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**SOBRE A ORGANIZAÇÃO DAS ESPÉCIES  
NAS COMUNIDADES: UMA ABORDAGEM  
GLOBAL COM PEIXES RECIFAIS**

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## RESUMO

A distribuição de espécies nas comunidades é mais influenciada por filtros locais derivados de interações de espécies ou fatores históricos e processos biogeográficos em escala regional? Que contribuição da riqueza regional seria esperada na compactação de espécies por unidade de área? Essas relações permanecem constantes em escalas espaciais hierárquicas de transectos a regiões? Num gradiente crescente de riqueza regional, a importância de fatores determinísticos vs. estocásticos nas regras de montagem (*assembly rules*) das comunidades locais se alterna? Categorizar espécies num conjunto reduzido de grupos funcionais muda os padrões supracitados? Por quê? Quão ampla deve ser a aplicabilidade de todos esses padrões entre diferentes grupos de organismos? Nesta dissertação, direciono respostas e discussões a esses desafios utilizando, provavelmente, o banco de dados quantitativo mais extenso geograficamente já compilado para peixes recifais – o grupo de vertebrados mais rico do planeta. Independentemente, eu e os colaboradores desse trabalho realizamos transectos padronizados em  $20 \times 2 \text{ m} = 40 \text{ m}^2$  paralelos ao recife até 30m de profundidade – um esforço total de 5.916 transectos. O escopo geográfico abrange 103 sítios distribuídos em 17 localidades englobadas em seis grandes regiões biogeográficas marinhas tropicais: 1) Caribe (Belize, Cuba e Bahamas); 2) Atlântico Sul Ocidental (sul, sudeste e nordeste do Brasil); 3) ilhas oceânicas do Atlântico Sul Ocidental (Arquipélagos de São Pedro e São Paulo, Fernando de Noronha e Trindade e Martim Vaz); 4) Atlântico Oriental (São Tomé e Cabo Verde); 5) Pacífico Oriental (México e ilha de Malpelo); 6) Pacífico Sul (Nova Caledônia, Tonga, Fiji e Polinésia Francesa). 989 espécies pertencentes a 301 gêneros e 83 famílias foram registradas. Através de regressões entre riqueza local e regional em três escalas espaciais hierárquicas observei que a riqueza local aumenta linearmente com o aumento da riqueza regional tanto em termos taxonômicos (riqueza de espécies) como funcionais (riqueza de grupos funcionais). Isso indica que processos atuando na escala regional (e.g., especiação, extinção, dispersão) devem ser mais influentes do que processos locais (e.g., competição, predação) na composição local de comunidades. O aumento da riqueza regional de peixes em função do aumento da riqueza regional de corais pode ser um indicativo de que diversidade gera diversidade em termos de riqueza de nicho. Nas 17 localidades, a dissimilaridade média entre amostras, medida através da distância de Jaccard, não diferiu do esperado ao acaso, i.e., gerado por

um modelo nulo que simulou colonizações no espaço. Esse padrão, observado em termos taxonômicos e funcionais, sugere que as espécies e grupos funcionais se distribuem de maneira estocástica na escala local da comunidade, entretanto outras abordagens nulas devem ser adotadas para confirmação do padrão encontrado. Meus resultados estão de acordo com a recente mudança de paradigma na Ecologia de Comunidades na qual as atenções voltaram-se para padrões regionais e macroecológicos ao invés de processos locais no entendimento da composição local da biodiversidade, ainda que tais regras sejam contingentes ao grupo de organismos analisado. Acredito que os resultados aqui apresentados possam refletir um padrão geral para metacomunidades ricas e relativamente abertas, nas quais comunidades locais são altamente influenciadas por processos regionais e talvez montadas ao acaso.

**Palavras-chave:** Diversidade  $\alpha$ ,  $\beta$  e  $\gamma$ . Escala. Regras de montagem. Grupos funcionais. Peixes recifais.

## ABSTRACT

Should species interactions determine their distribution in local communities or are they more influenced by biogeographical and historical processes? What is the contribution of increasing regional richness on their packing? Will this influence remain the same as spatial scale grows hierarchically (e.g., islands, regions)? As regional richness increases will community composition be assembled by chance rather than by deterministic factors? How the categorization of species into a smaller set of functional groups would change the observed results? Why? How broad should be the applicability of the answers to such questions between different species assemblages? In the present thesis, I address the answers and discussions to these challenges through the most geographically exhaustive community dataset compiled to date for reef fish – the most species-rich vertebrate assemblage on Earth. I and other colleagues have conducted visual censuses independently through area-standardized strip transects (incidence data in  $20 \times 2\text{m} = 40\text{m}^2$ ) between 0 and 30m of depth in rocky and coral reef systems – a total effort that summed 5.916 transects. The geographical range encompassed 103 sites spread through 17 major localities embedded in 6 main tropical biogeographical provinces: Caribbean (Bahamas, Belize and Cuba), Southwestern Atlantic (Northeastern, Southeastern and South Brazil), Southwestern Atlantic Oceanic islands (St. Paul's Rocks, Fernando de Noronha Archipelago and Trindade/MartimVaz Archipelago), Tropical Eastern Atlantic (Cape Verde and São Tomé), Tropical Eastern Pacific (Malpelo island and central Western Mexico) and South Pacific (New Caledonia, Fiji, Tonga and French Polynesia). This represents a regional richness gradient from approximately 60 to 1500 species. 989 species belonging to 301 genera and 83 families were recorded. Local vs. regional plots, both on taxonomical and functional perspectives, show that local community is positively enriched as regional richness increases, with no sign of approaching a saturation level. This indicates a strong influence of regional processes on the local composition of communities. The fact that reef fish regional richness responded linearly to coral regional richness might indicate that diversity begets diversity in terms of niche diversification or both corals and fish's evolution was driven by other factors in common. In the 17 localities analyzed, the observed mean beta diversity (Jaccard distance) did not differ from the random-placement null model, both in taxonomic and functional perspectives. This may indicate that species and

functional groups in local communities are stochastically assembled; however different null models should be applied in order to confirm such pattern. My results support the relatively recent change of paradigm in Community Ecology where attention has shifted from local to regional and macroecological processes if one tries to understand the underpinning rules of local biodiversity functioning, even though such patterns should be very contingent between different groups of organisms. I believe that the results herein presented should be applicable to rich and relatively open metacommunities, i.e., local communities are strongly influenced by regional processes and maybe their assembly is mostly driven by stochasticity.

**Keywords:**  $\alpha$ ,  $\beta$  and  $\gamma$  diversity. Scale. Assembly rules. Functional groups. Reef fish

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## **INTRODUÇÃO**



### *A problemática ambiental e o estudo da diversidade*

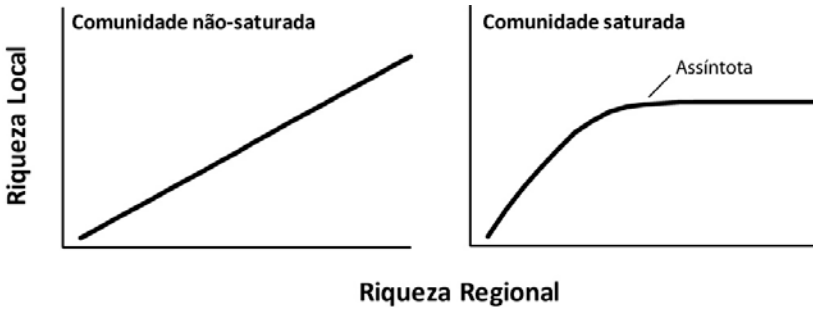
Ações antropogênicas vêm alterando a composição biológica das comunidades através de uma variedade de atividades que aumentaram a taxa de invasão e extinção de espécies, em todas as escalas, de local a global (Jackson et al. 2001, Hooper et al. 2005). Essas mudanças nos componentes da biodiversidade do planeta são preocupantes não só por razões éticas e estéticas, mas também por possuírem um grande potencial de alterar as propriedades ecossistêmicas e os benefícios e serviços que essa biodiversidade oferece à humanidade (Dobson 1995, Thompsom & Starzonski 2006, Keesing et al. 2010).

Nas duas últimas décadas, pesquisas abordando diversidade e riqueza de espécies vêm ganhando especial atenção (Ricklefs & Schluter 1993, Rosenzweig 1995, Cornell & Karlson 2000, Petchey & Gaston 2002, Cornell et al. 2008, Dahl et al. 2009), principalmente porque as políticas públicas conservacionistas utilizam medidas de diversidade e riqueza para justificar e direcionar os recursos destinados à conservação ambiental. O desafio está em medir a diversidade de maneira que possa ser bem interpretada (Purvis & Hector 2000). Assim, medidas comparáveis de riqueza (e.g. riqueza local ou diversidade alfa por unidade de área padrão) de diversos locais podem responder questões cruciais sobre como a diversidade conhecida está estruturada e qual a melhor maneira de conservá-la (Hooper et al. 2005, Cornell et al. 2007, Arias-González et al. 2008, Rodríguez-Zaragoza & Arias-González 2008). Conseqüentemente, os ecólogos distinguem tradicionalmente diferentes componentes da diversidade (=riqueza) de espécies, sendo três principais: diversidade local ou alfa ( $\alpha$ ), diversidade beta ou substituição ( $\beta$ ) e diversidade regional ou gama ( $\gamma$ ) (Whittaker 1972, Koleff et al. 2003).

### *A influência da escala regional*

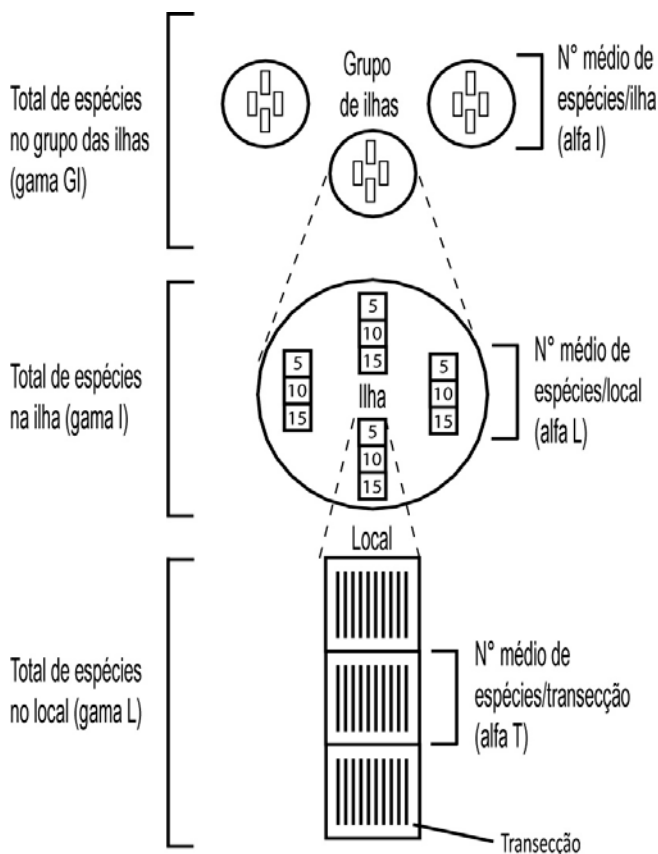
As últimas duas décadas representam uma importante mudança de paradigma na ecologia de comunidades de forma que muitos estudos têm frisado a grande importância de fatores atuantes na escala regional derivados de processos históricos e biogeográficos, ao invés da visão

clássica que atribuía maior importância e foco de trabalho em processos locais na formação das comunidades (Schluter & Ricklefs 1993, Karlson et al. 2004, Ricklefs 2008). Muitos avanços nesse novo conceito derivam de estudos avaliando como a riqueza local (ou diversidade alfa) se comporta ao longo de um gradiente de riqueza regional (diversidade gama) (Srivastava 1999, Loreau 2000, Soininen et al. 2007) (Figura 1).



**Figura 1.** Modelo conceitual ilustrando as duas interpretações básicas para as curvas de relação entre as riquezas local e regional. Ver texto para maiores explicações.

Classicamente se imaginava que, de modo geral, na natureza as comunidades seriam saturadas em espécies (Figura 1, direita) e, portanto, a composição local das mesmas seria fortemente determinada pelas interações competitivas entre espécies que as compunham (Schluter & Ricklefs 1993, Ricklefs 2008); entretanto, estudos recentes têm mostrado que a riqueza local aumenta com a riqueza regional, na maioria dos casos linearmente (Loreau 2000, Ricklefs 2000, Witman et al. 2004, Cornell et al. 2007, 2008), o que tem gerado interpretações muito exageradas: “curvas insaturadas” seriam típicas de comunidades insaturadas e não-interativas, enquanto “curvas saturadas” indicariam comunidades saturadas e altamente interativas (Cornell & Lawton 1992). Loreau (2000) sugere que curvas de riqueza local-regional em múltiplas escalas hierárquicas (transectos englobados em sítios, sítios englobados em ilhas, ilhas em arquipélagos; ver modelo esquemático em Figura 2) são muito mais confiáveis para se entender os padrões macroecológicos que regem o comportamento da biodiversidade (Cornell & Lawton 1992, Cornell & Karlson 2000, Karlson et al. 2004).



**Figura 2.** Exemplo de amostragem em escalas espaciais hierárquicas. 'Alfa T' indica a diversidade alfa (ou riqueza local) de um local (ou entre transectos), i.e., média de espécies entre transectos; 'Gama L' indica a diversidade gama (ou riqueza regional) do local, i.e., total de espécies amostradas dentro do local; 'Alfa L' representa a diversidade alfa da ilha, i.e., média de espécies entre locais; 'Gama I' indica a diversidade gama da ilha; 'Alfa I' indica a diversidade alfa do arquipélago, i.e., média de espécies entre ilhas; 'Gama GI' indica a diversidade gama, i.e., total de espécies, encontrada no arquipélago. Modelo adaptado de Cornell et al. (2007) utilizado para o estudo da diversidade de corais hermatípicos no Indo-Pacífico.

Em escalas espaciais hierárquicas, desde pequenos locais até grandes regiões biogeográficas, estudos mostram um incremento constante na riqueza local à medida que a riqueza regional aumenta, sem

sinais aparentes de atingir uma saturação ou assíntota (Figura 1; Lawton 1999, Karlson et al. 2004, Witman et al. 2004, Cornell et al. 2008, Soininen et al. 2007, Belmaker 2009). Isso basicamente indica que a composição das comunidades na escala local deve ser mais influenciada por processos atuantes na ampla escala temporal dos processos regionais (e.g. limite de dispersão, taxa de colonização, especiação e extinção) do que na escala das interações locais (e.g. competição, inibição, facilitação, predação).

### ***A diversidade beta***

A diversidade beta (*species turnover*) é uma medida da diferença na composição de espécies tanto entre duas ou mais assembléias locais como entre assembléias locais e regionais (Ricklefs & Schluter 1993, Condit et al. 2002, Soininen et al. 2007, Dahl et al. 2009). Desde a sugestão original de Whittaker (1972) de que a diversidade beta devesse ser medida como a proporção na qual a riqueza de espécies de uma região excede a riqueza média de uma única localidade dentro da mesma região, diversos estudos a têm empregado para mensurar a mudança na composição de espécies em diversas escalas para diversos fins (e.g. Cornell & Lawton 1992, Cornell & Karlson 2000, Magurran 2004, Cornell et al. 2007, 2008).

Para uma dada riqueza regional de espécies, localidades individuais se diferenciam mais marcadamente entre si e representam uma proporção menor das espécies que ocorrem na região à medida que a diversidade beta aumenta (Dahl et al. 2009). É, portanto, reconhecido que a diversidade beta captura uma faceta fundamental do padrão espacial da biodiversidade (Gaston & Williams 1996). Entretanto, estudos relacionados à diversidade beta são poucos quando comparados à diversidade local e regional, especialmente abordando a variação da riqueza de espécies e seus respectivos determinantes em ampla escala (Brown 1995, Gaston 2000, Lomolino et al. 2006).

Há uma generalização recorrente de que a diversidade beta aumenta em direção a baixas latitudes, fornecendo um provável mecanismo para a alta riqueza de espécies nos trópicos (Lomolino et al. 2006). Alguns estudos recentes têm testado empiricamente tais generalizações e os resultados são inconsistentes, sugerindo que os padrões provavelmente são fortemente contingentes no que diz respeito

a táxons ou região geográfica (Koleff et al. 2003, Soininen et al. 2007, Dahl et al. 2009).

### ***As regras de montagem ('assembly rules') das comunidades locais***

Os padrões que determinam como e quantas espécies ocorrem em comum entre duas comunidades são um dos temas centrais na ecologia de comunidades, sendo que esse debate data desde os trabalhos de Gleason (1927) e Clements (1938). Diamond (1975) propôs que a composição das comunidades deveria ser regida por regras de montagem ou "*assembly rules*", as quais poderiam ser preditas e determinadas por algumas variáveis chave, tais como riqueza regional de espécies, variáveis abióticas e interações interespecíficas (Chase 2003). O fato de comunidades ambientalmente similares apresentarem estruturas variáveis na composição levou à proposição de que as comunidades poderiam atingir múltiplos equilíbrios estáveis (Diamond 1975, Chase 2003, 2010).

Connor & Simberloff (1979) desafiaram essa idéia afirmando que as regras de montagem propostas por Diamond (1975) seriam "tautológicas, triviais ou – mais importante – um padrão similar ao obtido por um modelo nulo onde as espécies são estocasticamente distribuídas no espaço". A partir disso, muitos trabalhos consideraram a utilização de modelos nulos para testes em ecologia de comunidades, sendo que muitos outros modelos foram propostos e discutidos (ver revisões em Gotelli & Graves 1996, Gotelli 2000). Chase (2003) retoma a idéia das regras de montagem avaliando o papel da riqueza regional e produtividade nas mesmas, e ao longo de um experimento de sete anos (Chase 2010), demonstra que num gradiente crescente de riqueza regional e produtividade existe uma alternância de fatores determinísticos para estocásticos na montagem das comunidades levando as mesmas a múltiplos equilíbrios estáveis.

Verificar a possível aplicabilidade desses resultados em gradientes de riqueza regional para diferentes organismos permanece um desafio. Será que na maioria dos casos as comunidades regidas por fatores determinísticos passam a múltiplos equilíbrios estáveis (Chase 2003, 2010), ou são simplesmente organizadas ao acaso sem nunca atingir um equilíbrio propriamente dito?

### *Categorizando espécies em grupos funcionais*

Muito do que se sabe sobre as relações entre riqueza local e regional foi conduzido somente em termos taxonômicos, i.e., análises utilizando espécies como unidade biológica. Até o momento, não existem trabalhos que tenham realizado a mesma abordagem em termos de riqueza funcional, i.e., número de grupos funcionais ao invés de espécies. A categorização de espécies em grupos funcionais pode ser realizada através da combinação de atributos funcionais considerados importantes no nicho fundamental de cada espécie que compõe uma comunidade local (McGill et al. 2006, Halpern & Floeter 2008). Logo, espera-se que essa avaliação seja feita de forma particular para cada grupo de estudo. Tal processo deve resultar em uma diminuição de unidades biológicas, pois pode englobar várias espécies em grupos de comum função. Dessa maneira, seria possível avaliar se a composição funcional na escala local, assim como na perspectiva taxonômica, aumenta ao longo de um gradiente de riqueza regional ou atinge um nível de saturação – o que pode ser esperado caso o número de grupos funcionais seja bastante reduzido (Halpern & Floeter 2008).

### *Hipóteses*

Diante dos tópicos acima expostos foram elaboradas hipóteses sobre uma série de modelos conceituais de acordo com possíveis comportamentos da riqueza local em função da riqueza regional, tanto na perspectiva taxonômica quanto na funcional:

1) Se a riqueza taxonômica local for fortemente influenciada pela riqueza regional e esse padrão se repetir na perspectiva funcional, processos operando na grande escala regional devem exercer forte influência na composição local das comunidades;

2) Se a riqueza taxonômica local for fortemente influenciada pela riqueza regional mas a riqueza funcional local atinge uma assíntota, i.e., um teto máximo:

a) Filtros locais provocados por interações intra e interespecíficas promovem a restrição da composição das comunidades e as mesmas devem possuir regras fixas de montagem (Diamond 1975);



b) As comunidades são primariamente montadas de maneira determinística e, à medida que a riqueza regional aumenta, efeitos de prioridade (e.g., inibição e facilitação) se tornam mais intensos levando as comunidades a múltiplos equilíbrios estáveis (Chase 2003, 2010).

Nesta dissertação, testo em uma perspectiva taxonômica e também funcional se: 1) as comunidades locais são mais influenciadas por fatores em níveis locais de interação ou regionais; 2) a montagem ou organização das comunidades ocorre ao acaso ou é regida por fatores determinísticos. Utilizo provavelmente o banco de dados quantitativo geograficamente mais extenso já compilado para peixes recifais – o grupo de vertebrados mais rico do planeta– em um esforço total de 5.916 amostras em diversos locais do mundo. O escopo geográfico abrange 103 sítios distribuídos em 17 localidades englobadas em seis grandes regiões biogeográficas marinhas tropicais: 1) Caribe (Belize, Cuba e Bahamas); 2) Atlântico Sul Ocidental (sul, sudeste e nordeste do Brasil); 3) ilhas oceânicas do Atlântico Sul Ocidental (Arquipélagos de São Pedro e São Paulo, Fernando de Noronha e Trindade e Martim Vaz); 4) Atlântico Oriental (São Tomé e Cabo Verde); 5) Pacífico Oriental (México e ilha de Malpelo); 6) Pacífico Sul (Nova Caledônia, Tonga, Fiji e Polinésia Francesa).

Os resultados observados somente a partir de regressões entre riqueza local em função da riqueza regional podem não ser suficientes para gerar conclusões concretas (Cornell et al. 2008) já que seria difícil observar se existe algum ponto, ao longo de um gradiente de riqueza regional, onde há alternância entre fatores determinísticos e a estocasticidade na montagem das comunidades (Chase 2010). Uma abordagem complementar seria analisar em diferentes localidades, ao longo de um gradiente de riqueza regional, como a beta diversidade observada difere daquela obtida através de uma comunidade gerada ao acaso (Cornell et al. 2007, Anderson et al. 2011). Se a beta diversidade observada apresentar valores menores do que os obtidos numa comunidade gerada ao acaso, se conclui que existe forte determinismo na montagem das comunidades, ao passo que a igualdade de valores entre observado e nulo indicaria forte estocasticidade. A utilização de modelos nulos é uma das maneiras mais recomendadas para se entender os padrões de riqueza observados e seus respectivos mecanismos (Anderson et al. 2011).

Um estudo aponta a possibilidade de estocasticidade em comunidades de peixes recifais (Belmaker 2009). Entretanto os resultados estão restritos a um pequeno gradiente de riqueza regional

dentro de uma única região biogeográfica. Além disso, não foram analisados em uma perspectiva de riqueza funcional. Apesar de evidências mostrando regras de montagem nas comunidades de peixes recifais em ampla escala (Bellwood & Hughes 2001), detectar estocasticidade funcional na escala local desafiaria tanto essa possibilidade assim como a existência de múltiplos equilíbrios estáveis nas comunidades locais (Chase 2010).

## **CAPÍTULO ÚNICO**

### **HOW ARE SPECIES PACKED IN SPACE? THE ROLE OF REGIONAL RICHNESS AND STOCHASTICITY ON TAXONOMIC AND FUNCTIONAL COMMUNITY ASSEMBLY**



## HOW ARE SPECIES PACKED IN SPACE? THE ROLE OF REGIONAL RICHNESS AND STOCHASTICITY ON TAXONOMIC AND FUNCTIONAL COMMUNITY ASSEMBLY

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**Although great advances have emerged on the relationships between alpha, beta and gamma diversity, relatively little is known on how they interplay in a functional richness perspective. We addressed this gap through an unprecedented regional richness gradient using the geographically most exhaustive reef fish assemblage dataset compiled to date. Both at taxonomical and functional levels, alpha diversity increased with increasing gamma diversity, thus supporting the hypothesis that diversity begets diversity in terms of niche diversification. Our results indicate that, from the poorest to the richest locality, local richness in reef fish communities is more influenced by regional and historical processes. Relatively open and rich metacommunities local assembly may present a stochasticity-like pattern probably as a consequence of many simultaneous spatio-temporal dynamics.**

A great paradigm shift on the concept of community ecology has occurred in the last two decades, where many studies have brought the attention to regional and historical processes rather than local interaction influencing local community assembly (Schluter and Ricklefs 1993, Karlson et al. 2004, Ricklefs 2008). Many advances on this new idea were brought up by research focused on the relationship between the

three classical components of diversity, namely alpha (local), beta (turnover) and gamma (regional) diversity (Srivastava 1999, Loureau 2000, Soininen et al. 2007).

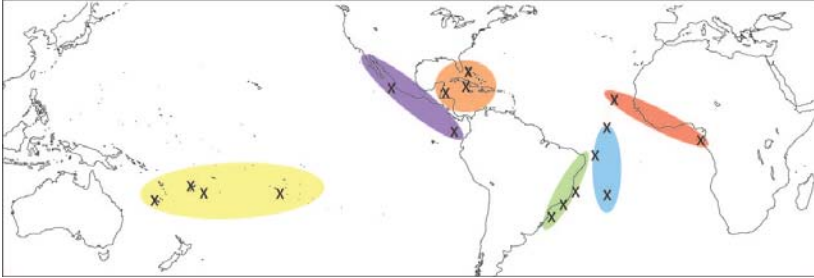
In many hierarchical scales, from local assemblages to entire landscapes and biogeographical regions, most studies show a local faunal enrichment following an increasing gradient of regional richness, with no sign of approaching a local level saturation (Lawton 1999, Karlson et al. 2004, Witman et al. 2004, Cornell et al. 2008, Soininen et al. 2007, Belmaker 2009). This basically means that community composition at the local scale is likely to be underpinned by regional processes (e.g., dispersal limitation, speciation and extinction rates) instead of local species interactions (e.g., competition, predation). However, we are not aware of any studies attempting to seek such trend in a functional richness perspective. Categorizing species into functional groups can be done by the combination of known functional traits considered important in community niche packing (McGill et al. 2006, Halpern and Floeter 2008), and that shall be particular to each group of study. In most cases, this approach is likely to reduce the number of biological units (functional groups instead of species) and could thus reveal whether local functional composition grows with increasing regional richness or achieves a level of functional saturation, i.e. as taxonomic richness increases, there will be an increasing level of biological redundancy as no more functions are added to the system. If local taxonomic richness is strongly influenced by regional richness and this pattern is also observed in a functional perspective, one might hypothesize that diversity begets diversity, where richer communities increasingly encompass a greater array of functions. However, if local functional richness reaches an asymptote and thus cannot trespass a niche packing “ceiling”, the assembly of communities can either be ruled uniquely by deterministic mechanisms or functional deterministic priority effects become more intense leading to communities presenting stochastic multiple stable equilibria (Chase 2003, 2010).

Nevertheless, the outcomes observed uniquely from local vs. regional plots might not be enough to draw precise conclusions (Cornell et al. 2008) as it would be very difficult to depict if there exists a threshold of regional richness at which community assembly starts being more influenced by stochasticity rather than deterministic processes (Chase 2010). A complementary way to achieve such answer would be to analyze how functional beta diversity differs from a hypothetical pattern merely expected by chance (Chase 2010) as regional richness increases (Cornell et al. 2007, see also mission statement V4b in

Anderson et al. 2011). If the observed community dissimilarity falls below the null expectation, then one would expect stronger determinism in community functional assembly while the lack of differences should indicate strong stochasticity. By addressing appropriate null models, one could disentangle the underpinning nature of the observed patterns and its related processes (Anderson et al. 2011).

In the present study, both in taxonomic and functional perspectives, we test whether local communities are open to regional influence and if deterministic processes or stochasticity are likely to rule their assembly. One previous study that we are aware of (Belmaker 2009) has already indicated the possibility of stochasticity in reef fish community assembly. However those findings were restricted to a single biogeographical region and were not analyzed in terms of functional richness. Despite the evidence that, in a large-scale context, reef fish may present assembly rules (Bellwood and Hughes 2001), detecting stochasticity in terms of functional richness in the local interactive scale will both challenge such view and recent evidence for multiple stable equilibria in rich and relatively productive localities (Chase 2010).

We have compiled the geographically most exhaustive assemblage dataset for reef fish species, the richest vertebrate assemblage on Earth. The authors, together with other trained colleagues, have conducted visual censuses independently through area-standardized strip transects (incidence data in  $20 \times 2 \text{m} = 40 \text{m}^2$ ) between 0 and 30m of depth in rocky and coral reef systems – a combined effort of 5.916 transects. The geographical range encompassed 103 sites spread through 17 major localities embedded in 6 main tropical biogeographical provinces (Fig. 1, Supplementary Table S1): Caribbean (Bahamas, Belize and Cuba), Southwestern Atlantic (Northeastern, Southeastern and South Brazil), Southwestern Atlantic Oceanic islands (St. Paul's Rocks, Fernando de Noronha Archipelago and Trindade/MartimVaz Archipelago), Tropical Eastern Atlantic (Cape Verde and São Tomé), Tropical Eastern Pacific (Malpelo island and central Western Mexico) and South Pacific (New Caledonia, Fiji, Tonga and French Polynesia). This represents a regional richness gradient from approximately 60 to 1500 species. 989 species belonging to 301 genera and 83 families were recorded. We have assigned a functional group to each species (McGill et al. 2006, Halpern and Floeter 2008) based on the combination of four functional traits (Supplementary Table S2) previously defined elsewhere (Chabanet et al. 2010).

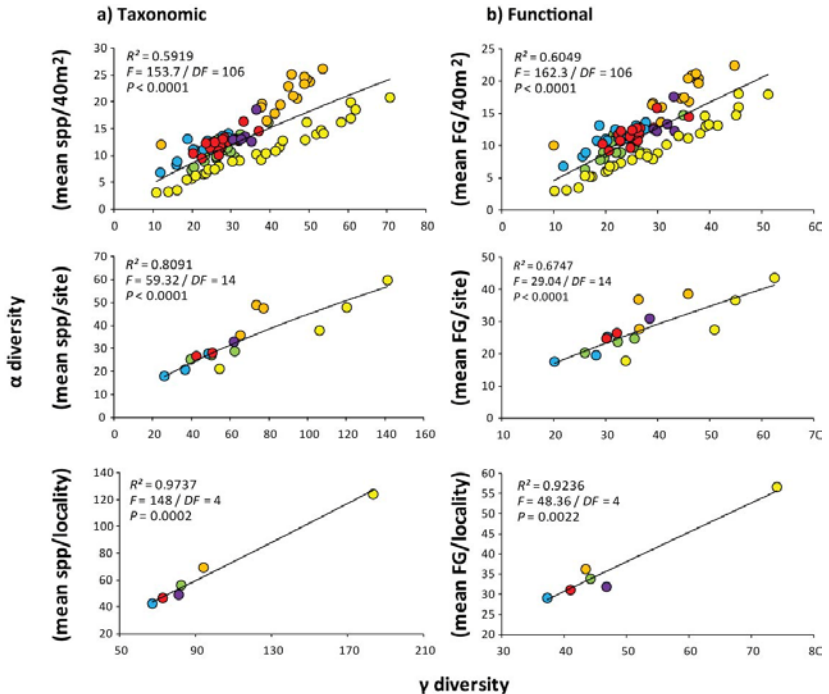


**Figure 1** The six biogeographical regions considered in the present article: Indo-West Pacific (yellow), Tropical Eastern Pacific (purple), Caribbean (orange), Southwestern Atlantic (green), Southwestern Atlantic oceanic islands (blue), Tropical Eastern Atlantic (red). “X” marks indicate where the seventeen localities are situated. Map illustration created in R version 2.12.1 for Windows (R Development Core Team 2010) using package MASS (Venables and Ripley 2002); map coordinates were obtained from the NOAA Database (<http://rimmer.ngdc.noaa.gov/mgg/coast>; coastline database WCL 1:5,000,000).

Local vs. regional plots were built using standardized hierarchical sampling (Loreau 2000, Cornell et al. 2007) of local richness (Supplementary Methods). Mean alpha diversity was analyzed at 3 increasing scales: between transects, between sites and between localities. This method was chosen in as much is likely to avoid potential methodological pitfalls (Srivastava 1999, Cornell et al. 2008). Results show that increasing regional richness enhances local richness at these three scales, both at the taxonomic and functional perspective (Fig. 2a,b). This corroborates the major trend in recent literature (Lawton 1999, Srivastava 1999, Loreau 2000, Karlson et al. 2004, Witman et al. 2004, Cornell et al. 2008) showing that reef fish assemblages are strongly influenced by processes acting at the regional level (but see discussions in Belmaker 2009).

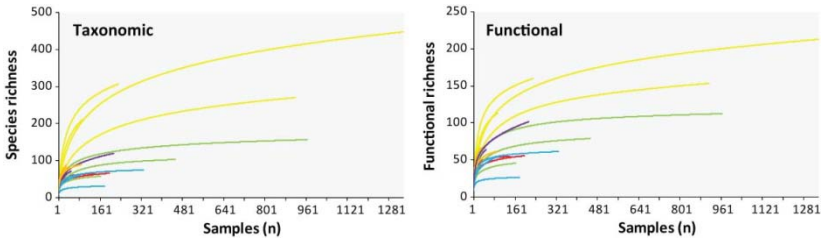
South-Pacific local richness becomes increasingly greater compared to the other regions as scale increases hierarchically most likely because of increasing beta diversity (Belmaker et al. 2008). Sampling the enormous regional species pool in the South-Pacific until exhaustion is a difficult task (Fig. 3) – however the present sampling effort covered a very significant proportion of the species available to UVC (underwater visual census) sampling.





**Figure 2** Local (alpha) vs. regional (gamma) richness plots using increasing area-standardized hierarchical sampling (from the top to the bottom, see Supplementary Methods), both in taxonomic (a) and functional (b) perspectives. Colors refer to different biogeographical regions: Indo-West Pacific (yellow), Tropical Eastern Pacific (purple), Caribbean (orange), Southwestern Atlantic (green), Southwestern Atlantic oceanic islands (blue), Tropical Eastern Atlantic (red).  $R^2$ ,  $F$ ,  $DF$ , and  $P$  values as well as the adjustment curve represent a fit from an alpha (log) vs. gamma (log) linear model (Cornell et al. 2008).

Moreover, in each locality we plotted the frequencies of the observed number of species grouped into octave classes (Fig. S1, Supplementary Methods) and observed that in the South-Pacific frequencies between octaves are more evenly distributed than in other localities. Conversely, Caribbean localities show higher frequencies concentrated at the greater octave class and therefore they present a considerable deviation from the adjustment model in the between-sites scale both in terms of alpha (Fig. 2) and beta diversity (Fig. 4).



**Figure 3** Sample-based rarefaction curves (100 runs) for each locality using the total available sampling effort (Supplementary Methods). Colors refer to different biogeographical regions: Indo-West Pacific (yellow), Tropical Eastern Pacific (purple), Caribbean (orange), Southwestern Atlantic (green), Southwestern Atlantic oceanic islands (blue), Tropical Eastern Atlantic (red). Analyses were run on Estimates version 8.2 for Windows (Colwell 2009).

Differences between sites embedded in the Pacific and sites from all other regions pooled together are observed at the between-transsects scale (Fig. 2, top) where Pacific sites show lower species packing despite its large regional species pool. Two possible distinct trends could be considered and therefore we have regressed the two groups separately and the results show a pattern even stronger in taxonomic (Pacific –  $R^2 = 0.975$ ,  $F = 1054$ ,  $DF = 27$ ,  $P < 0.0001$ ; Atlantic + TEP –  $R^2 = 0.7386$ ,  $F = 217.6$ ,  $DF = 77$ ,  $P < 0.0001$ ) and functional (Pacific –  $R^2 = 0.9397$ ,  $F = 1009$ ,  $DF = 27$ ,  $P < 0.0001$ ; Atlantic + TEP –  $R^2 = 0.6863$ ,  $F = 168.5$ ,  $DF = 77$ ,  $P < 0.0001$ ) perspectives.

One may argue that such differences could be a matter of sampling bias due to different observers in each site. However that is the general case for the whole dataset and when all other regions are pooled together there are no such apparent segregations. We believe that this somehow counter-intuitive difference might be due to a patchiness effect. Pacific reef systems are much wider, present more sand patches (or coral patches in sand) and many different zonations while Atlantic and Eastern Pacific ones are much homogeneous, steeper and present smaller available area – this could lead to a “compression of life” effect where species would have to pack more effectively in space. Besides, other studies have previously found clear differences between the Caribbean and the Pacific (Sale 1996) where, like herein observed, Caribbean sites can pack more species on average than Pacific sites of equivalent area (Fig. 2, Fig. S1, Smith 1978, Bohnsack and Talbot 1980). This issue deserves careful explanations possibly derived from different historical and evolutionary histories between the different

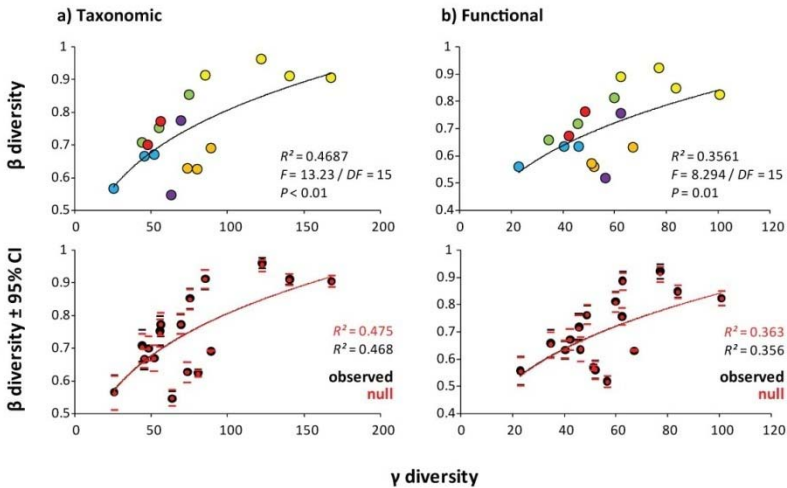
regions (Sale 1996, Lessios 2008) and those will be discussed more appropriately elsewhere.

Our findings show a strong local enrichment of reef fish functional richness with increasing regional pool and scale (Fig. 2b) supporting the idea that diversity begets diversity in terms of niche diversification, i.e., as regional richness increases communities encompass a greater array of functions. Studies have pointed habitat heterogeneity as one of the most credible proposed hypotheses which could explain regional variability in species richness for tropical forest trees (Condit et al. 2002) and other vertebrate taxa like mammals (Kerr and Packer 1997) and birds (Rahbeck and Graves 2001). Reef fish encompass wide phylogenetic, taxonomic and functional spectra (Bellwood 1998, Robertson 1998) and its modern lineages have been evolving in association with reef-building corals for at least 50 Ma (Renema et al. 2008). In an exploratory attempt, we considered scleractinian coral richness for each locality as a raw proxy of habitat heterogeneity and found that reef fish taxonomic and functional regional richness responded linearly to it (taxonomic –  $R^2 = 0.8097$ ,  $F = 63.81$ ,  $DF = 15$ ,  $P < 0.0001$ ; functional –  $R^2 = 0.6909$ ,  $F = 33.52$ ,  $DF = 15$ ,  $P < 0.0001$  functional; Fig. S2, Supplementary Methods). Such regional influence of coral richness on fish regional richness was already suggested elsewhere (Belmaker 2009) and was shown to be a consequence of the increase in beta diversity among regions once heterogeneity in coral habitat was accounted for (Arias-González et al. 2008, Belmaker et al. 2008). However, it is possible that shallow reef organisms' evolution is ruled by other extrinsic processes and therefore they have evolved in parallel.

We measured how beta diversity behaved in terms of regional richness in the between-sites scale (Supplementary Methods) and compared the observed values against values obtained running a random-placement null model (Fig. 4) built in order to disentangle the possible relative importance of stochastic versus deterministic mechanisms underlying community assembly (Chase 2010). Because within-locality biogeographical composition is likely to be more homogeneous with no strong inner barriers (Kulbicki 2007, Floeter et al. 2008, Robertson and Cramer 2009), overall community composition is not expected to present significant differences, i.e., a priori all species in the regional pool can potentially occupy all local samples. We used the Jaccard distance (1-Jaccard similarity) as a measure of beta diversity in as much it is based on incidence data (Magurran 2004). The null model shuffled species between samples (with samples equiprobable)

maintaining species totals fixed (Supplementary Methods). Conceptually this corresponds to a colonization scenario in which species colonize each sample randomly (Gotelli 2000) thus mimicking a sampling process relevant to the calculation of beta diversity (Nicholas J Gotelli, pers. comm.).

We observed an increase of beta diversity with increasing regional richness both in the taxonomic (Fig. 4a) and functional richness perspective (Fig. 4b). Although some studies suggested beta diversity to be uncorrelated with regional richness (Srivastava 1999, Koleff et al. 2003), others predict (Chase 2003) or show (Belmaker et al. 2008) the same pattern as ours at the taxonomic level and such differences could be a consequence of the very small scale herein analyzed – similarity between 40m<sup>2</sup> transects – where species interactions are most likely to be observed (Loreau 2000, Belmaker et al. 2008).



**Figure 4** Beta diversity (Jaccard distance) regressed against an increasing gradient of regional (gamma) richness in taxonomic (a) and functional (b) terms. Colors refer to different biogeographical regions: Indo-West Pacific (yellow), Tropical Eastern Pacific (purple), Caribbean (orange), Southwestern Atlantic (green), Southwestern Atlantic oceanic islands (blue), Tropical Eastern Atlantic (red). Graphs at the bottom show the comparison between the observed values (black circles) and values obtained from a random-placement null model (red circles) (see text and Supplemental information).  $R^2$ ,  $F$ ,  $DF$ , and  $P$  values

and the adjustment curve represent a fit from a beta (log) vs. gamma (log) linear model (Cornell et al. 2008).

Not only the observed beta diversity did not differ from the null expectation (Fig. 4, bottom) but also they were surprisingly indistinguishable from it and, again, the results were very much alike in both perspectives adopted. Taxonomic stochasticity is not a novelty for reef fish assemblages (Belmaker 2009). Reef fish may represent a model of relatively open metacommunities (Mora and Sale 2002), being dispersed through larval stage with different patterns of dispersal limitation, settlement and habitat choice (Leis 2002) in addition to many post-recruitment events (Jones 1991) constraining their survival ability. Moreover, while some reef fish species may be dependent and constrained by the habitat (Belmaker 2009) many others are not believed to be so (Sale 1996, Chittaro and Sale 2003). Reef fish can present high feeding versatility (Bellwood et al. 2006), and studies show that their colonization success may be in agreement with the competitive lottery hypothesis (Sale 1978, Munday 2004).

This highly contingent and multifaceted scenario may drive community assembly to a complete stochasticity. However, taxonomic stochasticity might also be observed if many species in the regional richness pool share similar functional traits so that initial colonization by one species will be followed by substitution of other functionally similar species, creating multiple stable equilibria (Chase 2003, 2010). However, that may not seem to be the present case. From the poorest (32 species / 27 functional groups sampled in St. Paul's Rocks, Table S1) to the richest locality (448 species / 213 functional groups sampled in New Caledonia), the observed beta diversity did not deviate from the null expectation in the functional richness perspective, i.e., observed between-sample similarity of functional groups does not differ from a pattern generated by chance. This could possibly indicate a complete stochasticity in reef fish local community assembly rather than multiple stable equilibria (Chase 2010, however different null models (Anderson et al. 2011) should be analyzed in concert in order to confirm such findings. For instance, our results are in accordance with other studies which have also pointed stochasticity in community assembly for freshwater fish (Muneepeerakul et al. 2008), fynbos shrubland (Latimer et al. 2005) and tropical forests (Condit et al. 2002, Volkov et al. 2003). Although reef fish local assembly could be stochastic, we believe that it should be due to the fact that reef fish face many dynamic spatio-temporal processes ultimately leading to no assembly predictability.

Future analyzes applying an explicit neutral-model are necessary to solve this puzzle. Reef-building corals assemblages, for example, are also strongly influenced by regional processes (Cornell et al. 2008); however differ from neutral-model predictions (Dornelas et al. 2006). Results herein showed may also be applied to other relatively open and rich metacommunities. Understanding the scale in which processes act to assemble local communities, e.g., assembly rules or the lack thereof, are of fundamental importance for the present century conservation agenda where biodiversity manipulation becomes increasingly necessary.

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**SUPPLEMENTARY INFORMATION**



## METHODS

### Field sampling

In the Atlantic Ocean (except Belize) and Tropical Eastern Pacific, reef fish communities were surveyed through strip transects visual censuses of standardized area –  $20 \times 2 \text{m} = 40 \text{m}^2$  (Floeter et al. 2007) – between 0 and 30m of depth. In Belize and the Indo-West Pacific, strip transects were larger ( $100 \times 2 \text{m}$  and  $50 \times 4 \text{m}$  respectively) nevertheless were partitioned in each 10m long and 1m wide in such a way that it was possible to reduce them to  $40 \text{m}^2$  without making any sort of data approximation. Only data from outer reef and reef crest were incorporated for the Indo-West Pacific.

All transects started and ended approximately at the same depth (within 3 meters of depth variation) and were conducted parallel to the reef. Except for data collected in the Caribbean where it was recorded only species presence x absence data, all individuals within the transect area were identified to the species level and recorded. All authors and collaborators have wide experience with such methodology (Kulbicki et al. 2005, Mellin et al. 2006, Floeter et al. 2007, Luiz Jr et al. 2008).

### Defining functional groups

We assigned a functional group to each recorded species. Functional categorization (Halpern & Floeter 2008) was based on the combination of four community functional traits (Table S2): 1) Trophic mode (4 categories); 2) Maximum published total length (6 categories); 3) Mobility (4 categories); 4) School-size (5 categories). Traits have been previously defined elsewhere (Chabanet et al. 2010). One may notice that not all combinations are realistic in nature (e.g. a solitary and territorial zooplanktivorous species larger than 80cm), resulting therefore in less observed combinations out of the total pool available (171 observed of  $480 = 4 \times 6 \times 4 \times 5$ ).

Information regarding taxonomy followed the Catalog of Fishes (<http://research.calacademy.org/redirect?url=http://researcharchive.calacademy.org/research/Ichthyology/catalog/fishcatmain.asp>) however recent changes suggested in Westneat and Alfaro (2005) and Craig et al.

(2007) were incorporated. All information regarding functional traits were obtained from the published literature and online databases (Randall 1967, Humann and Deloach 2002, Kulbicki et al. 2005, Floeter et al. 2008, Robertson and Allen 2008) and also based on the authors' expertise.

## **Hierarchical sampling approach**

The last two decades have provided a broad and enriching literature on the concept of community saturation (or the lack thereof) based on local vs. regional richness plots (Lawton 1999, Srivastava 1999, Karlson et al. 2004, Witman et al. 2004, Cornell et al. 2008, Harrison and Cornell 2008). It is now widely accepted that any attempt to understand whether communities approach saturation at certain level of regional richness should be done through a hierarchical sampling design (Loureau 2000, Cornell et al. 2007). Therefore we adapted the hierarchical sampling strategy proposed by Cornell et al. (2007):

Scale 1) Transect – site: here, alpha diversity is the mean species richness between transects while gamma diversity is the total amount of species found in each site;

Scale 2) Site – locality: alpha is the mean richness between sites embedded in a given locality while gamma is the total richness in each locality;

Scale 3) Locality – region: alpha is the mean richness between localities embedded in a given biogeographical region and gamma is the total richness of each region.

One may notice this proposed hierarchical sampling approach is based on biogeographical criteria rather than pre-determined geographical distance. The literature on reef fish biogeography provides enough support to consider the six proposed regions (Briggs 1974, Floeter et al. 2008) and to separate them into biologically different localities. Sites are distant 5km to 200km from each other and lack marine biogeographical barriers between them therefore it should configure no significant differences in community composition. Localities are found more than 300km apart and already present significant changes in biological composition (Kulbicki 2007, Floeter et al. 2008, Robertson and Cramer 2009).

## Obtaining alpha and gamma diversity

Since each site had a different total sampling (Table S1), we brought all of them to the minimum sampling effort available ( $n = 5$ ) in order to perform all analyses and comparisons based on the regional richness (gamma) obtained from the same standardized total area (Gotelli and Colwell 2001). To capture a more realistic frame of the average packing in Scale 1, in each site, five transects were randomly chosen from the available pool and then alpha and gamma at Scale 1 were obtained. This procedure was repeated 1,000 times to obtain an average value and its 95% confidence interval. Manly (1995) states that the resulting  $P$  value from this type of procedure may be positively biased if the number of randomizations is not large enough and Bejder et al. (1998) showed that the  $P$  value should stabilize using 20,000 iterations. We compared  $P$  values obtained running the proposed 20,000 repetitions with the ones obtained with 1,000 and observed no substantial differences.

The number of sites between localities was not the same. Therefore, based on the minimum available ( $n = 4$ ), four sites were randomly chosen so the average alpha and total gamma diversity at Scale 2 could be obtained. The same applies to Scale 3 where two localities were randomly selected to calculate alpha and gamma.

All data manipulation was conducted using Software R version 2.12.1 for Windows (R Development Core Team 2010).

One may argue that the gamma values calculated in all scales does not represent the true regional richness of each site as surely five strip transects of  $40\text{m}^2$  fall much below the necessary to capture the total number of existing species, even in the poorest site. However, we aim to answer: given the same standardized area between all possible sites, does regional richness strongly influence local richness as hierarchical scale increases?

## Beta diversity

As in the case of local vs. regional plots, a great amount of attention has been paid to beta diversity in such a fashion that many descriptors and approaches for it have been broadly discussed and some have emerged recently (Koleff et al. 2003, Chao et al. 2005, Anderson et

al. 2011). In a recent review, Anderson et al. (2011) gave an elucidative roadmap for the analysis of beta diversity providing a series of mission statements within two main types of approaches: the turnover and variation.

Here we analyzed how community variation within each of the 17 proposed localities behaves in terms of a regional richness gradient (please refer to mission statement V4b in Anderson et al. 2011). For that, the Jaccard distance (the same as 1-Jaccard index of similarity) was used in as much it is based on presence x absence data (1 x 0) (Magurran 2004).

In a similar fashion as described above, localities were leveled to the same number of samples based on the site with smaller sample effort (Bahamas  $n = 30$ , Appendix I) in order to compare localities on a progressive regional richness gradient on the basis of the same sample effort (Gotelli and Colwell 2001). In each locality, thirty censuses were randomly chosen 5,000 times (enough number of iterations where  $P$  values stabilized), the gamma and beta diversity were calculated. All data manipulation was conducted using scripts developed in R and the calculation of dissimilarity indices were conducted using package *vegan* (Oksanen et al. 2010).

## **Null model**

We developed a simple algorithm written in R environment (see script below) to perform randomization of species in the observed data matrices. The null model shuffled species between samples (with samples equiprobable) maintaining species totals fixed (please refer to SIM2 in Gotelli 2000). Conceptually this corresponds to a colonization scenario in which species colonize each sample randomly (Gotelli 2000) thus mimicking a sampling process relevant to the calculation of beta diversity (Nicholas J Gotelli, pers. comm.).

This randomization process is likely to produce degenerate matrices, i.e., it might have resulted in samples with marginal totals equal to zero. If it did, such samples were excluded. One might argue that this would affect the gamma diversity (total number of species in every iteration) and thus could not be used for comparisons with the observed value on the basis of same gamma diversity. However gamma diversity obtained through 5,000 iterations was identical to the real data in all localities.



In each locality, 5,000 random draws of 30 censuses was performed (see *Beta diversity* item) and for each of these the null model was applied and the Jaccard distance was calculated. The final mean and 95% confidence interval were used to compare with the observed values. If the observed values fall below the null expectation it should indicate there are some deterministic factors underpinning community assembly; if not, stochastic mechanisms must be prevailing (Chase 2010).

```
#####
#FUNCTION_SHUFFLE_SIM2#
#####
```

```
shuffle.sim2 <- function(data)
{
  data.results<- matrix(0, nrow(data), ncol(data))
  for (j in 1:ncol(data))
  {
    data.results[,j] <- sample(data[,j])
  }
  data.results
}
```

```
#####
#FUNCTION_NULL_BETA#
#####
```

```
library(vegan)
```

```
null.beta<-function(data,census)
{
  step1<-data
  step2<-step1[sample(1:nrow(step1),census),]
  step3<-step2[,which(colSums(step2)!=0)]
  step4<-shuffle.sim2(step3)
  step5<-step4[which(rowSums(step4)!=0),which(colSums(step4)!=0)]
  step6<-vegdist(step5,method="jaccard")
}
```

```

step7<-as.numeric(ncol(step3))
step8<-mean(step6)
step9<-c(step7,step8)
step9
}

#####
#FUNCTION_NULL_BETA_II#
#####

null.beta2<-function(data, census, iter)
{
mat1<-matrix(0,iter,2)
for(i in 1:iter)
{
                                mat1[i,]<-null.beta(data, census)
                                }
mat1
ci1<-quantile(mat1[,1], probs<-c(0.025, 0.975), type=2)
ci2<-quantile(mat1[,2], probs<-c(0.025, 0.975), type=2)
gamma<-data.frame(mean(mat1[,1]), ci1[1], ci1[2])
jaccard<-data.frame(mean(mat1[,2]), ci2[1], ci2[2])
final<-data.frame(cbind(gamma,jaccard))
names(final)<-c("gamma_mean", "gamma_2.5%", "gamma_97.5%",
"jaccard_D_mean", "jaccard_D_2.5%", "jaccard_D_97.5%")
final
}

#####
#EXAMPLE#
#####

#creating a hypothetical community matrix with presence x absence
data#

a<- c(1,0,0,0,1,0,1,1,0,1); b<- c(1,0,1,1,0,0,1,0,0,1); c<-
c(1,1,0,0,1,0,1,1,1,0);
d<- c(1,0,0,1,0,1,0,0,0,0); e<- c(1,0,1,0,0,0,1,0,0,1); f<- a; g<- b; h<- c;
i<- d; j<- e

```

```
com.ex<-as.matrix(rbind(a,b,c,d,e,f,g,h,i,j)) #final matrix
com.beta.null<-null.beta2(com.ex, 7, 100) #7 census taken at random
running 100 iterations#
com.beta.null #see results
```

### **Calculating the frequency of species occurrences in octaves**

In each locality we plotted the frequencies of the observed number of species grouped in octaves (Preston 1948, Lobo and Favila 1999). Thirty censuses were randomly chosen 5,000 times (enough number of iterations where *P* values stabilized), and the mean frequency of each class and its respective 95% CI upper bound were calculated. Only one locality per region is shown to illustrate major biogeographical differences (Fig. S1).

### **Coral richness vs. reef fish regional richness**

We compiled coral richness related to each locality gathering data from published literature (Spalding et al. 2001) and ReefBase online database (Tupper et al. 2011). Average fish gamma diversity obtained from 5,000 random draws of 30 transects (see *Beta diversity* item) was used in the simple linear regression analyses between coral richness and fish gamma diversity (Fig. S2).

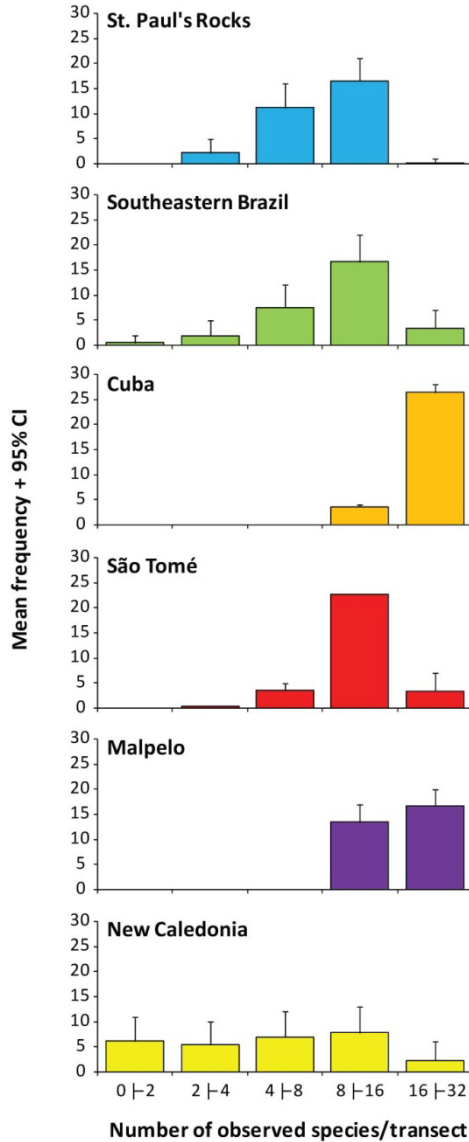
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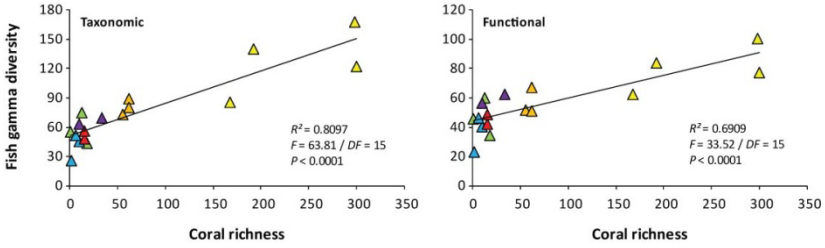
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**Figure S1** Frequency of species occurrences classified into octaves. Only one locality per region is shown for illustration purposes (see main text for further explanations).



**Figure S2** Simple linear regression analyses between fish gamma diversity and coral richness in each locality in taxonomic (left) and functional richness (right) perspective.



**Table S1** Sites, localities and biogeographical regions herein considered.

<b>Region</b>	<b>Locality</b>	<b>Site</b>	<b>Census (n)</b>	<b>Spp</b>	<b>Funct. Groups</b>
<b>Caribbean</b>	<i>Bahamas</i>	BAH1	6	47	32
		BAH2	6	52	33
		BAH3	6	44	25
		BAH4	6	45	30
		BAH5	6	57	37
	<i>Belize</i>	BEL1	5	38	22
		BEL2	10	51	32
		BEL3	20	67	40
		BEL4	5	12	10
		BEL5	10	56	32
		BEL6	40	67	37
	<i>Cuba</i>	CUB1	13	66	33
		CUB2	8	57	34
		CUB3	5	47	28
		CUB4	7	54	32
	<b>Indo-West Pacific</b>	<i>Tonga</i>	TON1	100	39
TON2			8	77	55
TON3			28	99	62
TON4			55	94	63
TON5			81	98	62
TON6			60	111	73
<i>Fidji</i>		FIJ1	28	98	72
		FIJ2	108	196	116
		FIJ3	52	151	93
		FIJ4	68	176	104
		FIJ5	80	177	106
		FIJ6	68	162	95
<i>New Caledonia</i>		NWC1	29	46	33
		NWC2	72	204	79

		NWC3	333	262	98
		NWC4	601	342	84
		NWC5	20	89	50
		NWC6	293	223	90
	<i>French</i>	FPO1	70	85	47
	<i>Polynesia</i>	FPO2	102	105	59
		FPO3	88	88	52
		FPO4	117	137	68
		FPO5	115	108	55
		FPO6	44	120	61
		FPO7	118	112	64
		FPO8	31	27	22
		FPO9	98	90	47
		FPO10	68	75	45
		FPO11	35	80	44
		FPO12	31	68	38
<b>Southwestern Atlantic</b>	<i>Northeastern Brazil</i>	NEB1	44	33	21
		NEB2	25	39	26
		NEB3	50	45	27
		NEB4	45	50	31
	<i>South Brazil</i>	SB1	40	46	29
		SB2	71	58	38
		SB3	62	42	29
		SB4	134	75	45
		SB5	82	67	41
		SB6	64	59	37
	<i>Southeastern Brazil</i>	SEB1	94	77	47
		SEB2	108	70	40
		SEB4	391	115	57
		SEB5	130	80	43
		SEB6	64	60	32
		SEB7	55	69	40
		SEB8	71	63	34

		SEB9	39	47	29
<b>Southwestern Atlantic (Oceanic Islands)</b>	<i>St. Paul's Rocks</i>	SPR2	5	21	16
		SPR3	138	29	20
		SPR4	10	21	17
		SPR5	22	20	17
		<i>Fernando de Noronha Archipelago</i>	NOR1	12	36
	NOR2		12	27	22
	NOR3		20	36	30
	NOR4		10	36	28
	NOR5		10	24	17
	NOR6		18	43	29
	NOR7		7	13	10
	<i>Trindade &amp; Martim Vaz Archipelago</i>	TRI1	37	44	28
TRI2		54	61	36	
TRI3		17	38	26	
TRI4		22	46	29	
TRI5		40	47	28	
TRI6		17	32	21	
TRI7		12	29	18	
TRI8		37	49	30	
TRI9		6	33	21	
TRI10		26	39	26	
TRI11		47	50	31	
TRI12		14	35	20	
<b>Tropical Eastern Atlantic</b>	<i>Cape Verde</i>	CVD1	19	38	27
		CVD2	34	54	36
		CVD3	18	40	30
		CVD4	11	34	26
		CVD5	11	36	25
		CVD6	19	39	29
		CVD7	15	40	27
		CVD8	15	37	26
		CVD9	23	36	27

		CVD10	16	33	22
		CVD11	17	35	25
	<i>São Tomé</i>	STM1	28	46	26
	<i>Island</i>	STM2	8	43	32
		STM3	13	26	19
		STM4	39	47	32
		STM5	27	43	29
		STM6	13	35	24
		STM7	11	27	22
<b>Tropical</b>	<i>Malpelo</i>				
<b>Eastern Pacific</b>	<i>Island</i>	MAL1	49	72	42
	<i>Mexico</i>	MEX1	88	69	40
		MEX2	39	54	34
		MEX3	36	71	42
		MEX4	51	88	46

---

**Table S2** Detailed description of functional traits herein used to categorize species into functional groups after Chabanet et al. (2010).

<b>Functional traits</b>	<b>Categories</b>	<b>Meaning</b>
Trophic group	P	Piscivore
	C	Carnivore
	H	Herbivore
	Z	Zooplanktivore
Length (Maximum published TL)	1	0 – 7 cm
	2	7.1 – 15 cm
	3	15.1 – 30 cm
	4	30.1 – 50 cm
	5	50.1 – 80 cm
	6	> 80 cm
Mobility*	1	Territorial
	2	Sedentary
	3	Mobile
	4	Very mobile
School-size	1	Single fish
	2	Pair
	3	3 – 20 fish
	4	20 – 50 fish
	5	> 50 fish

\* **Territorial**: species which stay within a very restricted area (less than 20m<sup>2</sup>) as adults, usually display specific behaviors to exclude conspecifics or species with similar behavior; **Sedentary**: species staying within an area less than 1000m<sup>2</sup> for very long periods (several months and usually years). May display specific behavior to defend against intruders, but usually only weekly aggressive, except towards conspecifics; **Mobile**: species which tend to stay on a given reef (up to several hectares) for prolonged periods, but which will move regularly to other reefs; **Very mobile**: species constantly on the move, usually will not stay on the same reef more than a day or two and often less.



## **CONCLUSÃO**





Os resultados mostram que a riqueza local nas comunidades de peixes recifais aumenta à medida que aumenta a riqueza regional, i.e., apresentam um padrão de comunidades insaturadas (Figura 1, esquerda). Esse padrão foi observado em todas as escalas – transecto-sítio, sítio-localidade, localidade-região – tanto na perspectiva taxonômica como funcional. Esses resultados indicam fortemente que a composição das espécies na escala local é influenciada por processos históricos e biogeográficos atuando em nível regional, tais como dispersão, colonização, especiação e extinção. Resultados semelhantes têm sido descritos na literatura para corais (Karlson et al. 2004, Cornell et al. 2008), organismos bentônicos (Witman et al. 2004), peixes (Belmaker 2009), aves (Ricklefs 2000) e diversos outros grupos (ver revisões em Lawton 1999 e Srivastava 1999).

O padrão linear de enriquecimento local com aumento de riqueza regional foi observado em todas as escalas, tanto na perspectiva taxonômica quanto funcional. Tal resultado suporta a idéia de que diversidade gera diversidade em termos de diversificação de nicho. Idéias prévias encontradas na literatura indicam a heterogeneidade de habitat como um dos principais fatores regendo a riqueza regional de espécies (Kerr & Packer 1997, Rahbeck and Graves 2001, Condit et al. 2002, Belmaker et al. 2008, Belmaker 2009).

O grupo “peixes recifais” engloba uma ampla diversidade filogenética, taxonômica e funcional (Bellwood 1998, Robertson 1998) e suas linhagens recentes têm evoluído em associação próxima aos corais formadores de recife por pelo menos 50Ma (Renema et al. 2008). Assim, foi testado, de maneira exploratória, como a riqueza regional padronizada por unidade de área nas diferentes localidades se comporta em função da respectiva riqueza regional de corais. Os resultados mostraram um aumento positivo da riqueza regional de peixes recifais em função da riqueza regional de corais, corroborando os dados de Belmaker (2009). A riqueza regional de corais deve proporcionar novas possibilidades de nicho em termos de alimentação, refúgio e reprodução de peixes recifais de maneira que possibilite o surgimento de novos grupos funcionais no ambiente. Entretanto, há a possibilidade de que esses organismos, peixes e corais, assim como os demais organismos de mares rasos, tenham evoluído em paralelo sujeitos a outros fatores evolutivos.

Apesar de alguns trabalhos na literatura terem apontado falta de relação entre diversidade beta e riqueza regional (Srivastava 1999, Koleff et al. 2003) outros previram (Chase 2003) ou encontram (Belmaker et al. 2008) padrão semelhante ao aqui encontrado, onde a

diversidade beta aumenta com a riqueza regional. Essa discrepância provavelmente se deve à pequena escala local analisada – dissimilaridade média entre transectos de 40m<sup>2</sup> – onde interações locais são provavelmente observadas (Loreau 2000, Belmaker et al. 2008), ao contrário de outros estudos que estabeleceram a falta de relação em escalas espaciais muito maiores.

O fato da beta diversidade não diferir do modelo nulo em ambas as perspectivas, taxonômica e funcional, pode indicar que as comunidades de peixes recifais se organizam estocasticamente no espaço. Esse fato não é novidade para peixes recifais, entretanto (Belmaker 2009). Peixes recifais representam modelos de metacomunidades relativamente abertas (Mora & Sale 2002), sendo dispersos durante a fase larval com diferentes limites de dispersão, assentamento e escolha de habitat (Leis 2002), além de estarem sujeitos a diversos fatores pós-recrutamento (Jones 1991) que podem restringir o sucesso de colonização. Ainda, a estrutura das comunidades não deve ser dependente do habitat (Sale 1996, Chittaro & Sale 2003) pois podem apresentar alta versatilidade alimentar (Bellwood et al. 2006) e, além disso, estudos mostram que a capacidade de colonização de peixes recifais está de acordo com a hipótese de loteria competitiva (Sale 1978, Munday 2004). Esse cenário altamente contingente, dinâmico e multifatorial pode fazer com que a montagem das comunidades ocorra ao acaso.

Estocasticidade taxonômica, entretanto, pode também ser observada caso muitas espécies do '*pool*' regional compartilhem atributos funcionais de maneira que a colonização inicial por uma espécie precede a substituição de outra funcionalmente semelhante, levando a comunidade a múltiplos equilíbrios estáveis (Chase 2003, 2010). Entretanto, como aqui mostrado e de acordo com a literatura, esse não deve ser o caso. Da localidade regionalmente mais pobre (32 espécies / 27 grupos funcionais amostrados no Arquipélago de São Pedro e São Paulo; Table S1) a mais rica (448 espécies / 213 grupos funcionais amostrados na Nova Caledônia) a diversidade beta não diferiu de um padrão gerado ao acaso em termos de riqueza funcional. Isso pode indicar estocasticidade na montagem local das comunidades de peixes recifais ao invés de possíveis múltiplos equilíbrios estáveis (Chase 2010). Entretanto, análises futuras abordando diferentes modelos nulos são necessárias para a confirmação de tal padrão.

De fato, a rica biodiversidade pode estar relacionada à falta de estabilidade (Naeem 2002, Pfisterer & Schmid 2002) e os resultados podem estar sustentando essa idéia com o grupo de vertebrados mais

rico do planeta. Outros estudos também apontam para estocasticidade na montagem das comunidades locais em outros grupos e sistemas ricos como peixes de água doce (Muneepeerakulet al. 2008), mata arbustiva de *fyndbos* (Latimer et al. 2005) e florestas tropicais (Condit et al. 2002, Volkov et al. 2003). Apesar da possibilidade de que as comunidades de peixes recifais sejam organizadas ao acaso, acredito que isso se deva ao fato de que peixes recifais enfrentam muitos processos espaço-temporalmente dinâmicos levando a imprevisibilidade de estruturação. Análises futuras direcionadas a modelos nulos explícitos são necessárias para resolver essa questão. As comunidades de corais formadores de recife, por exemplo, são, da mesma forma que as de peixes recifais, fortemente influenciadas por processos atuando em escala regional (Cornell et al. 2008), entretanto diferem de previsões derivadas da teoria neutra (Dornelas et al. 2006). Provavelmente os resultados obtidos por essa dissertação podem ser aplicados para outras metacomunidades ricas e relativamente abertas. Entendendo a escala em que processos atuam para organizar as comunidades, e.g., regras de montagem ou a falta das mesmas, são de fundamental importância para a agenda de conservação do século presente onde a manipulação da biodiversidade tem se tornado cada vez mais necessária.

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