouillot *et al*., 2014).

This level of redundancy in species' functional roles thus mediates the impact of species' loss over ecosystem functioning (Halpern & Floeter, 2008, Bellwood *et al.* 2004). Since rare species are certainly the first to disappear under multiple pressures (Hawkins *et al*., 2000; Munday, 2004; Van Calster *et al*., 2008), the amount of overlap in the functions supported by rare vs. common species across ecosystems is a major issue. Recently Mouillot *et al*. (2013a) have shown that vulnerable functions, *i.e.* those with low redundancy, are overwhelmingly supported by rare species while, at the same time, many rare species share similar roles with common species. This study urges to identify the rare species having very distinct combinations of traits from the rest of the pool since their local extinction would induce a major drop in functional diversity. It also urges to identify the most vulnerable communities to biodiversity erosion, *i.e.* those primarily composed of rare species supporting unique functions.

Tropical marine reefs host an extraordinary diversity of life while being heavily impacted by multiple human activities (overfishing, pollution, habitat loss, etc.) (Jackson *et al*., 2001; Halpern *et al*., 2008). Fish are known to perform a large variety of roles upon which the functioning of reefs critically depends such as the removing of algae that may outcompete corals (Bellwood *et al*., 2004, 2006). Among essential roles, some are supported by rare or threatened species; thus beyond the quantity of biodiversity it is also its quality that matters to sustain ecological processes even in such species-rich ecosystems. However, the spatial distribution of functional rarity remains to be explored in reef fish communities while it would provide relevant information to the conservation of the most vulnerable species and communities within the context of intense disturbances and high uncertainty. This is especially important in the current scenario of coral reef decline (Jackson *et al*., 2001; Bellwood *et al*., 2004; Hughes *et al*., 2010) and the multiple threats affecting reef fish species (Hawkins *et al*., 2000; Munday, 2004; Graham *et al*., 2011; Bender *et al*., 2013b). Here we assessed the global patterns of functional rarity within reef fish communities through the use of an extensive dataset comprising local abundances, regional occupancies and functional traits for 1,474 reef fish species. In this study, we aimed to investigate: (i) differences in the functional space filled by rare and common species across reef fish communities; (ii) the functional distinctiveness of rare species relative to the total species pool; and (iii) the functional loss in reef fish communities following the potential removal of rare species.

METHODS

Dataset

Our sampling was carried out in 9,681 underwater visual transects of $40m^2$ (2m x 20m) over 252 sites distributed across six marine biogeographic regions (*sensu* Kulbicki *et al.*, 2013). The sites where transects were conducted were grouped in 93 locations and then assembled into 25 subregions. A total of 1,474 reef fish species were recorded. All individuals greater than 4 cm in length were identified at the species level and counted (Appendix S1).

The functional strategy of each reef fish species was determined based on a combination of six different categorical traits (Guillemot *et al.*, 2011). These traits include maximum body size of the species, mobility, position in the water column, period of activity, schooling behaviour, and diet (Appendix S2).

Rarity estimations

Under such hierarchical spatial structure (Fig. S1) we estimated abundance and occupancy of reef fish species, two out of three main components of rarity (Rabinowitz, 1981; Gaston, 1994; Mouillot *et al.*, 2013a). More precisely, occupancy was measured as the extent of occurrence, *i.e.* the number of samples where the species was present in a given site while local abundance was measured as the mean number of individuals over samples where the species was present in a given site. From the values obtained across sites we computed the abundance and occupancy values for 93 locations, taking into account only sites where species were present (Mouillot *et al.*, 2013a). Such rationale was also employed to estimate species abundances and occupancies at the subregion scale. Our local scale corresponds to the location scale (*e.g.* Abrolhos Bank, Lifou, Moorea) and the regional scale is defined by subregions (*e.g.* Southeastern Brazil, New Caledonia, French Polynesia). Rare species were defined as those with less than 5% of the maximum observed value of abundance or occupancy across the species pool in each location and subregion (Mouillot *et al.*, 2013a).

By contrast, species commonness at the local scale corresponds to the species mean abundance across samples where the species is present, and is expressed as a percentage of the maximum observed abundance value in the ecosystem. At the regional scale, commonness corresponds to the number of occurrences over all samples, and is also expressed as a percentage of the maximum observed occupancy value.

Functional Distinctiveness

Recently, metrics that assess the ecological distinctiveness of species have been developed within a conservation context. The rationale is that species sharing less biology with the rest of pool are of major importance (Isaac, 2007). For instance species phylogenetic distinctiveness, *i.e.* that measure the lack of genetic relatedness between a species and the rest of the community, has entered into the design of conservation priorities (Cadotte & Davies, 2010). By analogy, the functional distinctiveness, that quantifies the uniqueness of a species combination of biological traits from the rest of the species pool, has been previously applied (Mouillot *et al.*, 2013a) but never used to map the biogeography of functional rarity. Basically, we estimated species functional distinctiveness as the sum of branch lengths divided by the number of species subtending those branches along the functional dendrogram. When a species has a unique combination of traits it has a long branch with few species making it highly distinctive.

We have estimated species functional distinctiveness across each location. The distinctiveness of species considering the global species pool has also been estimated, in order to assess the relationship between functional distinctiveness and species commonness – the opposite of rarity –, both at local and regional scales. We have tested the relationship between species' functional distinctiveness and commonness through ordinary least squared regressions and quantile regressions (95th and 99th quantiles) to detect triangular relationships if any (Mouillot *et al.,* 2013). Analyses were conducted in R 2.14.2 software (R Core Team, 2012) using package ADE4 and specifically, the *originality* function, for functional distinctiveness measurements; and package QUANTREG and *rq* function for quantile regressions.

Functional diversity

Each reef fish species was placed in a multidimensional functional space according to its trait values (Villeger *et al.*, 2008). The first step involves the computation of the Gower distance between all pairs of species within communities (Gower & Legendre, 1986; Legendre & Legendre, 1998). The second step is the Principal Coordinate Analysis (PCoA), which is applied on the Gower distance matrix (Villeger *et al.*, 2008, 2011), providing coordinates for the placement of species – based on their functional traits – in a multidimensional functional space. Once species are set in a functional space, we can estimate the amount of space, a surrogate of functional diversity, filled by rare vs. common species. This space is measured through the volume inside the convex hull enclosing species (Cornwell *et al.*, 2006; Villeger *et al*., 2011). The convex hull and therefore functional diversity were estimated using the R package GEOMETRY version 0.3.3 and the function *convhulln*.

We further assessed the loss of functional diversity within reef fish communities following the removal of an increasing number of species: from the most abundant, or common, to the “rarest” ones; and, from the “rarest” species to the most abundant ones. We tested whether the observed values of functional diversity loss were significantly different than expected by chance, by contrasting observed values to the 95% confidence limits obtained through the null model. Under the null model, an increasing number of species were randomly removed from the assemblage, and after species removal, functional diversity loss was computed. In each location we simulated a random removal (1000 random draws) of each number of species (1 species, 2 species, and so on). This analysis was conducted using both rarity measures: abundance and occupancy.

Finally, we have investigated the set of functional traits of those rare species that lie outside the functional space occupied by common species, *i.e.*, the functions that are only supported by rare species. This was achieved by identifying the points that are outside the convex polytope that represents the functional space of common species (function *outconvex,* available upon request). All data analyses were conducted using the software R 2.14.2 (R Core Team, 2012).

RESULTS

Rare species filled a greater part of the functional space of reef fish communities when compared to common species (mean±sd; rare: 0.18±0.05; common: 0.12±0.05), across the majority of locations (Fig. 1a,b). This contribution of rare fish species to the functional diversity of communities is particularly high in locations of the Southwestern Atlantic, as well as in the Hawaiian Islands, French Polynesia and New Caledonia, in the Pacific Ocean (see Fig. 1a,b).

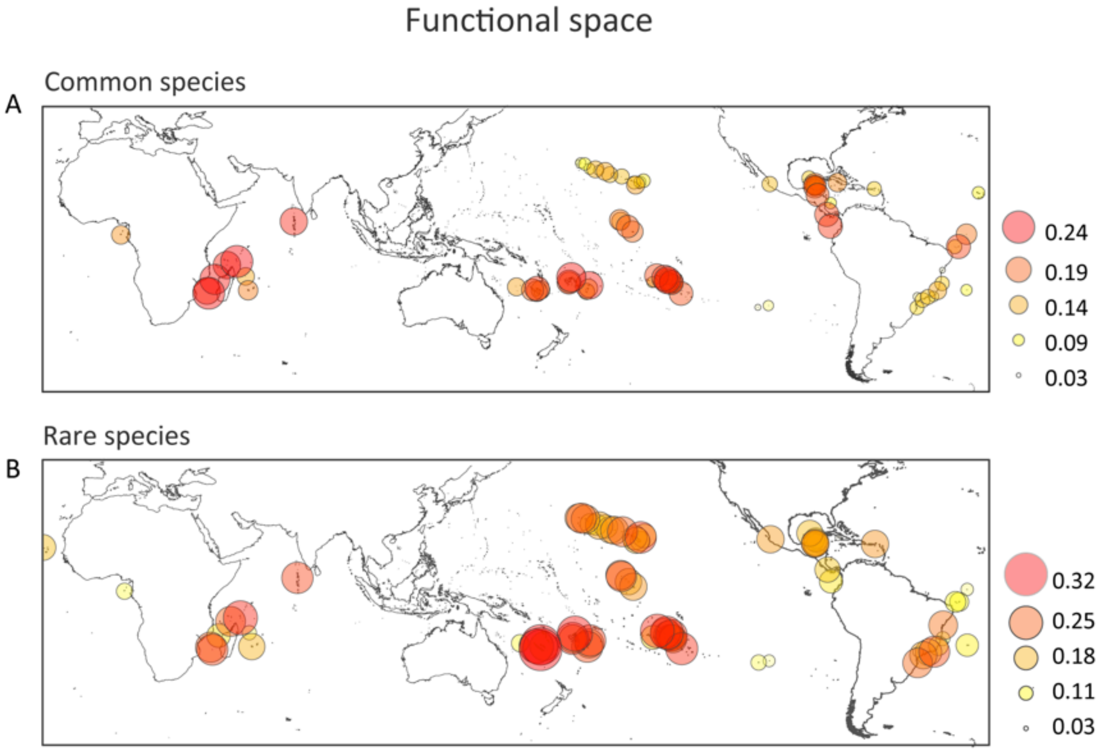

Figure 1. The amount of functional space, used as a surrogate for functional diversity, filled by the top 5% common (A) vs. rare (B) reef fish species across locations. Species commonness vs. rarity was measured at the local scale as the mean abundance over all samples where the species is present (see methods). The amount of functional space is expressed as a proportion of that filled by the entire assemblages

The functional distinctiveness of common vs. rare species in communities – expressed as the mean distinctiveness of rare and common species from the local pool – differed across locations (Fig. 2a, b). Those reef fish communities where rare species carried the most distinct combinations of traits were St. Paul's Rocks Archipelago, Rio de Janeiro, Roca's Atoll, Fernando de Noronha Archipelago and Cape Verde, all located in the South Atlantic. The rare species of Hawaii (Eastern Hawaii), Taiaro and Tekokota Atolls (French Polynesia), and Tromelin (Western Indian) also exhibited high functional distinctiveness. In addition to several locations in the Southwestern Atlantic, the reef fish communities of Hikueru Atoll (French Polynesia), Kure Atoll (Northwestern Hawaiian Islands) and Easter Island exhibited common species with high functional distinctiveness. When contrasting the functional distinctiveness of common and rare species within the same community, one can notice the increased distinctiveness of rare species in communities of the Western Indian Ocean, Easter Island and São Tomé (Eastern Atlantic) (see Fig. 2a,b)

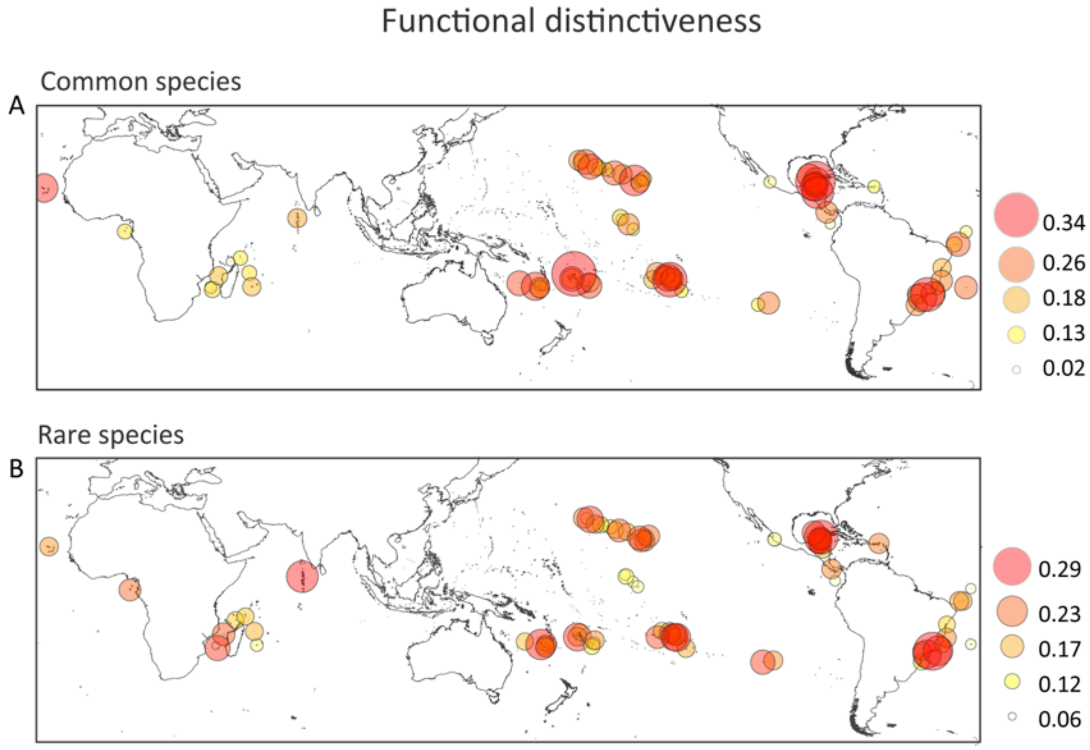

Figure 2. The mean functional distinctiveness of the top 5% common (A) vs. rare (B) reef fish species across locations. Functional distinctiveness quantifies the uniqueness of species traits from the rest of species in communities (see methods). Colour gradient (pale yellow to red) and increasing circle-size gradient denote increasing values, *e.g.* functional distinctiveness, in each map.

Functional distinctiveness of species across locations was negatively related to commonness, when commonness was estimated as local abundance (Fig. 3a), but not for occupancy at the regional scale. The most distinct combinations of functional traits – with the highest functional distinctiveness – are found in rare reef fish species, whereas species with low functional distinctiveness were either rare or common. For regional occupancy, the regressions were not significant suggesting independence between species functional distinctiveness and their rarity (Fig. 3b).

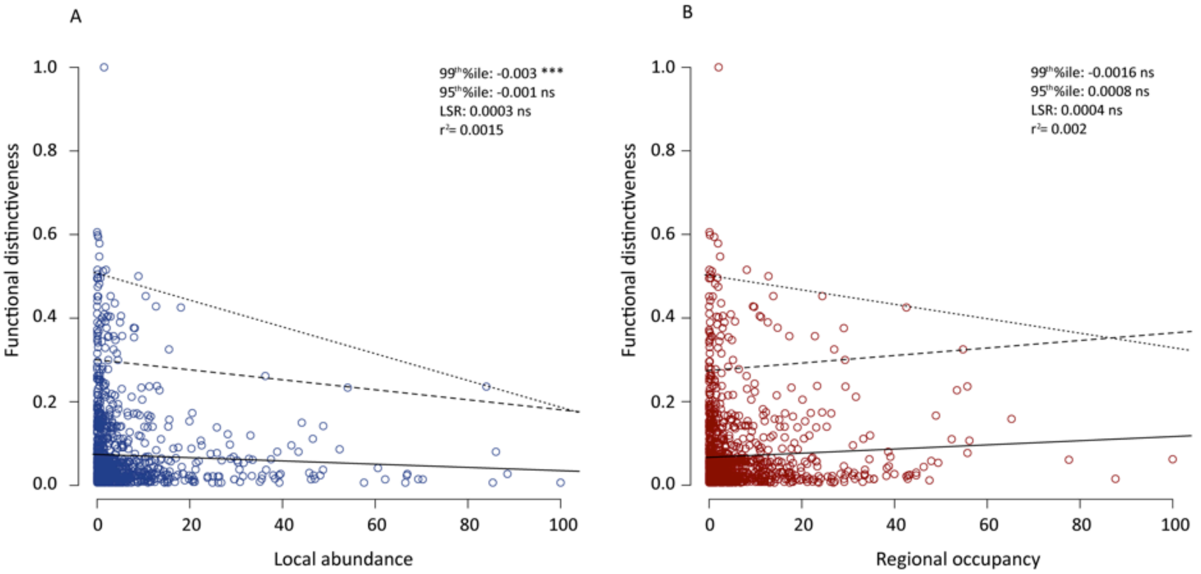

Figure 3. Functional distinctiveness of reef fish species as a function of commonness. Commonness was assessed at the local (a) and regional (b) scales. At the local scale, commonness was measured as the mean abundance across samples where the species is present and expressed as a percentage of the maximum observed value. At the regional scale, commonness was measured as the number of occurrences over all samples, and is also expressed as a percentage of the maximum observed value. Solid lines represent ordinary least squared regressions (LSR), dashed and dotted lines represent the 95th and 99th quantile regressions. ns $p>0.05$, ***$p<0.001$.

When species were gradually removed from communities in each location, along an increasing gradient of commonness, *i.e.* from the “rarest” species to the most abundant one, there was a significant reduction in the functional diversity of communities (Fig. 4). The estimated loss following the removal of the collection of rare species (from 8 to 237 species) from communities varied from 20% to ~80% of the functional space across most locations (Appendix S3, Fig.S3.1, S3.2). Nevertheless, when the most common species were removed from reef fish communities – along a decreasing commonness gradient –, a substantial number of these common species were removed before there was considerable loss in the functional diversity of communities (Fig. 4).

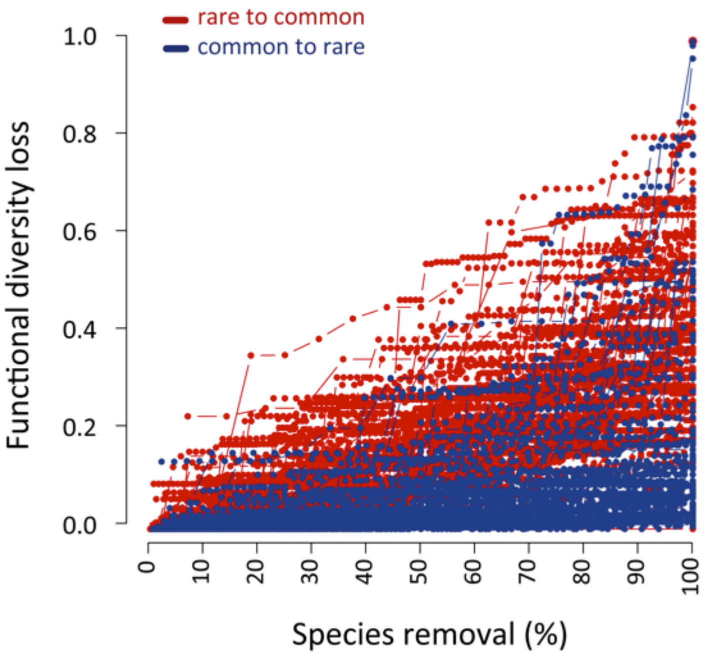

Figure 4. The amount of functional diversity loss across all reef fish communities (locations) following the successional removal of species according to two extreme scenarios: from the most abundant, or common, to the "rarest" ones (blue dots), and from the "rarest" species to the most abundant ones (red dots).

This pattern of functional diversity loss following the removal of rare species from communities was particularly striking for Southwestern Lagoon (New Caledonia), Kure Atoll, Salvador (Brazilian coast, Southwestern Atlantic), Necker Island (British Virgin Islands, Caribbean) Eastern Hawaii (Main Hawaiian Islands) and Sala y Gomez Island (South Pacific). Furthermore, the functional loss identified for reef fish communities across different biogeographic regions was not related to total species richness nor to the number of rare species in communities (Appendix S3, Fig.S3.3). Finally, the traits that appeared more frequently among rare species – those lying outside the functional space occupied by common ones –, were solitary species, those of diurnal activity, piscivores and planktivores, in addition to invertivores, solitary species and species living in small groups (Appendix S4).

DISCUSSION

Our study reveals that rare species support most of functional diversity found in tropical reef fish communities given their wide spectra of trait combinations. Moreover, the most functionally distinct species across reef fish communities are rare in terms of local abundance. This pattern identified for global reef fish communities is in agreement with that identified for reef fishes of New Caledonia, Tonga, Fiji and French Polynesia, and also for communities of alpine plants and tropical trees (Mouillot *et al.*, 2013a). The functions of rare species include, for instance, the key role of a fish species in reef regeneration through macroalgae growth control (Bellwood *et al.*, 2006; Mouillot *et al.*, 2013a). Thus the extirpation of rare species from reef fish might compromise the breath of functions supporting key ecological processes.

When species are rare both in terms of local abundance and geographic range they are said to face a “double jeopardy” (Gaston, 1994). Hence, the proper conservation of species functional roles relies on the knowledge of whether locally rare species are also rare in terms of geographic range size. Our study reveals that the most functionally distinct species have low local abundance and are regionally sparse. Although we did not directly assess the relationship between the geographic range and local abundance of species, the rarity pattern across scales (local – region) can provide important information to management strategies, which are mostly applied at small spatial scales.

Classic conservation prioritizations are commonly based on various taxonomic diversity components such as total species richness, endemism, rarity or threatened species, reflecting patterns of species occurrence (Lamoreux *et al.*, 2005; Guilhaumon *et al.*, 2008; Jenkins *et al.*, 2013). The biodiversity hotspots, for instance, are locations where exceptional concentrations of endemic species meet high levels of habitat loss (Roberts *et al.*, 2002; Myers *et al.*, 2004). Nevertheless, it is also acknowledged that the breadth of functions performed by species is also a crucial component that is worth preserving within the context of massive biodiversity decline (Naeem *et al.*, 2012). A recent study based on a functional approach has suggested new global hotspots of reef fish biodiversity considering species abundances and functional traits (Stuart-Smith *et al.*, 2013). However this study did not identify critical locations where the most distinct combinations of traits are supported by rare species. Our assessment of functional distinctiveness and potential functional diversity erosion across different marine biogeographic regions offers interesting insights towards conservation strategies. Despite the outstanding species richness and high functional redundancy in most tropical reef fish communities (Bellwood *et al.*, 2004; Halpern & Floeter, 2008; Mouillot *et al.*, 2014), considerable functional loss following the removal of its rare species may happen. For instance, the highly diverse reef fish communities of Lifou in New Caledonia (190 species) may loose up to 60% of functional diversity if 110 rare species were to disappear. In the well-preserved reefs of Palmyra Atoll and Kingman (Northern Line Islands) (Stevenson *et al.*, 2007; Sandin *et al.*, 2008), the loss of rare reef fishes (100 and 95 species, respectively), would also compromise nearly 40% of the functional diversity. Indeed, the losses of 100 or 95 species represent unrealistic scenarios, yet they highlight that the amount of rare species in reef fish ecological communities do contribute a lot to the functional diversity of such communities – from 20 to 80% of the functional space.

The combination of rarity – measured in terms of abundance – and functional distinctiveness indicates which are the “rarest” species carrying unique combinations of traits in reef fish communities. When we look at the global species pool, rare species with unique functional traits include the arrow blenny, *Lucayablennius zingaro* (Chaenopsidae), a very small invertebrate feeder occurring in the Caribbean; the shortstripe goby, *Elacatinus chancei* (Gobiidae), which occurs associated tube sponges also in the Caribbean region, and the orange-spotted grouper *Epinephelus coioides* (Epinephelidae), a large-bodied piscivore. These, among other species, combine high functional distinctiveness and low abundance values relative to other species from the global pool. At the local scale, the functions supported by rare species presenting low redundancy, *i.e.* low functional insurance, are primarily associated with traits such as large body size, piscivore, mobile invertivore or planktivore diet categories, and solitary behaviour. Large-bodied reef fishes tend to be rarer when compared to species of small and medium body sizes (Munday & Jones, 1998), which is possibly related to energetic and space (*e.g.* home range) requirements (Jones et al., 2002; Brown *et al.*, 2004). This highlights the local rarity and functional distinctiveness of top predator species. Their loss may greatly alter the breadth of functions performed in reef fish communities and imperil ecosystem functioning (Heithaus *et al*., 2008). Additionally, large-bodied fish species are more prone to declines or extinctions (Jennings *et al*., 1999; Bender *et al*., 2013b) given the correlated life-history traits that render their populations highly vulnerable to exploitation (Reynolds *et al*., 2005).

Our results call for new thinking and improved approaches into the preservation of the ecological roles supported by rare species in order to maintain the extant set of functions in reef fish communities. It also discloses that the functional loss following the removal of rare taxa might compromise not only species-poor communities, but also highly diverse reef fish communities. The patterns of rarity, functional diversity loss and distinctiveness of rare fish species remain to be explored in many regions, in particular in the Indo-Australian Archipelago (the Coral Triangle), the largest marine biodiversity hotspot hosting the greatest reef fish and coral diversity in the world (Roberts *et al*., 2002; Cowman & Bellwood, 2013).

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Appendix S1

Transect size standardization procedure and hierarchical sampling structure

Our analysis were conducted using one of the largest databases of underwater visual censuses compiled to date and assembling data collected across over 250 reef sites distributed in five major biogeographic regions (Kulbicki *et al*., 2013). Transects were oriented parallel to the reef, starting and ending at approximately the same depth. In each transect, fish were counted and identified to the species level. Reef fish communities of the Southwestern Atlantic, Eastern Atlantic and Eastern Pacific were surveyed through transects of 40 m^2 (2 m x 20 m). In the Caribbean transects were of 60 m^2. Visual censuses in Mexico, Honduras, Colombia (San Andres Archipelago), Easter and Salas y Gomez Islands, spanned over 100 m^2. In the Hawaiian Islands, Northern Line Islands and US Virgin Islands transects were of 100 and 200 m^2. And finally, in locations of the South Pacific and Western Indo-Pacific, transects were of 250 m^2 (Chabanet *et al*., 2010). Since transects varied in size we adopted a standardization method that randomly subsamples individuals from original transects to an area equivalent to 40 m^2 (Mora *et al*., reference). Under this standardization procedure, individuals are randomly sub-sampled within the fraction of transects that equals 40m^2 (Mora *et al*., 2011).

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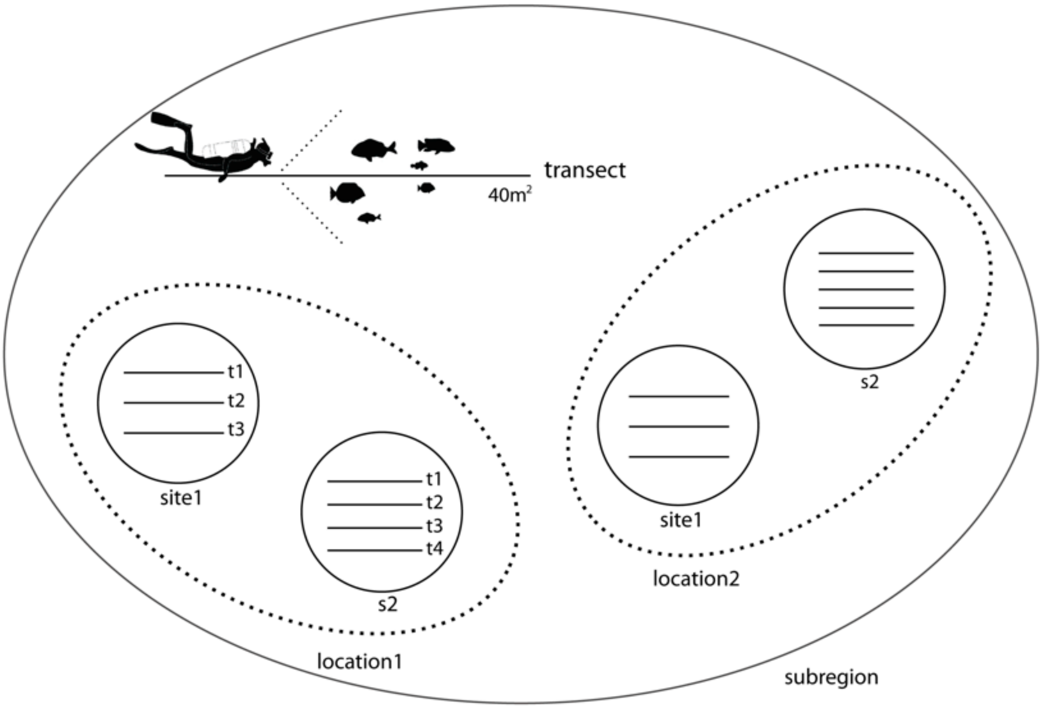

Figure S1. Schematic drawing of the hierarchical sampling structure of reef fish communities. Underwater visual transects (t1, t2, ...) of $40m^2$ were conducted across different sites (s1, s2, ...). These sites are gathered locations, which in its turn comprise a subregion. Our database comprises 93 locations gathered in 25 subregions distributed across six marine biogeographic regions.

Appendix S2

Reef fish species were classified into one of the 6 maximum body size categories: 0-7 cm, 7.1-15 cm, 15.1-30 cm, 30.1-50 cm, 50.1-80 cm and >80 cm. Fish species were also classified according to its mobility, in one of the 3 categories: sedentary (including territorial species), mobile within a reef and mobile between reefs. Period of activity also includes 3 ordered categories: diurnal, both diurnal and nocturnal, and nocturnal. Schooling behavior refers to 5 categories: solitary, pairing, or living in small (3-20 individuals), medium (20-50 individuals) or large groups (>50 groups). Vertical position in the water column includes 3 ordered categories: benthic, bentho-pelagic and pelagic. Species were also classified according to its diet, based on the main items consumed by each species, which led to 7 trophic categories: herbivore-detritivores (*i.e.* fish feeding on turf or filamentous algae and/or undefined organic material), macro-algal herbivores (*i.e.* fish eating large fleshy algae and/or seagrass), invertivores targeting sessile invertebrates (*i.e.* corals, sponges, ascidians), invertivores targeting mobile invertebrate (*i.e*. benthic species such as crustaceans), planktivores (*i.e.* fish eating small organisms in the water column), piscivores (including fish and cephalopods) and omnivores, *i.e.* fish for which both vegetal and animal material are important in their diet. Trait values for adult life-stages were extracted from FishBase and from more specific works for Indo-Pacific (Kulbicki *et al*., 2010), for Tropical Eastern Pacific (Robertson & Allen, 2008), and for Atlantic (Halpern & Floeter, 2008) fish faunas.

Reference list:

Halpern, B.S. & Floeter, S.R. 2008. Functional diversity responses to changing species richness in reef fish communities. Marine Ecology Progress Series 364, 147–156.

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Appendix S3

Functional space loss across reef fish communities

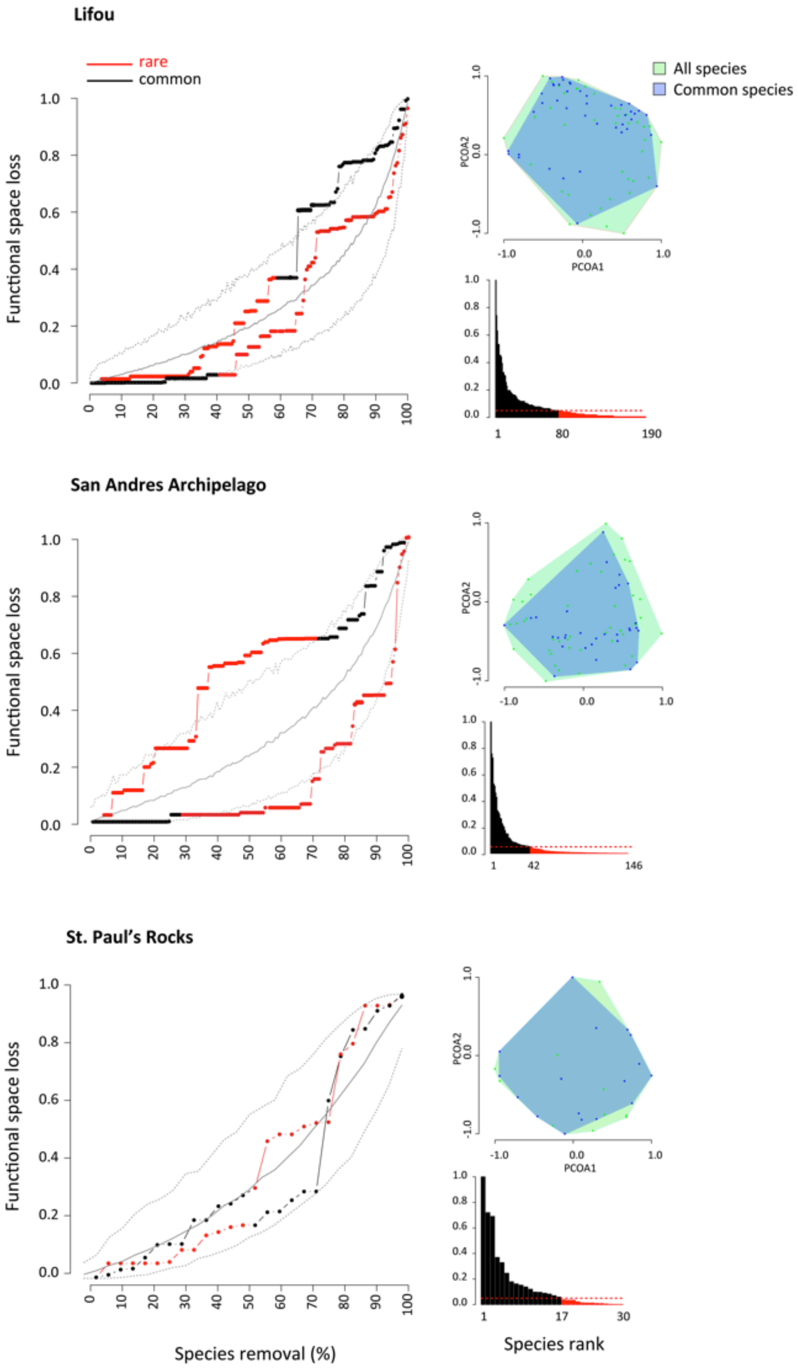

Figure S3.1. Plots for the amount of functional space loss – used as a surrogate for functional diversity –, the functional space of filled by species in the community and species abundance ranks (SARs) for Lifou (New Caledonia, Central Pacific), San Andres Archipelago (Colombia, Caribbean), and St. Paul's Rocks (Brazil, Southwestern Atlantic) communities. On the left hand-side, the loss of functional diversity was estimated after the successional removal of species from the most abundant, or common, to the "rarest" ones (black dots to red dots), and from the "rarest" species to the most abundant ones (red dots to black dots). Red dots represent rare species in communities (5% of the most abundant species), and black dots represent common species. Grey lines denote the 95% confidence intervals for the null model, in which functional diversity loss was measured following the random successional removal of species from communities. On the right, two dimensions of the functional space of all species in the communities (green) and the space filled by common species (blue); the SAR for the community (rare species in red, common in black).

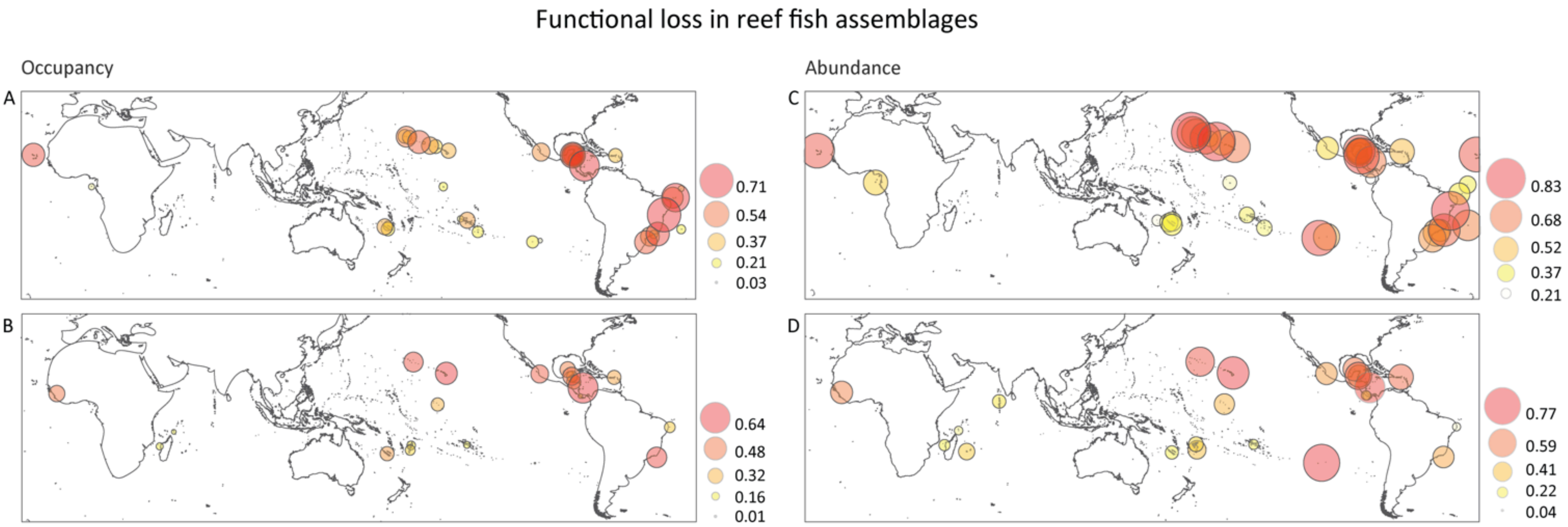

Figure S3.2. The functional loss in reef fish communities following the removal of rare species. The functional loss in communities when rarity is estimated through occupancy, at the local (A), and regional scales (B); and also when rarity is measured as the relative abundance at the local (C), and regional scales (D). Notice that at the local scale, when rarity is estimated in terms of species abundances, the functional loss is greater and reaches 80% of the functional space of communities. Colour gradient (pale yellow to red) and increasing circle-size gradient denote increasing functional loss

The loss in the functional space of fish communities is greater when rarity is measured through species abundance, and at the local scale (80% functional space loss) (c, d). Nevertheless, a considerable loss in the breath of functions present in communities is still detected when rarity is measured through occupancy, at the local and regional scales – up to 70% of functional loss (a, b). The functional loss identified for reef fish communities across different biogeographic regions is not related to total species richness nor to the number of rare species in communities.

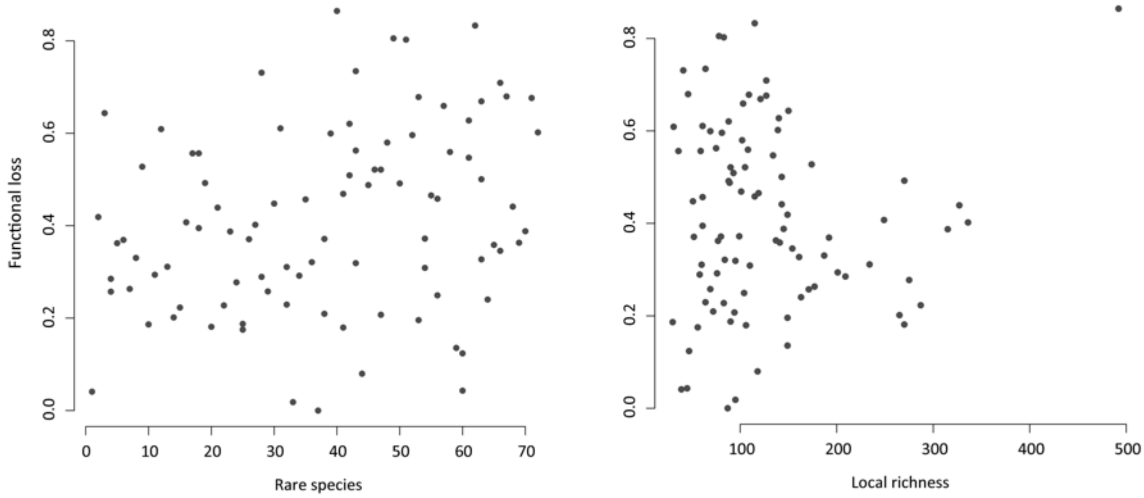

Figure S3.3. The relationship between functional loss and the number of rare species in communities (left); and functional loss and total species richness in reef fish communities (right).

Appendix S4

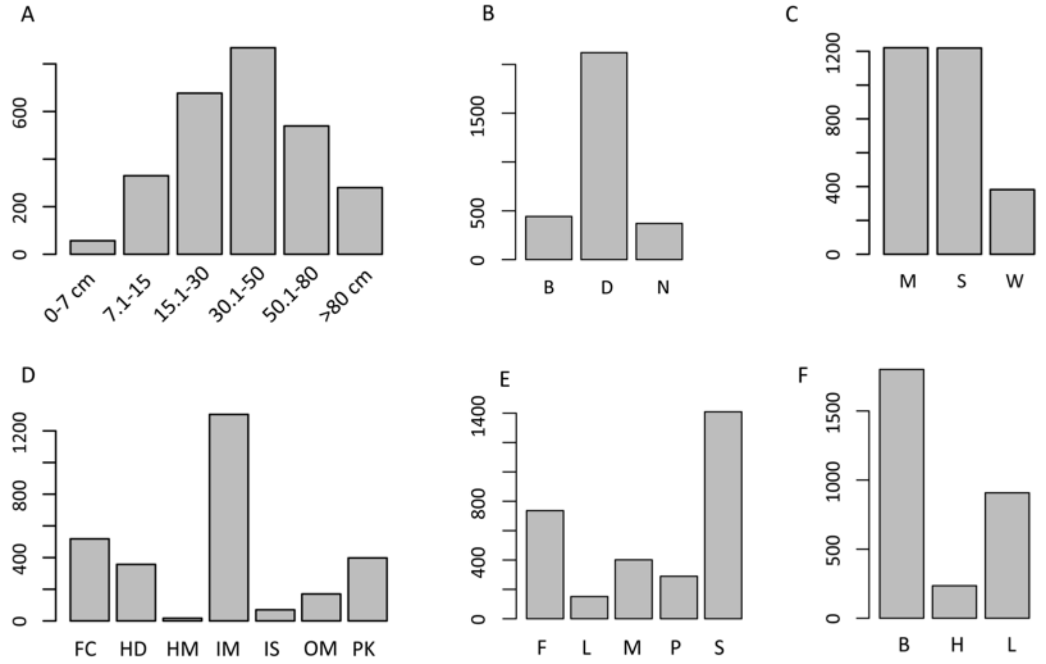

Figure S4. The traits of rare species across reef fish communities. Rare reef fish species body size categories (A), period of activity (B), mobility (C), diet categories (D), schooling behaviour (E), and position in the water column (F). The occurrence of traits was counted across each rare fish species in each one of the 25 subregions. Rarity was measured in terms of abundance at the subregion scale. Period of activity: D – diurnal, N – nocturnal, B – both. Mobility: S – sedentary, M – mobile within reef, B – mobile between reefs. Diet: HD – herbivore-detritivores, HM –macro-algal herbivores, IS – invertivores targeting sessile invertebrates, IM – invertivores targeting mobile invertebrates, PK – planktivores, FC – piscivores, and OM – omnivores. Schooling behavior: S – solitary, P – pairing, F – small, M – medium or L – large groups. Position in the water column: L – benthic, B – bentho-pelagic and H – pelagic.

CONCLUSÃO

CONCLUSÃO

Nas últimos 30 anos, a ecologia de comunidades têm utilizado abordagens baseadas em atributos biológicos para compreender a estruturação de comunidades (Grime, 1974; McGuill *et al*., 2006; Weiher *et al*., 2011). O estudo de padrões e processos por trás da estruturação de comunidades de peixes recifais iniciaram na década de 70 e foram, em sua maioria, focados na estrutura taxonômica deste conjunto de espécies (Sale, 1977; Syms *et al*., 1998; Bellwood & Hughes, 2001; Mora *et al*., 2003). No entanto, na última década, um número crescente de estudos de comunidades de peixes recifais também foram conduzidos a partir de uma perspectiva funcional, em que as características das espécies e seus impactos sobre os processos do ecossistema são considerados (Bellwood *et al*., 2002; 2003; 2004; 2006; Halpern & Floeter, 2008; Guillemot *et al*., 2011). Esta perspectiva com foco em um outro componente de comunidades ecológicas – além do componente taxonômico – é de grande relevância, visto que cada processo pode afetar de maneira distinta os componentes da diversidade (Devictor *et al*., 2010; Mouillot *et al*., 2011; Meynard *et al.,* 2011). Além disso, a escala na qual os padrões de estruturação de comunidades e mecanismos relacionas são investigados pode resultar em diferentes respostas. Apesar dos processos de estruturação de comunidades de peixes recifais terem sido investigados anteriormente em grandes escalas espaciais (Bellwood & Hughes, 2001; Bellwood *et al*., 2006), inclusive focando nos atributos das espécies (Bellwood *et al*., 2006), estes componentes raramente são avaliados em conjunto, e em múltiplas escalas espaciais. O objetivo principal deste trabalho foi revelar os padrões e processos de estruturação de comunidades de peixes recifais em múltiplas escalas espaciais, avaliando tanto grupos taxonômicos quanto funcionais sob uma abordagem complementar. Especificamente, eu estudei os determinantes da estrutura funcional e taxonômica de assembléias de peixes recifais dentro do Oceano Atlântico e demais regiões biogeográficas, com a intenção de separar os efeitos de processos histórico-evolutivos, biogeográficos e ambientais, sobre os padrões de estruturação das assembléias. Eu também explorei os padrões de estrutura das comunidades de peixes recifais através de regiões biogeográficas distintas – Indo-Pacífico, Pacífico Tropical Oriental e Atlântico – para entender se os padrões e processos destas regiões foram moldados principalmente por diferenças em sua história evolutiva.

Além disso, eu investiguei se as comunidades de peixes recifais apresentam um padrão aninhado, onde as comunidades com menor riqueza de espécies são subconjuntos daqueles locais ricos em espécies, e entidades funcionais "universais" estão presentes em todos os locais. Por fim, estudei as funções representadas por espécies raras e comuns em comunidades de peixes recifais de 93 locais diferentes, distribuídos em cinco regiões biogeográficas.

De maneira geral, os resultados revelam que processos dentro de cada região, como a história-evolutiva, são responsáveis por padrões na estrutura taxonômica e funcional em cada região, *i.e.* no Indo-Pacífico, Pacífico Tropical Oriental e Atlântico. Além disso, a disponibilidade de habitat em escala local – como a area recifal – , isolamento e temperature de superfície do oceano (Sea Surface Temperature, SST), têm papel central na estruturação dos componentes de comunidades ecológicas de peixes recifais. Estes fatores ambientais interagem com os atributos das espécies – tamanho do corpo e categoria trófica – determinando a composição de espécies nas comunidades. Os atributos de peixes recifais, por sua vez, interagem com os filtros ambientais através do potencial de dispersão/ colonização de espécies, bem como dos recursos necessários às espécies. Para peixes recifais, tamanho corporal grande implica em distribuições mais amplas, maior potencial para colonizar novos habitats e para expandir sua distribuição através de barreiras de dispersão (Luiz *et al*., 2012; 2013). Entretanto, peixes recifais de tamanho pequeno têm distribuição restrita e especificidade de habitat (Hawkins *et al*., 2000), estando associados à complexidade estrutural dos recifes de coral (Munday & Jones, 1998; Bender *et al*., 2013). Espécies de tamanho pequeno predominam em locais com grandes áreas cobertas por recifes de coral, como o Caribe e o Indo-Pacífico Central, enquanto que espécies de tamanho grande predominam em assembléias associadas a locais periféricos, com menor riqueza de espécies e isolados dos centros de diversidade. Considerando grupos tróficos, existem diferenças marcantes na contribuição de cada grupo ao longo das diferentes regiões biogeográficas (Capítulo II) e também dentros de cada região (Capítulo I). Enquanto piscívoros podem representar até 20% da riqueza de espécies no Pacífico Oriental Tropical, eles não ultrapassam 12% nas áreas mais ricas em espécies no Arquipélago Indo-Australiano. No Atlântico, espécies que se alimentam de invertebrados representam um grande proporção da riqueza de espécies em comunidades de peixes recifais, enquanto no Indo-Pacífico existe uma proporção maior de planctívoros. A temperatura interage com o tamanho das espécies, dieta, comportamento alimentar e categoria trófica, e também influencia a disponibilidade de recursos ambientais (Harmelin-Vivien, 2002), sendo um importante fator que afeta a estrutura de comunidades de peixes recifais (Bender *et al*., 2013a). Apesar das variações existentes, assembléias globais de peixes recifais são compostas por um número reduzido de configurações taxonômicas e funcionais ao longo de seu extraordinário gradiente de riqueza de espécies.

Quando os atributos biológicos das espécies – tamanho do corpo e categoria trófica – são combinados para definir um conjunto de entidades funcionais (EF) e os padrões de distribuição destas entidades são estudados, as comunidades de peixes recifais apresentam estruturas funcionais semelhantes dentro de cada região biogeográfica. A estrutura funcional de comunidades com menor riqueza de espécies representam subconjuntos da estrutura funcional encontrada naqueles locais mais ricos, e este padrão se mantém para a maior parte das regiões. Entretanto, este padrão aninhado não é encontrado para a estrutura taxonômica (*i.e.* número de espécies/ família) das comunidades. Provavelmente, isto resulta da homogeneidade na composição taxonômica de comunidades de peixes recifais dentro de cada região, o que foi encontrado no Capítulo II. Devido à redundância funcional, um padrão aninhado da estrutura funcional foi identificado mesmo para locais muito isolados. O aninhamento funcional pode estar associado às funções "universais": aquelas EF que são essenciais para os processos do ecossistema são mantidas ao longo das localidades, apesar do *turnover* de espécies dentro destas EF. Os padrões de estruturação identificados estão associados ao potencial de dispersão e/ ou recursos necessários às espécies, os quais interagem com gradientes de isolamento e área.

Apesar das comunidades de peixes recifais poderem apresentar uma estrutura funcional básica/ universal ao longo de amplos gradientes de riqueza, algumas funções podem estar associadas à espécies raras – aquelas com distribuição restrita ou população pequena (Rabinowitz, 1981; Gaston, 1994). Esta questão levou ao Capítulo IV, no qual eu avalio o grau de sobreposição nas funções de espécies raras e comuns em comunidades de peixes recifais de diferentes oceanos. As espécies de peixes raras preenchem a maior parte da gama de atributos funcionais presentes nas comunidades avaliadas, e muitas vezes têm funções únicas. Também avaliei as reduções na diversidade funcional das comunidades após a remoção de espécies raras, e mostei que a perda de espécies raras pode comprometer seriamente a diversidade funcional de comunidades. Estes resultados mostram a vulnerabilidade de papéis ecológicos de espécies raras, mesmo nas mais diversas comunidades de peixes recifais.

Esta tese mostra que os padrões da estrutura taxonômica e funcional de comunidades de peixes recifais foram moldadas por um conjunto de fatores e/ou processos: história evolutiva, biogeografia (isolamento, latitude, distância do centro da diversidade) e fatores ambientais (SST, recife rochoso vs. biogênico, riqueza de espécies de coral, etc.). Além disso, revelamos os papéis relativos de cada fator na estruturação dos componentes taxonômico e funcional das comunidades de regiões biogeográficas. A interação entre isolamento e a estrutura funcional das comunidades destaca a importância da conectividade entre comunidades de peixes recifais. Disponibilidade de habitat é uma característica ambiental importante no processo de estrutuação de comunidades de peixe recifal, independente da escala espacial (Bellwood & Hughes, 2001; Hubert *et al*., 2011; Bender *et al*., 2013a; Parravicini *et al*., 2013). Além disso, a temperatura foi identificada como uma variável que afeta a estrutura funcional das comunidades de peixe no Indo-Pacífico. Este conjunto de resultados contribui para o entendimento dos padrões de estruturação das comunidades de peixe recifal em grande escala espacial, e também para orientar futuros esforços de conservação dos ambientes recifais, os quais devem priorizar a conectividade entre recifes a fim de manter o conjunto de funções existente nestas comunidades.

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