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**MACROECOLOGIA DE INTERAÇÕES AGONÍSTICAS EM
PEIXES RECIFAIS**

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PEIXES RECIFAIS:
DE PADRÕES ESPACIAIS A REDES ECOLÓGICAS**

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Para meu casal favorito, mãe e pai, que significam o mundo pra mim;
Para o oceano, minha fonte de energia e inspiração.

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Quem quer ninguém segura!

“just keep swimming”
Dory, the optimistic *Paracanthus hepatus*

Retirado do filme ‘Finding Nemo’

RESUMO

A diversidade e coexistência de espécies vêm sendo estudada por décadas, o que desencadeou no desenvolvimento de diversas teorias ecológicas a fim de compreender os processos envolvidos na estruturação de comunidades. A composição e a distribuição de espécies são regidas por processos regionais (e.g. dispersão, especiação) e interações bióticas (e.g. competição, predação). No entanto, pouco se sabe sobre a influência de processos regionais e filtros espaciais na distribuição de espécies em comunidades locais. Em ecossistemas marinhos, peixes recifais exibem um gradiente longitudinal de riqueza de espécies em larga escala que está fortemente associado a processos regionais. Por outro lado, interações interespecíficas, como competição, atuam sobre a dinâmica de populações de peixes recifais e podem desempenhar um papel fundamental sobre a composição de espécies desse grupo. No presente estudo, investigamos a relação entre a riqueza de espécies e a diversidade de interações agonísticas de peixes recifais em diferentes escalas espaciais ao longo de sete recifes tropicais distribuídos em cinco províncias biogeográficas (Atlântico Oeste, Caribe, Polinésia, Pacífico Central e Indo-Pacífico Central). Ainda, para cada recife foi construída uma rede de interações agonísticas entre espécies de peixes recifais, para comparar a estrutura dessas interações entre os sete recifes. Dados de riqueza de espécies e diversidade de interações agonísticas foram coletados através de um total de 350 amostras de vídeos em recifes biogênicos rasos e abrigados. Cada amostra possui duração de 10 minutos e abrange uma área de 2m². Foi observado maior acúmulo de espécies em comunidades locais regionalmente mais ricas e uma relação positiva entre riqueza regional e local. A riqueza local, composta apenas por espécies que interagiram agonisticamente, demonstrou essa mesma tendência de acúmulo de espécies, porém uma relação fraca entre a riqueza regional e local, ou seja, o número de espécies interagindo em escala local não aumenta de acordo com número de espécies. Este contraste entre acúmulo de espécies e relações espaciais de riqueza pode ser explicado através do aumento da diversidade beta *turnover* de espécies que interagem conforme o aumento da riqueza regional, e sugere uma segregação espacial destas espécies em comunidades locais regionalmente ricas. As redes agonísticas em escala regional diferiram quanto à complexidade topológica, porém exibiram semelhanças na composição filogenética e

funcional das espécies. Pomacentrídeos, labrídeos e acanthurídeos predominaram na composição das redes e o grupo funcional de herbívoros territoriais desempenhou um papel central em todas as sete localidades. Portanto, a contextualização empírica de comportamento agonístico de peixes recifais frente a diferentes escalas espaciais sugere que a riqueza regional é fundamental na estruturação de comunidades em diversas escalas espaciais, porém espécies que potencialmente competem pelos mesmos recursos podem ter sua distribuição espacial determinada por fatores locais (e.g. disponibilidade de recursos e atributos funcionais das espécies).

Palavras-chave: diversidade, recifes de coral, antagonismo, padrões de escala espaciais, coexistência.

Abstract

Diversity and coexistence of species have been studied for decades and triggered several ecological theories to understand the process involved in community assemblages. The composition of species pools is influenced by regional processes (e.g. dispersion, speciation and extinction) and biotic interactions (e.g. competition, predation). However, how these processes operate over species distributions across different spatial scales is poorly known. In marine ecosystems, reef fishes exhibit a longitudinal large-scale gradient of species richness and regional processes are strongly associated with community assembly. Conversely, interspecific interactions, such as competition, influence population dynamics of reef fishes and may have an essential role in shaping the community composition of this group. In this study, we aimed to investigate the relationship between species richness and the structure of agonistic interactions of fishes across different spatial scales, from tropical reefs in seven localities across five biogeographic provinces (south-western Atlantic, Caribbean, Polynesian, Central Pacific and Central Indo Pacific). Moreover, agonistic networks of reef fishes were built to compare the structure of these interactions among the seven studied localities. Species richness and agonistic interactions data were collected through a total of 350 samples of remote videos in shallow sheltered reefs, each sample consisting of a 2m² area during 10 minutes. We observed a higher species accumulation in regionally richer localities and a positive relationship between local and regional richness. For the local pool composed only by interacting species, we observed the same pattern in species accumulation, but not the local and regional positive relationship. This pattern can be explained by the increasing species turnover towards regionally richer areas suggesting higher spatial segregation of interacting species in richer local communities. Moreover, the topological complexity of agonistic networks, defined by modularity and centralization values, increased according to the regional richness gradient. Pomacentrids, labrids and acanthurids were predominant at network composition in all seven localities and territorial herbivores performed a central role in all local communities. Combined, our findings suggest that regional richness of reef fishes plays an essential role on the composition of local species pool, and that local processes (e.g. resource availability and species intrinsic attributes) probably drive the agonistic behavior and the spatial distribution of species. Furthermore, the empirical

contextualization of agonistic behavior in reef fish across different spatial scales highlights the importance of a better understanding of the balance among different mechanisms regulating the spatial distribution and resource use partition in reef fish communities

Keywords: diversity, antagonism, coral reefs, spatial-scale patterns, coexistence.

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INTRODUÇÃO GERAL

A macroecologia busca padrões empíricos e mecanismos responsáveis pela estruturação e dinâmica dos ecossistemas ao longo de escalas espaciais e temporais (Brown 1995). A identificação desses mecanismos se torna fundamental para evitar a perda de serviços ecossistêmicos indispensáveis para a manutenção da biodiversidade (Ricklefs 1987, Bellwood and Connolly 2001). Atualmente, observa-se um crescimento no número de estudos que abordam hipóteses sobre a predominância de processos que operam em larga escala sobre as comunidades através de comparações, ao longo de escalas espaciais, entre diferentes táxons, ambientes e regiões geográficas (revisado por Cornell e Harrison 2014). No entanto, um dos maiores desafios da macroecologia é o estabelecimento das escalas de estudo para compreensão dos processos ecológicos e biogeográficos envolvidos no delineamento dos padrões de biodiversidade (Witman & Roy 2009).

A elucidação de alguns padrões de diversidade e de coexistência das espécies encontrados nos sistemas terrestres e marinhos motivou o desenvolvimento de teorias ecológicas capazes de explicar os mecanismos por trás da estruturação das comunidades. As teorias pioneiras foram embasadas em mecanismo de partição de nicho, que sugere que a coexistência é possível devido à capacidade das espécies de utilizar os recursos de maneiras distintas, evitando a sobreposição de nichos (Dobzhansky 1950, Hutchinson 1957). Posteriormente, a teoria de biogeografia de ilhas (McArthur & Wilson 1967) sugeriu que a composição e distribuição das espécies são regidas por eventos de dispersão e despertou uma série de novas teorias (e.g. teoria neutra de Hubbell 2001), propondo o domínio de processos estocásticos de larga escala (e.g. dispersão, especiação, extinção) sobre a estruturação das comunidades. A divergência entre essas teorias gerou uma ampla linha de pesquisa a fim de investigar a prevalência de processos regionais e locais sobre a diversidade de espécies.

Nos últimos 30 anos, a grande variação de resultados sobre a influência de processos de diferentes escalas sobre a estrutura das assembleias (revisado por Cornell e Harrison 2014) suporta a ideia que há uma interação entre fatores regionais e locais e que a ecologia é dependente de escala (McGill 2010, Mittelbach e Schemske 2015). Apesar do balanço evidente entre estes processos (Fig 1), pouco se sabe sobre a extensão espacial da influência de fatores macroecológicos sobre a biodiversidade de espécies. Esse fato acarretou no desenvolvimento de

modelos matemáticos para tentar detectar a importância de filtros espaciais sobre a composição do *pool* de espécies. O modelo teórico linear mais clássico e utilizado (Gaston 2000, Ricklefs 1987) consiste na correlação entre a riqueza regional e local de espécies. Este modelo propõe dois cenários: se a riqueza local é diretamente proporcional a, porém menor, que a riqueza regional, processos em larga escala são mais importantes para determinar a diversidade local. Contrariamente, se a riqueza regional aumenta, porém a riqueza local atinge uma assíntota, processos locais regem a estrutura de comunidades em pequena escala. Para incorporar dados empíricos ao modelo, a riqueza regional deve ser definida pelo grupo de espécies capazes de dispersar e estabelecer-se em comunidades locais. A riqueza local, por sua vez, é composta pelo grupo de espécies presentes em uma escala cuja distribuição pode ser potencialmente influenciada por interações bióticas (Sristrava 1999).

A predominância de fatores locais, como interações bióticas (e.g. competição), está relacionada com a dinâmica entre disponibilidade de recursos e espécies residentes, que podem, conseqüentemente, impedir o estabelecimento de novos colonizadores em determinada escala espacial. Esta hipótese é reforçada pelo impacto causado por interações antagonistas (e.g. parasitismo, herbivoria, predação) sobre a estrutura de comunidades (Jabot and Bascompte 2012, Ings et al. 2009). Nos últimos anos, alguns estudos iniciaram a integração de processos espaciais e interações bióticas através de análise redes ecológicas (Maglianese et al. 2015, Tylianakis et al. 2007). Esta ferramenta analítica pode fornecer informações sobre o papel funcional de espécies (Guimarães et al. 2007, Schleuning et al. 2015) e permitir a identificação de processos-chave (e.g. evolução de espécies, gradientes ambientais, papel funcional) para manutenção da diversidade (Dunne et al. 2002). As redes ecológicas são compostas por nós, que podem representar diferentes níveis taxonômicos (e.g. indivíduos, espécies, famílias). Estes são conectados por *links* que ilustram as interações bióticas presentes na comunidade ou população. Apesar das redes desempenharem um importante papel analítico para o entendimento na estrutura, dinâmica e evolução de interações biológicas, a maioria dos estudos aborda apenas ambientes terrestres (poucas exceções como Guimarães et al. 2011). Assim, há uma lacuna do conhecimento sobre a estrutura de interações bióticas em ambientes marinhos inseridos em um contexto macroecológico.

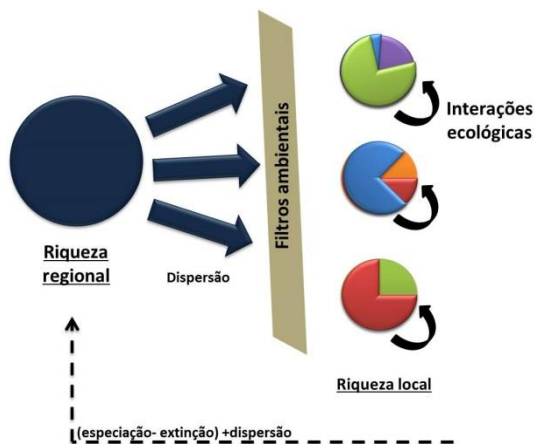


Figura 1. Modelo conceitual da dinâmica entre processos regionais e locais responsáveis pela formação da riqueza de espécies em escalas locais (adaptado de Mittelbach e Schemske 2012)

Em ecossistemas marinhos, a influência da dispersão larval na dinâmica de populações locais possui um robusto suporte através de modelos empíricos e estatísticos (Gaines and Roughgarden 1985, Lewin 1986). Em peixes recifais, o notável e bem definido gradiente longitudinal de diversidade de espécies permite explorar padrões da estrutura de comunidade ao longo de diferentes escalas espaciais. O Arquipélago Indo-Australiano é considerado o centro de origem e atual *hotspot* de espécies marinhas. A diversidade de corais, por exemplo, aumenta longitudinalmente em direção a este ponto e pode diminuir em até 50 vezes em direção leste deste centro (Briggs 2005, Kulbicki et al. 2013, Mora et al. 2003, Roberts et al. 2002). No caso de peixes recifais, o padrão de diversidade é semelhante aos corais e há uma grande variação de riqueza entre províncias biogeográficas, desde 2000 espécies no Indo-Pacífico a 300 no Atlântico Sul (Kulbicki et al. 2013). Ao longo do Pacífico, comunidades de peixes recifais exibem uma proporção semelhante de determinadas famílias, fato que pode evidenciar a força de processos de larga escala e estocásticos sobre a estruturação de peixes recifais (Bellwood and Hughes 2001, Connolly et al. 2005). No entanto, a alta diversidade de peixes registrada em pequenas escalas em algumas regiões (Bellwood et al. 2006) propõe que outros mecanismos relacionados à coexistência de espécies e interações bióticas desempenham um papel fundamental, porém ainda desconhecido, em comunidades locais.

Dentre as interações bióticas existentes, a competição entre peixes recifais é comumente evidenciada através da sobreposição de uso de recursos e comportamentos territoriais presentes em diversas espécies (e.g. Forrester et al. 2015, Munday et al. 2001, Roberston 1995) e, pode aumentar a frequência de interações agonísticas (Blowes et al. 2013, Kerry e Bellwood 2015). Como consequência, a competição interespecífica entre peixes recifais é capaz de alterar padrões de distribuição e abundância de populações (Robertson 1996), influenciar sobre taxas de crescimento e reprodução (Forrester 1990, Jones and McCormick 2002) e afetar a mortalidade de algumas espécies (Hixon & Webster 2002). Esses diferentes efeitos da competição sobre a abundância, metabolismo e sobrevivência em peixes recifais sugere que a partição de recursos e outros potenciais mecanismos associados a interações agonísticas atuam, em desconhecida escala, sobre padrões de distribuição espacial e estruturação de comunidades.

A incorporação de interações interespecíficas no contexto macroecológico é abordada, em grande parte, sob uma perspectiva latitudinal. Padrões de intensidade e especialização de interações bióticas ao longo de latitudes podem estar relacionados à riqueza de espécies e restrições fisiológicas devido a mudança de temperatura que varia de acordo com a latitude (Schemske et al. 2009, revisado por Moles e Ollerton 2015). Neste estudo, a fim de isolar potenciais efeitos da temperatura, investigamos a relação espacial entre riqueza regional/local e diversidade de interações agonísticas em peixes recifais de sete localidades ao longo do amplo gradiente de diversidade (Fig. 2). Uma vez que processos de larga escala exercem forte influência sobre a estruturação de comunidades em ambientes marinhos, nossa hipótese consiste na relação proporcional entre a riqueza regional e local de espécies, e no maior número de espécies disputando recursos através de eventos agonísticos em escala local conforme o aumento da riqueza regional. Desta forma, esse cenário evidenciaria a força de processos regionais sobre estruturação de comunidades em escalas extremamente reduzidas. A riqueza de espécies e interações entre peixes foi obtida através de vídeos (Fig. 3), que nos permitiu criar um banco de dados padronizado e robusto para todas as sete localidades. Dessa maneira, o presente estudo é o pioneiro, em ambientes marinhos, a testar as relações da diversidade espécies em diversas escalas espaciais associadas a redes de interações agonísticas diante de um contexto macroecológico, a fim de prover novos conhecimentos sobre mecanismos que regulam a distribuição e composição de peixes recifais.

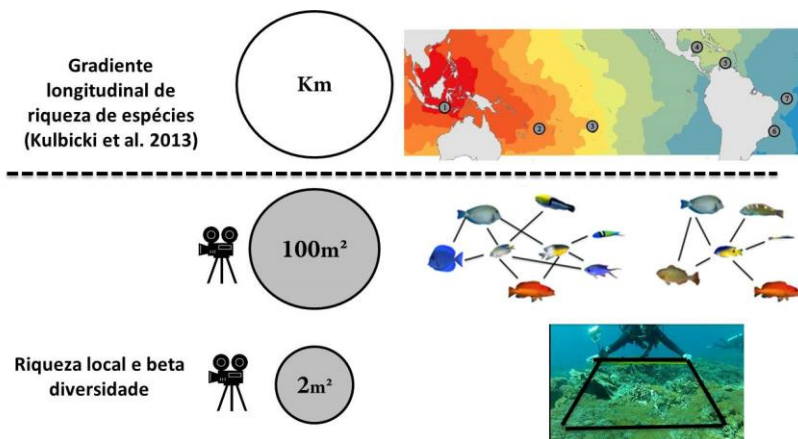


Figura 2. Escalas espaciais abordadas no presente estudo. O gradiente de riqueza longitudinal (Km) é dado pelo número de espécies de peixes recifais em distintas províncias geográficas. Baseado na marcante distinção da riqueza de espécies em amplas escalas, o presente estudo trabalhou em uma escala regional (100m²) e escala local (2m²) a partir de dados de filmagem remota. A riqueza regional e construção de redes agonísticas representam a escala de 100m², enquanto a riqueza local e medida da beta diversidade de espécies foram estimadas na escala local de 2m².

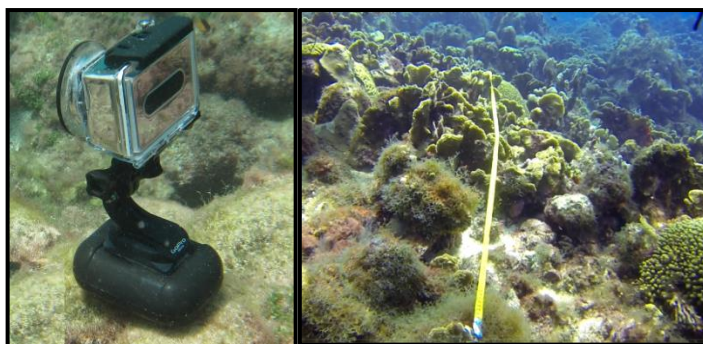


Figura 3. Método de filmagem remota (Longo e Floeter, 2012) utilizado para estimar a riqueza regional, local e interações agonísticas de peixes recifais. Uma câmera é lastreada e posicionada sobre o recife de coral. Após delimitar uma área de 2m² com o auxílio de uma trena, o mergulhador se afasta por aproximadamente 10 minutos e retorna para remover a câmera.

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Capítulo Único

The macroecology of agonistic interactions in reef fishes

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The macroecology of agonistic interactions in reef fishes

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Abstract

Diversity and coexistence of species have been studied for decades and triggered several ecological theories to understand the process involved in community assemblages. The composition of species pools is influenced by regional processes (e.g. dispersion, speciation and extinction) and biotic interactions (e.g. competition, predation). However, how these processes operate over species distributions across different spatial scales is poorly known. In marine ecosystems, reef fishes exhibit a longitudinal large-scale gradient of species richness and regional processes are strongly associated with community assembly. Conversely, interspecific interactions, such as competition, influence population dynamics of reef fishes and may have an essential role in shaping the community composition of this group. In this study, we aimed to investigate the relationship between species richness and the structure of agonistic interactions of fishes across different spatial scales, from tropical reefs in seven localities across five biogeographic provinces (south-western Atlantic, Caribbean, Polynesian, Central Pacific and Central Indo Pacific). Moreover, agonistic networks of reef fishes were built to compare the structure of these interactions among the seven studied localities. Species richness and agonistic interactions data were collected through a total of 350 samples of remote videos in shallow sheltered reefs, each sample consisting of a 2m² area during 10 minutes. We observed a higher species accumulation in regionally richer localities and a positive relationship between local and regional richness. For the local pool composed only by interacting species, we observed the same pattern in species accumulation, but not the local and regional positive relationship. This pattern can be explained by the increasing species turnover towards regionally richer areas suggesting higher spatial segregation of interacting species in richer local communities. Moreover, the topological complexity of agonistic networks, defined by modularity and centralization values, increased according to the regional richness gradient. Pomacentrids, labrids and acanthurids were predominant at network composition in all seven localities and territorial herbivores performed a central role in all local communities. Combined, our findings suggest that regional richness of reef fishes plays an essential role on the composition of local species pool, and that local processes (e.g. resource availability and species intrinsic attributes) probably drive the agonistic behavior the spatial distribution of species. Furthermore, the empirical

contextualization of agonistic behavior in reef fish across different spatial scales highlights the importance of a better understanding of the balance among different mechanisms regulating the spatial distribution and resource use partition in reef fish communities

Keywords: diversity, antagonism, coral reefs, spatial-scale patterns, coexistence.

Introduction

The identification of processes driving the diversity and spatial distribution of species across different spatial scales has been a key question in Ecology (e.g. Caley and Schluter 1997, Mittelbach & Schesmke 2015, Ricklefs 1987). Studies on species coexistence and on diversity variation across spatial-scales triggered the development of ecological theories aiming to explain the mechanisms behind community structure. Earlier theories were based on niche partitioning, suggesting it as the main mechanism to allow species coexistence and, as a consequence, biodiversity in natural ecosystems (Dobzhansky 1950, Hutchinson 1957). Later on, the theory of island biogeography (McArthur & Wilson 1967) suggested a dependence of species pool composition on dispersion events and evoked new theories (e.g. neutral theory from Hubbell 2001), proposing the dominance of stochastic and large scale processes (e.g. dispersion, extinction, speciation) to determine community assemblages. Therefore, the divergence between these theories proposes the prevalence of local (e.g. biotic interactions) or large scale processes in determining local communities.

In the past 30 years, the wide variation on studies results encompassing different scale-processes over community assemblages (reviewed by Cornell and Harrison 2014) supports the idea that large scale forces interact with local factors and ecology is scale-dependent (McGill 2010, Mittelbach and Schesmske 2015). Despite an evident interplay between regional and local processes on species distributions, the extent of the influence of evolutionary processes over biodiversity across different spatial scales remains poorly know. To address questions involving the strength of regional and local processes, a theoretical linear model, consisting in a correlation between local and regional richness in community species composition, has been proposed (Gaston 2000, Ricklefs 1987). This model consists of two scenarios: if local richness is directly proportional to, but less than, regional richness, large scale processes are more important to determine the local diversity. Alternatively, if regional richness increases but local richness attains a ceiling (e.g. asymptotic curve), local processes are stronger predictors in shaping local communities. To incorporate the model on empirical data, regional richness should be defined as the set of species capable to disperse and to establish in smaller communities, while the local species pool corresponds to the species present in a scale in which

biotic interactions can potentially influence species distributions (Sristrava 1999). Furthermore, the proper definition of species pool is crucial to avoid misleading interpretation about the strength, especially of local factors over community structure (Gonçalves-Souza et al. 2013, Szava-Kovats et al. 2013).

The dominance of local factors, as competition, over species pool composition is, in general, related to resource depletion caused by resident species and, hence, controls the establishment of new colonizers in same area. This hypothesis is reinforced by the impact of biotic interactions involving antagonistic relationships among species (e.g. parasitism, herbivory, predation) on community structure (Jabot and Bascompte 2012, Ings et al. 2009; Paine 1966). In recent years, a number of studies have started to integrate biotic interactions and spatial processes by ecological networks analysis (Maglianese et al. 2015, Tylianakis et al. 2007). The network approach can provide information about species roles in community structure (Guimarães et al. 2007, Schleuning et al. 2015) and permits to identify key processes (e.g. phylogeny and species evolution, abiotic gradients, functional similarities) that maintain biodiversity (Dunne et al. 2002). In community studies, the nodes in the network are comprised of individuals that make up populations, and the links connecting them propose population effects. Although networks have been key to understand the structure, evolution and dynamics of ecological interactions, few studies have used this approach in marine systems (Guimarães et al. 2011) and none have integrated across large spatial scales.

In marine ecosystems, the influence of regional dispersal on the dynamics of local populations is well established through empirical measures and statistical models (Gaines and Roughgarden 1985, Lewin 1986). In corals and reef fishes, the remarkable longitudinal downgrading diversity permits robust comparisons between local and regional richness. The Indo-Australian Archipelago is considered the center of origin and current hotspot of species. Within this region, coral reef biodiversity increases longitudinally, as one moves towards this hotspot (Briggs 2005, Kulbicki et al. 2013, Mora et al. 2003, Roberts et al. 2002) and decreases two- to 50- fold as one moves East across the Pacific. Fishes, for example, range, approximately, from over 2000 species in the Indo-Pacific to 300 species in the Brazilian coast (Kulbicki et al. 2013). Therefore, on the last decade studies on reef fishes across multiple spatial scales suggested that local community composition is under strong influence of regional processes and may be

structured by simple assembly rules like stochastic events of dispersion (Bellwood and Hughes 2001, Connolly et al. 2005). However, due to high diversity of reef fishes at small scales in some regions (Bellwood et al. 2003), mechanisms of species coexistence and the role of biotic interactions (e.g. competition) on local communities remain open to question.

Competition in reef fishes is an evident local process by the existence of resources use overlap and territorial behavior in a number of species (e.g. Forrester et al. 2015, Munday et al. 2001, Roberston 1995), which may enhance the frequency of agonistic interactions among reef fishes (Blowes et al. 2013, Kerry & Bellwood 2015). Indeed, interspecific competition among reef fishes has been shown to drive patterns of abundance and distribution across coral reef habitats (Robertson 1996), to influence energetic factors such as growth and reproduction (Forrester 1990, Jones and McCormick 2002), and to strongly affect fish mortality (Hixon & Webster 2002). These different effects of competition on reef fish abundance, fitness and survivorship suggests that resource partitioning and other potential mechanisms involving agonistic interactions may have an essential role in shaping the community structure of these species.

The incorporation of biological interactions in macroecological context is mostly associated to the latitudinal perspective. Patterns of intensity and specialization of biotic interactions across latitudes may be related to species richness or physiological constrains due temperature changes that covary with latitude (Schemske et al. 2009, reviewed by Moles and Ollerton 2015). To isolate any potential influence of temperature, we aimed to investigate the spatial relationship between regional richness and agonistic interactions in reef fishes in seven localities across a longitudinal global diversity gradient where temperatures were approximately constant. Species richness and interactions were assessed with remote videos, which allowed us to build a standardized and robust empirical database for all studied localities. This is the first marine ecology study to test regional and local richness relationships associated to agonistic networks providing novel insights about the processes involved on the species distribution across different spatial scales.

Methods

Study areas

We surveyed seven localities from two ocean basins (Table 1): four at the Atlantic (Rocas Atoll, Abrolhos, Curaçao, Yucatán) and three at the Indo-Pacific (Moorea, Fiji, Bali). All localities include tropical biogenic reefs at similar annual mean sea surface temperature—between 27 and 29°C (NOAA, 2014)—and span over four distinct biogeographic regions (*sensu* Kulbicki et al. 2013; Table 1) along a pronounced, large-scale gradient of species richness (Parravicini et al. 2013). Differences in biological traits (e.g. diet, size, home ranges; Moulliot et al. 2014) define resource-use patterns among reef fish species (Bellwood et al. 2006); thus their spatial distribution are influenced by habitat heterogeneity and complexity (Syms & Jones 2000, Vergés et al. 2012). Therefore, to maximize the probability of sampling a larger portion of the assemblage of each locality, we sampled at least three distinct shallow (from 2 to 10 meters) and sheltered sites that encompassed a clear variation in habitat complexity and benthic community (e.g. coral species with different morphologies, predominance of epilithical algae matrix, presence of coral rubble).

Table 1. The seven study localities, characterized as tropical biogenic reefs, and their respective biogeographic province and regional richness based on checklists (Kulbicki et al. 2013).

	Locality	Biogeographic province	Regional richness
1	Bali	Central Indo-Pacific	3689
2	Fiji	Central Pacific	1809
3	Moorea	Polynesian	1076
4	Yucatán	Caribbean	774
5	Curaçao	Caribbean	774
6	Abrolhos	South-western Atlantic	356
7	Rocas Atoll	South-western Atlantic	356

Data sampling: species richness and agonistic interactions

Our primary dataset consisted of species' agonistic interaction lists obtained through remote, standardized video samples. A remote video sample consisted of a 15-minute shot by a high-definition camera, fixed and focused on a 2m² reef area previously delimited by a diver (details in Longo & Floeter 2012). We sampled 50 videos in at least three sites for each study locality (details in Supplementary Material Table 1) to maximize probability of recording a broader portion of the species using the sites. Video samples were played back to identify all species and agonistic interaction events between pairs of fish of different species within the 2m² area for the 10 minutes in-between per video sample. We considered as agonistic interactions chasing events between fishes of different species, which is a well-documented behaviour representing interspecific disputes for different types of resources (Kerry and Bellwood 2015, Robertson 1996). Since proper detection of individuals of less than 5 cm body length is impaired in remote video analysis, we focused on species larger than this threshold.

Species-area relationships

We investigated the relation between regional richness and local species pools, and how agonistic interactions between species respond to spatial-scale richness variations, by considering three measures of local species richness as follows. The “detected species” richness corresponded to all species identified per locality; the “non-interactive species” richness corresponded to species identified but not involved in any agonistic interaction; finally, the “interactive species” richness corresponded only to the species that were detected interacting agonistically at a given locality.

We built sample-based accumulation curves to evaluate how species richness increase with sampling effort in each locality. We used the Coleman method (Coleman et al. 1982), calculating the 95% confidence intervals of the accumulation curves to assist the comparison among localities.

We built linear regression models to test the potential relationship between local and regional richness. Local richness was estimated as the mean of the species identified per video sample for each locality; the regional richness was estimated as the sum of all species identified in all video samples per locality. The high correlation between the regional pool identified in our video sampling and the regional pool defined by species checklists (available in Kulbicki et al. 2013) ensured

the reliability of our regional richness estimates (Supplementary Material Fig. 1). To investigate the spatial variation of interactive species richness at a local scale, we calculated the species turnover component of beta diversity using the Sorensen dissimilarity index for each locality. This index was appropriate to evaluate concurrence of interactive species on video samples, since it emphasizes the shared, rather than unshared, species between samples. These analyses were performed in R environment with assistance of the packages *vegan* (Oksanen et al. 2015) and *betapart* (Baselga & Orme 2013).

Agonistic interaction networks

We applied the network formalism to investigate large-scale patterns of agonistic interactions among reef fishes across the seven localities. It is important to highlight that networks represent the regional scale and nodes are composed by all species recorded interacting agonistically in each locality. We opted for a regional scale (regional scale correspond to the regional richness and was estimated as the sum of all species identified in all video samples per locality) in order to identify spatial heterogeneity in species distributions and taxonomical association patterns among reef fishes. We plotted the binary adjacency matrices for each locality (in which an element $a_{ij} = 1$ when species i interacted agonistically with species j , and $a_{ij} = 0$ otherwise) as one-mode undirected networks. In the network depiction, species represented by nodes are connected by links whenever an agonistic interaction between them was recorded in the video samples..

Considering that agonistic interactions can be promoted by similar species traits and phenotypes (Blowes et al. 2013, Best et al. 2013), we used two topological metrics to identify patterns of taxonomic predominance and associations over a large-scale gradient of species richness. The first metric was closeness centrality, the inverse of the average distances to all other nodes in the network; Wasserman & Faust 1994). Closeness indicates the tendency of some nodes to be more connected than the others in the network; thus within the agonistic networks, it indicated fish species with higher potential to directly interact with other species. We also used closeness to calculate centralization, i.e. a network-level centrality score to be compared across agonistic networks. Centralization was used as a summary metric to infer on the distribution and heterogeneity of agonistic interactions along the regional species diversity gradient. The second topological metric was modularity, which we used to evaluate the existence of

subsets of cohesive nodes that are more connected within each other than to the rest of the network (see Newman 2006). A modular network in our case would indicate compartmentalization of the agonistic interactions among species. We calculate modularity for each network using the spectral partitioning algorithm (Newman 2006), recommended for small networks (Marquiti et al. 2014).

We assessed the significance of the network metrics with a null model approach. We compared empirical centralization and modularity values with a null distribution calculated for 1,000 theoretical networks with same size (number of nodes) and connectance (proportion of realized links) as the empirical networks. We used a null model to create binary theoretical adjacency matrices, in which the probability of each matrix cell being occupied was proportional to the row and column sums of the original matrices (original null model 2 in Bascompte et al. 2003, modified by Pires et al. 2015 for squared matrices). The empirical network metrics were considered significant when they fell outside of the 95% confidence intervals of the null distribution. Significant values of modularity and centralization indicate that the topology of networks is robust and non-randomly structured. Network analyses were performed in R environment, using the package *igraph* (Csardi & Nepuz 2006).

Results

Species richness patterns

The sampled tropical reefs covered a large-scale longitudinal gradient of species richness with regional pool ranging from 26 species at the poorest locality (Rocas Atoll) to 256 at the richest locality (Bali). Such species pools we estimated from remote video sampling tallied with the estimates via checklist methods (Table 1; Supplementary Material Fig.1).

Regardless the species richness type considered, accumulation curves showed an overall similar pattern: higher species accumulation in localities with higher regional species richness (Fig. 1). However, the curves of interactive species (Fig. 1c) differed in three fundamental ways: a) the confidence intervals of some localities overlapped, unlike for richness of detected (Fig. 1a) and non-interactive species (Fig. 1b); b) the curve for Curacao (Caribbean) accumulated a higher number of species than would be predicted by regional richness (i.e., richness was higher than the richer Moorea in the Indo-Pacific); finally, c) the curve

for Yucatan (Caribbean) accumulated a smaller number of species than would be predicted by regional richness (i.e. converging to the poorer Rocas and Abrolhos localities in the Southwestern Atlantic). Combined, these findings suggest that underlying mechanisms driving richness of species that engage in agonistic behavior may be similar, but not necessarily identical/proportional, to those driving the richness of the entire reef fish assemblage.

Species-area relationships

We found a positive relationship between local and regional richness for detected and non-interactive species (Fig 2; $r^2=0.71$, $F_{1,5}=19.73$, $p=0.007$; $r^2=0.67$, $F_{1,5}=9.98$, $p=0.0251$; respectively). Detected local species richness varied from 7 to 22 species at Rocas and Bali, respectively, while non-interactive species richness varied from 2 to 9 species at Abrolhos and Bali, respectively. On the other hand, for interactive species, the variation in local richness was only between 1 and 4 species at Yucatán and Bali, respectively. Moreover, there was no linear relationship with regional richness (Fig 2, $r^2=0.06$, $F_{1,5}=0.09$, $p=0.7$).

Agonistic interactions

Despite regional species richness differences, the proportion of total interactive species tended to be similar among sites (Fig. 3; Bali = 24%, Fiji = 23%, Moorea=25%, Yucatan=21%, Abrolhos=30%), excepting for Rocas and Curaçao (53% and 44%, respectively). Furthermore, in all sites, species from Labridae, Acanthuridae and Pomacentridae composed more than 50% of the interactive species pools (Fig. 3).

While proportions demonstrated similarities among localities, the turnover of interactive species (Sorensen index component) demonstrated a gradual increase among localities with greater regional richness (Fig. 4a and 4b), excepted for Curaçao, whose species turnover was superior than for Yucatan and Moorea.

The network structure increased in complexity along the regional species richness gradient (Fig 4a): in species-rich localities there were more species engaged in agonistic behavior (i.e. more nodes and links; Fig. 4b) as well as more heterogeneity in that behavior (centralization; Fig. 4c). In general, agonistic networks were

predominantly composed by nodes representing species of Pomacentridae and Labridae (in Fig. 3 the green and blue nodes, respectively). None of agonistic networks, except from Bali, were organized into cohesive groups of interacting species — the empirical modularity values were not different than the null expectancy (Table 2). But the agonistic networks were centralized (closeness centralization values higher than expected by chance, Table 2) and such centralization decreased with species turnover and regional richness. We observed a recurrent star structure around one or two central, more connected species in networks; however, this pattern was less evident in Bali and Yucatan. Closeness centrality was homogeneously distributed among species in larger networks (i.e. with more species) (Fig 3.). In general, species of *Stegastes* were more central (higher closeness) in the networks (centrality values per species in Supplementary Material Table 2 and detailed networks in Supplementary Material Fig 2.).

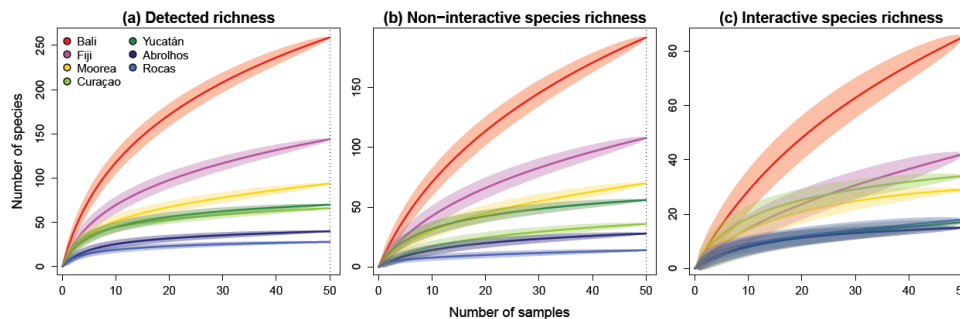


Figure 1. **Sample-based accumulation curves of reef fish species in seven tropical reefs along a longitudinal species richness gradient.** The solid lines represent the cumulative number of species registered (y-axis) as a function of the cumulative number of 2m² video plot samples (x-axis), with 95% confidence intervals. Note different y-axis scales reflecting the distinct number of species between local richness types. (a) Detected species richness: all species identified on each sample; (b) Non-interactive species richness: species identified but not involved in agonistic interactions; (c) Interactive species richness: only species detected interacting agonistically. Color code indicates species richness gradient

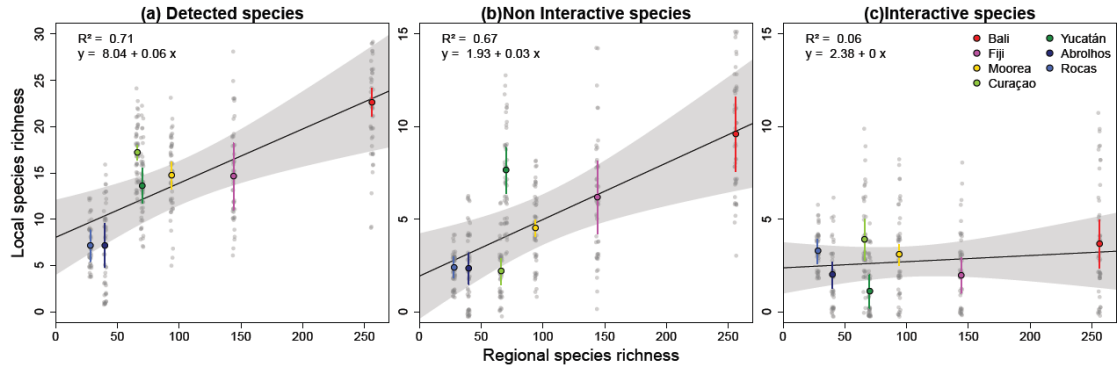


Figure 2. **Reef fish species-area relationship between local and regional richness in seven tropical reefs.** (a) Detected species (b) Non- interactive species (c) Interactive species. Colored circles represent the local richness of each study locality; whiskers represent standard errors of the mean. Shadow areas represent the 95% confidence intervals estimated from predicted values of the linear model. Grey points represent the total reef fish species identified in each video sample per tropical reef locality but were not included in the linear model. Color code follows the longitudinal species richness gradient.

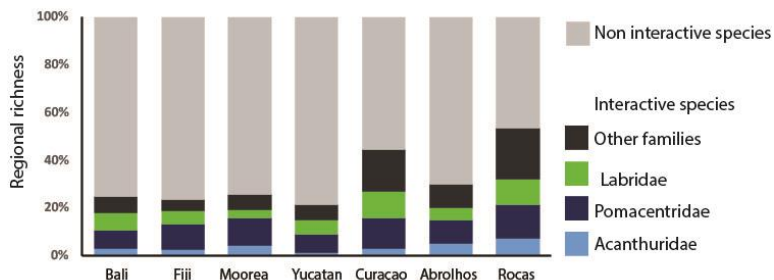


Figure 3. **Proportion of reef fishes engaged in agonistic interactions along the longitudinal regional richness gradient.** Bars represent regional richness of each tropical reef locality as estimated by remote video sampling. Colors represent five categories: interactive species of Acanthuridae; Labridae; Pomacentridae; interactive species of other fish families; and non-interactive species.

Table 2. **Modularity and centralization for network of agonistic interaction among reef fish species of each locality.** Empirical values were considered significant (*) when they fell outside of the 95% confidence intervals (CI) of the theoretical distribution created with a null model.

Locality	Modularity	2.5%CI	97.5%CI	Centralization	2.5%CI	97.5%CI
Bali	0.583*	0.494	0.559	0.231*	0.067	0.201
Fiji	0.498	0.360	0.550	0.476*	0.104	0.361
Moorea	0.225	0.274	0.448	0.532*	0.139	0.405
Curaçao	0.216	0.238	0.359	0.497*	0.164	0.397
Yucatán	0.341	0.216	0.458	0.362*	0.131	0.362
Abrolhos	0.111	0.152	0.452	0.818*	0.09	0.545
Rocas	0.303	0.216	0.520	0.652*	0.147	0.509

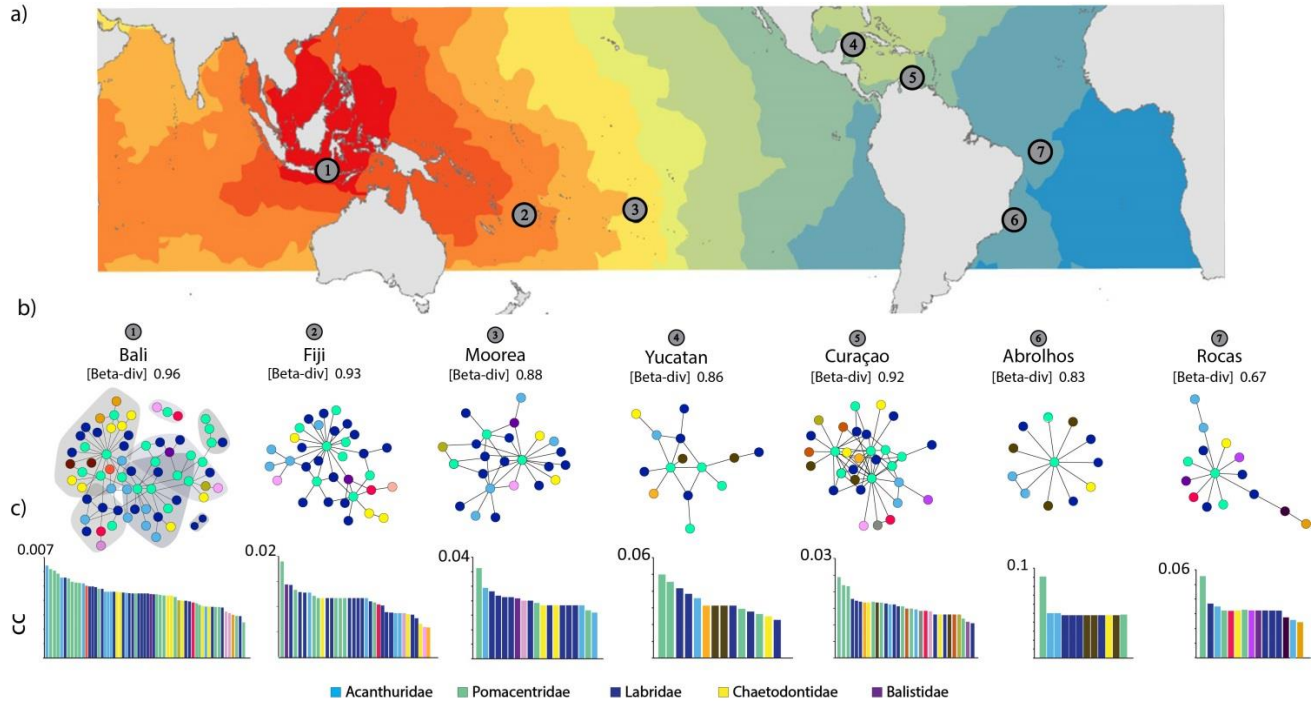


Figure 4. **Reef fish agonistic networks along the longitudinal species richness gradient.** a) Enumerated points represent sampled localities and colors represent the longitudinal species richness gradient (from higher (red) to lower (blue) species richness); b) Agonistic networks: reef fish species (nodes color-coded by family) linked whether recorded engaged in

agonistic behavior; Shadow areas in Bali represent the modularity index. Beta-div values represent the species turnover component of Sorensen dissimilarity index; Network centralization: bars represent closeness centrality (CC) for each species (color-coded by fish family). Predominant families and their respective colors are presented below the bar graphs.

Discussion

We present the first empirical contextualization of agonistic behavior in the marine environment at a cross-oceanic scale, meeting the need for integration of network thinking and macroecology (Kissling and Schleuning 2015). By showing that regional and local species richness are strongly, positively related across seven reef fish communities distributed along four biogeographic regions, our study supports that large scale processes influence community structure of reef fish at local scales (Bellwood and Hughes 2001, Connolly et al. 2005). However, this relationship became weaker when we focus on the local pool of species that compete directly for resources, evidenced by agonistic interactions. The tendency for richer communities to have more species engaged in direct competition suggests these species may be more spatially segregated at a fine scale, since the spatial distributions of species tend to be mediated by competition at smaller scales when large-scale processes promote regional coexistence (Boulangeat et al. 2012, Godsoe et al. 2015). Combined, our findings suggest that regional richness of reef fish species plays an important role defining the local pool of species, and local processes (e.g. resource availability) probably drive the frequency and strength of agonistic behavior among species.

The positive relationship between the local pool of reef fishes (detected and non-interactive species) and regional richness strengthens the evidence that highly diverse ecosystems contain, proportionally, more species at local scales (Caley and Schutler 1997, Ricklefs 1987, Witman et al. 2004). In reef fish, a global study investigated the functional redundancy among six tropical-reef fish faunas (Mouillot et al. 2014) and observed positive relationship between functional entities and species number and in richer regions several vulnerable functions supported by just one species. Such species packing at local scales and functional entities at regional scales suggest that niche partitioning can be a major underlying mechanism structuring reef fish assemblages (see niche theory: Hutchinson 1957). In contrast, reef fish communities in the Pacific may display a constant contribution of some families to the total species pool, suggesting that reef fish biodiversity may follow a simply assembly rule where species

proportions are highly predictable regardless of location (Bellwood and Hughes 2001). Here, we found similar proportions of the total number of species that compete directly for resources and families among sites compared to their respective regional richness (e.g. Bali and Yucatán contained 24% and 21%, respectively, of total interactive species). The similarity between species contribution in agonistic interactions between sites leads to the question: could the same assembly rules (Bellwood and Hughes 2001) operate at finer scales, influencing the diversity of interactions in local reef fish communities? A negative answer would emphasize the prevalence of large-scale and neutral processes structuring reef fish communities (Barneche et al. 2016, Hubbell 2001).

The roles, if any, played by neutral processes and niche partitioning in structuring ecological communities is a long-standing debate in ecology (Barneche et al. 2016, Godsoe et al. 2015, Soberón 2010). The stochastic niche and ‘lottery’ theory (Sale 1974, Tilman 2004) attempted to alleviate this conflict by positing that species propagules are vulnerable to stochastic mortality and dispersion, but growth and survival will depend on the resources left unconsumed by established species. Recent empirical evidence for this theory came from a tropical forest system (Karger et al. 2015): niche overlap decreases with increasing species pool, influenced by environmental gradients and local factors. Our findings harmonize with the stochastic niche theory, since there was a higher species accumulation and turnover but no difference between local interactive species richness among sites. We suggest two main drivers for this pattern: habitat complexity and functional similarities of species.

Habitat complexity in coral reefs is primarily given by coral diversity and percent coverage (Kulbicki et al. 2014, Wilson et al. 2010), both of which are primary structuring drivers of reef fish assemblages (Graham et al. 2007, Wilson et al. 2008). The presence of several coral morphs may enhance the number of refuges and food availability for reef fishes and, hence, increase habitat suitability for the settlement of a wide variety of fish species. Furthermore, corals and reef fishes are structured by similar historical processes (Bellwood and Hughes 2001, Burgess et al. 2010), and follow the same longitudinal species richness gradient

(Connolly et al. 2005, Karlson et al. 2004). Thus, taking coral diversity as a proxy of resources availability and interspecific agonistic interactions as a surrogate for interference competition between reef fishes, our empirical results disagree with the theoretical expectation for local richness to be a constant fraction of the total species pool, given enough limiting factors (Allesina and Levine 2011). The controversy could be explained, in our study, by the role of intrinsic attributes of fish species that present interspecific agonistic behavior, combined with the spatial boundaries promoted by small scales. Interspecific aggression is a clear evidence of resource competition among reef fishes (reviewed by Bonin et al. 2015). Contrasts in resource use by different fishes can affect the frequency and strength of agonistic behavior (Peiman and Robinson 2010), depending on their diet overlap, territorial behavior and phylogenetic similarity (Bellwood et al. 2006, Blowes et al. 2013, Roberston 1961).

In the agonistic networks observed in our study, nodes were generally dominated by a subset of species from three fish families: Pomacentridae, Acanthuridae and Labridae. Several species of these families have similarities in functional attributes, such as limited home range and herbivorous diet (Moulliot et al. 2014), that could reflect on the agonistic behavior and competition for similar resources. Furthermore, territorial behavior is frequently reported for those interactive species (van Rooij et al. 1996, Roberston et al. 1976, Robertson and Polunin 1981) and is a relevant characteristic to determine spatial distributions of reef fishes (Robertson and Lassig 1980). A study conducted across different spatial scales with Danish avifauna demonstrated the importance of territoriality on species distribution even in large scales (Gotelli et al. 2010) and suggests that interspecific competition plays an important role even at the large scale of an entire country. In our study, we were not able to detect the influence of agonistic interactions on local richness of the detected species. However, the similar local richness and turnover gradient of interactive species may support the idea of spatial segregation of species subset with functional similarities at finest scales (2m²). A comparable pattern is described for plants and animals, which are likely to reduce local pools and to increase the beta diversity between communities due antagonistic interactions (e.g.

herbivory and parasitism) (Jabot and Bascompte 2012). Associated to interactive species turnover, we expected a modularity gradient on the agonistic networks as a consequence of spatial species segregation and association of species taxonomically closer. In mutualistic networks, modules identify potential specialists and generalist species and provide relevant information about ecosystem resilience (Olesen et al. 2013, Schleuning et al. 2015). However, in this study, network modularity values were not significant and may not represent the best global metric to identify patterns in the structure of reef fish agonistic interactions. Centralization, on the other hand, was higher than expected by chance and decreased according to species richness, thus suggesting that richer sites have, potentially, a wider distribution of interactions among species compared to poor sites, which tend to present one or two dominant central species.

The same pattern of distribution emerged on species closeness centrality among sites, as in richer sites the species dominance became weaker according to evenness in centrality values. Despite differences in closeness centrality, pomacentrid species displayed the most central roles among sites. Similarly to food webs dynamics, the central species of agonistic networks pertain to particular taxonomic group which are expected to play an important dynamic role independent of their particular ecological community (Stouffer 2012). Furthermore, as animal-plant mutualistic networks, the conservation of species functional roles across communities is strongly influenced by their evolutionary histories (Rezende et al. 2007, González et al. 2015). In the agonistic networks, the dominant central species is represented by the territorial herbivores, a functional group widely distributed among coral reefs (Ferreira et al. 2004, Kulbicki et al. 2014, Robertson 1996, Robertson and Polunin 1981). These species may influence the benthic community diversity, coral settlement, algal growth, and also affect the distribution, feeding activity and growth rate of other reef fishes at local scales (Gochfeld et al. 2010, Hixon and Brostoff 1996, James et al. 1992, Wellington et al. 1982). Therefore, due to this relevant functional role of damselfishes in coral reefs, we suggest that, in the studied agonistic networks, the loss of central species in poorer sites (e.g. Rocas and Abrolhos) may lead to a rapid and evident ecosystem change.

While our study highlights the importance of large- and local-scale processes that function in tandem shaping the structure and dynamics of reef fish communities, a better understanding of the underlying mechanisms regulating the interplay between agonistic behavior and resource use partition in reef fish assemblages begs further research. We recommend incorporating ecological (e.g. species abundance, body size) and evolutionary factors (e.g. phylogeny) into weighted network modeling (e.g., Rezende et al. 2007, Vázquez et al. 2009, Woodward et al. 2005) to insert agonistic behavior within the larger architecture other ecological interactions operating over differed spatial scales. A refined approach on the influence of habitat complexity is a timely challenge given the rapid, global decline of coral reef ecosystems (Hughes et al. 2004, Ash 2016).

We show that higher regional pool of reef fish species can potentially promote the establishment of a larger number of species at local communities. Additionally, the increased habitat heterogeneity and complexity provided along the coral species gradient could also affect the suitability for a wide variety of species at fine spatial scales. This may explain higher values of species turnover and accumulation in richer sites we observed here, but is not enough to explain the lack of relationship between local and regional richness of species that invest in agonistic behavior to deal with competition. While evaluating the contribution of competition exclusion is out of the scope of this study, the restricted number of species displaying agonistic behavior at small scales, as well as the similar network structure across the richness gradient, suggest that species attributes, especially home range and diet, are the strongest explanatory candidates of the patterns in agonistic interactions and influence local spatial distribution of potential competitors. Finally, the fact that local communities can support an higher species number influenced by regional richness but only a small fraction displayed agonistic behavior reinforce questions about energetic constrains and niche partition theories on highly diverse ecosystems.

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Supplementary Material

Figure 1. Correlation regional richness video plot and checklist (Spearman Rank = 0.988)

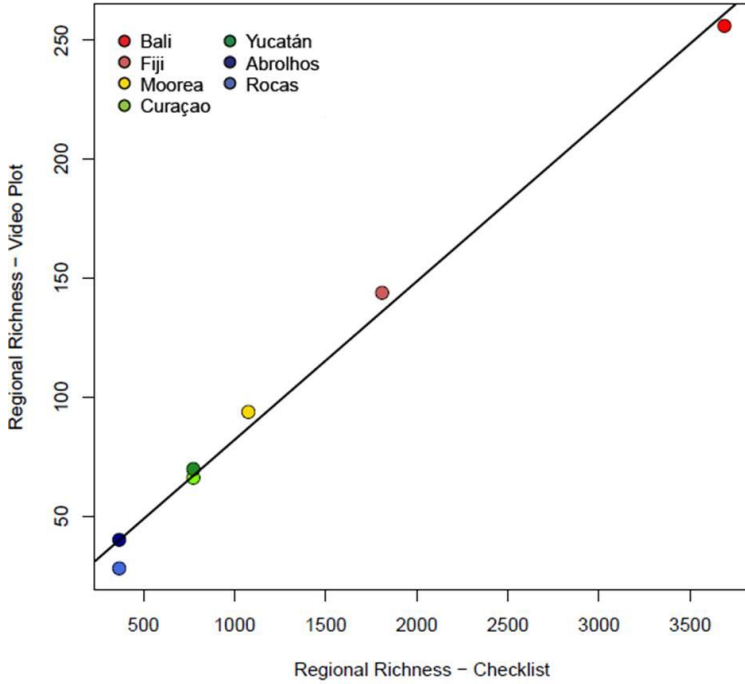


Table 1- Sample summary of the field effort at the study sites

Site	Coordinates	Depth	N samples	Year
Bali				
Amed	8°20'15.0"S 115°39'37.7"E	4-5m	13	2013
Nusa	8°40'09.4"S 115°26'30.3"E	3-5m	11	2013
Lembongan	8°16'32.2"S 115°35'50.5"E	5-10m	17	2015
Padang Bay	8°32'04.0"S 115°30'46.8"E	3-6m	9	2015
Fiji				
Lai Lai	18°11'24.7"S 177°37'13.6"E	2-3m	16	2010
Namada	18°11'24.7"S 177°37'13.6"E	2-3m	7	2010
Votua	18°12'14.7"S 177°42'33"E	3-6m	27	2011
Moorea				
East Moorea	17°29'01.8"S 149°52'00"W	1-3m	16	2012
West Moorea	17°29'14.8"S 149°54'50.5"W	1-3m	29	2012
Tiahura	17°48'61"S 149°91'05"W	1-3m	5	2012
Yucatán				
Barracudas	20°38'41'' N 87°02'91'' W	7-8m	11	2013
Jardines	20°37'27'' N 81°01'55''W	6-8m	10	2013
Moche	20°38'41'' N 84°18'47'' W	6-8m	5	2013
Sabalos	20°34'87'' N 87°06'58'' S	6-7m	9	2013
Paraíso	20°28'12'' N 86°59'01''W	12m	15	2013
Curaçao				
Oostpunt	12°02'14'' N 68°47'85'' W	9-12m	21	2013
Snake Bay	12°08'39'' N 68°59'82'' W	9-12m	10	2013
Water Factory	12°06'32''N 68°57'15''W	9-12m	11	2013

Westpunt	12°22'55''N 69°09'49''W	9-12m	9	2013
Abrolhos				
Chapeirões	17°58'38''S 38°43'19''W	6-10m	20	2010
Mato Verde	17°57'54''S 38°42'05''W	4-10m	10	2010
Portinho Norte	17°57'44''S 38°42'38''W	3-10m	10	2010
Siriba	17°58'11''S 38°42'38''W	4-10m	10	2010
Rocas				
Âncoras	03°52'51'' S 33°48'16''W	2-3m	13	2012
Falsa Barreta	03°51'64'' S 33°49'40''W	1-4m	14	2012
Podes Crer	03°52'20''S 33°48'45''W	1-3m	15	2012
Salão	03°52'29''S 33°48'33''W	8-10m	8	2012

Table 2. List of all interactive species of each site and their respective closeness centrality index.

Locality	Species	Family	Closeness centrality
Bali	<i>Acanthurus grammoptilus</i>	Acanthuridae	0.00463
	<i>Acanthurus lineatus</i>	Acanthuridae	0.005618
	<i>Acanthurus mata</i>	Acanthuridae	0.00463
	<i>Acanthurus nigricans</i>	Acanthuridae	0.004545
	<i>Acanthurus nigricauda</i>	Acanthuridae	0.00463
	<i>Acanthurus tristis</i>	Acanthuridae	0.003571
	<i>Amanses scopas</i>	Monacanthidae	0.004587
	<i>Amphiprion melanopus</i>	Pomacentridae	0.003546
	<i>Anampses melanurus</i>	Labridae	0.004505
	<i>Balistapus undulatus</i>	Balistidae	0.004464
	<i>Bodianus mesothorax</i>	Labridae	0.00463
	<i>Cantherhines dumerilii</i>	Monacanthidae	0.003012
	<i>Centropyge tibicen</i>	Pomacanthidae	0.003226
	<i>Centropyge vrolikii</i>	Pomacanthidae	0.003125
	<i>Cephalopholis argus</i>	Serranidae	0.003861
	<i>Chaetodon kleinii</i>	Chaetodontidae	0.004587
	<i>Chaetodon lineolatus</i>	Chaetodontidae	0.003571
	<i>Chaetodon melannotus</i>	Chaetodontidae	0.004329
	<i>Chaetodon trifascialis</i>	Chaetodontidae	0.00463
	<i>Chaetodon trifasciatus</i>	Chaetodontidae	0.00361
	<i>Chaetodon ulietensis</i>	Chaetodontidae	0.003984
	<i>Chlorurus bleekeri</i>	Scaridae	0.004444
	<i>Chlorurus sordidus</i>	Scaridae	0.00495
	<i>Chlorurus strongylocephalus</i>	Scaridae	0.003559
	<i>Chromis atripes</i>	Pomacentridae	0.004367
	<i>Chromis margaritifer</i>	Pomacentridae	0.004505
	<i>Chromis opercularis</i>	Pomacentridae	0.005263
	<i>Chromis ternatensis</i>	Pomacentridae	0.005236

<i>Chromis viridis</i>	Pomacentridae	0.003802
<i>Chromis weberi</i>	Pomacentridae	0.004237
<i>Cirrhilabrus exquisitus</i>	Labridae	0.002915
<i>Coris gaimard</i>	Labridae	0.004505
<i>Ctenochaetus striatus</i>	Acanthuridae	0.006452
<i>Epibulus insidiator</i>	Labridae	0.004505
<i>Gomphosus varius</i>	Labridae	0.004525
<i>Halichoeres hortulanus</i>	Labridae	0.003984
<i>Halichoeres trimaculatus</i>	Labridae	0.004505
<i>Hemigymnus fasciatus</i>	Labridae	0.003937
<i>Hemigymnus melapterus</i>	Labridae	0.003509
<i>Heniochus varius</i>	Chaetodontidae	0.004329
<i>Labroides dimidiatus</i>	Labridae	0.004566
<i>Neoglyphidodon melas</i>	Pomacentridae	0.005882
<i>Parupeneus multifasciatus</i>	Mullidae	0.004016
<i>Plectroglyphidodon dickii</i>	Pomacentridae	0.00369
<i>Plectroglyphidodon lacrymatus</i>	Pomacentridae	0.006211
<i>Pomacentrus adelus</i>	Pomacentridae	0.006098
<i>Pomacentrus amboinensis</i>	Pomacentridae	0.003546
<i>Pomacentrus auriventris</i>	Pomacentridae	0.002488
<i>Pomacentrus bankanensis</i>	Pomacentridae	0.004831
<i>Pomacentrus burroughi</i>	Pomacentridae	0.005319
<i>Pomacentrus coelestis</i>	Pomacentridae	0.004405
<i>Pomacentrus lepidogenys</i>	Pomacentridae	0.005556
<i>Pomacentrus moluccensis</i>	Pomacentridae	0.004444
<i>Pseudanthias dispar</i>	Serranidae	0.004505
<i>Pseudanthias huchtii</i>	Serranidae	0.004545
<i>Pteragogus enneacanthus</i>	Labridae	0.004505
<i>Scarus niger</i>	Scaridae	0.005
<i>Scarus psittacus</i>	Scaridae	0.004831
<i>Stegastes nigricans</i>	Pomacentridae	0.002933
<i>Thalassoma hardwicke</i>	Labridae	0.005618

	<i>Thalassoma lunare</i>	Labridae	0.005
	<i>Zanclus cornutus</i>	Zanclidae	0.005051
	<i>Zebrasoma scopas</i>	Acanthuridae	0.005208
Fiji	<i>Abudefduf sexfasciatus</i>	Pomacentridae	0.011905
	<i>Acanthurus auranticavus</i>	Acanthuridae	0.009174
	<i>Acanthurus thompsoni</i>	Acanthuridae	0.009174
	<i>Anampses neoguinaicus</i>	Labridae	0.00885
	<i>Balistapus undulatus</i>	Balistidae	0.014706
	<i>Centropyge bispinosa</i>	Pomacanthidae	0.009174
	<i>Chaetodon citrinellus</i>	Chaetodontidae	0.009009
	<i>Chaetodon ephippium</i>	Chaetodontidae	0.011905
	<i>Chaetodon pelewensis</i>	Chaetodontidae	0.006993
	<i>Cheilinus chlorourus</i>	Labridae	0.010753
	<i>Chlorurus bleekeri</i>	Scaridae	0.011905
	<i>Chlorurus spilurus</i>	Scaridae	0.012987
	<i>Choerodon anchorago</i>	Labridae	0.011905
	<i>Chromis margaritifer</i>	Pomacentridae	0.011905
	<i>Chrysiptera taupou</i>	Pomacentridae	0.011905
	<i>Ctenochaetus striatus</i>	Acanthuridae	0.012987
	<i>Dascyllus aruanus</i>	Pomacentridae	0.011905
	<i>Epinephelus merra</i>	Serranidae	0.010989
	<i>Halichoeres trimaculatus</i>	Labridae	0.014493
	<i>Labroides bicolor</i>	Labridae	0.011905
	<i>Labropsis australis</i>	Labridae	0.011905
	<i>Oxycheilinus digramma</i>	Labridae	0.011905
	<i>Parapercis hexophthalma</i>	Pinguipedidae	0.00813
	<i>Pomacentrus spilotoceps</i>	Pomacentridae	0.011111
	<i>Scarus chameleon</i>	Scaridae	0.011905
	<i>Scarus dimidiatus</i>	Scaridae	0.011905
	<i>Scarus globiceps</i>	Scaridae	0.009434
	<i>Scarus prasiognathos</i>	Scaridae	0.011236
	<i>Stegastes albifasciatus</i>	Pomacentridae	0.013514

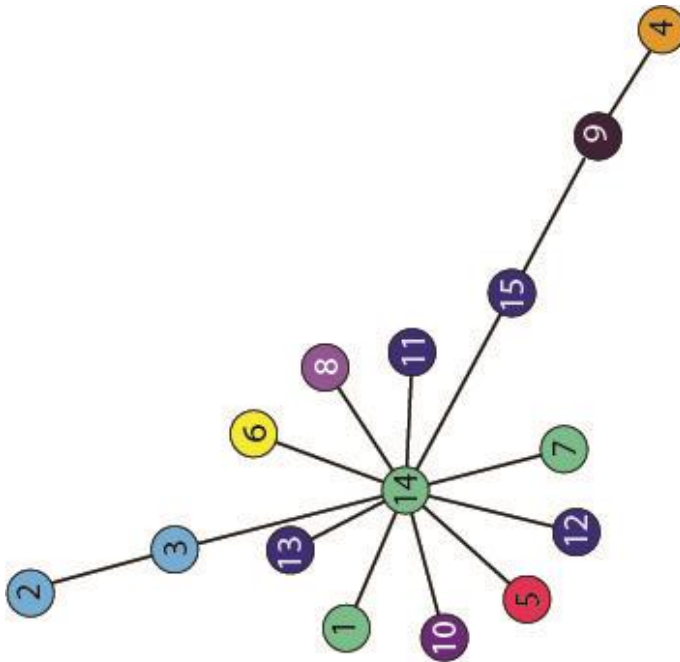
	<i>Stegastes nigricans</i>	Pomacentridae	0.019231
	<i>Stegastes punctatus</i>	Pomacentridae	0.012346
	<i>Stethojulis bandanensis</i>	Labridae	0.009259
	<i>Thalassoma hardwicke</i>	Labridae	0.013158
	<i>Zebrasoma scopas</i>	Acanthuridae	0.011905
Moorea	<i>Acanthurus triostegus</i>	Acanthuridae	0.015873
	<i>Aspidontus dussumieri</i>	Blenniidae	0.015873
	<i>Balistapus undulatus</i>	Balistidae	0.020833
	<i>Centropyge flavissima</i>	Pomacanthidae	0.02
	<i>Chaetodon citrinellus</i>	Chaetodontidae	0.018519
	<i>Cheilinus fasciatus</i>	Labridae	0.021739
	<i>Chlorurus spilurus</i>	Scaridae	0.023256
	<i>Chrysiptera leucopoma</i>	Pomacentridae	0.016667
	<i>Ctenochaetus striatus</i>	Acanthuridae	0.02439
	<i>Epibulus insidiator</i>	Labridae	0.018519
	<i>Forcipiger longirostris</i>	Chaetodontidae	0.018519
	<i>Gomphosus varius</i>	Labridae	0.021277
	<i>Halichoeres hortulanus</i>	Labridae	0.018519
	<i>Halichoeres trimaculatus</i>	Labridae	0.018519
	<i>Naso lituratus</i>	Acanthuridae	0.014286
	<i>Parupeneus multifasciatus</i>	Mullidae	0.015385
	<i>Scarus oviceps</i>	Scaridae	0.02
	<i>Scarus prasiognathos</i>	Scaridae	0.015873
	<i>Scarus psittacus</i>	Scaridae	0.021277
	<i>Stegastes nigricans</i>	Pomacentridae	0.03125
	<i>Stegastes punctatus</i>	Pomacentridae	0.019231
	<i>Stethojulis bandanensis</i>	Labridae	0.013514
	<i>Thalassoma hardwicke</i>	Labridae	0.018519
	<i>Zebrasoma scopas</i>	Acanthuridae	0.018519
Yucatán	<i>Acanthurus coeruleus</i>	Acanthuridae	0.002747
	<i>Bodianus rufus</i>	Labridae	0.001748
	<i>Canthigaster rostrata</i>	Tetraodontidae	0.002404

	<i>Chaetodon striatus</i>	Chaetodontidae	0.001923
	<i>Chromis cyanea</i>	Pomacentridae	0.002024
	<i>Haemulon parra</i>	Haemulidae	0.002404
	<i>Haemulon sciurus</i>	Haemulidae	0.002404
	<i>Microspathodon chrysurus</i>	Pomacentridae	0.002262
	<i>Scarus taeniopterus</i>	Scaridae	0.002404
	<i>Sparisoma aurofrenatum</i>	Scaridae	0.003205
	<i>Sparisoma chrysopterum</i>	Scaridae	0.002137
	<i>Stegastes adustus</i>	Pomacentridae	0.003846
	<i>Stegastes partitus</i>	Pomacentridae	0.003497
	<i>Thalassoma bifasciatum</i>	Labridae	0.002959
Curaçao	<i>Abudefduf saxatilis</i>	Pomacentridae	0.014706
	<i>Acanthurus coeruleus</i>	Acanthuridae	0.016129
	<i>Acanthurus tractus</i>	Acanthuridae	0.014706
	<i>Aulostomus maculatus</i>	Aulostomidae	0.014493
	<i>Bodianus rufus</i>	Labridae	0.013333
	<i>Canthigaster rostrata</i>	Tetraodontidae	0.016667
	<i>Cephalopholis cruentata</i>	Serranidae	0.014493
	<i>Chaetodon capistratus</i>	Chaetodontidae	0.016667
	<i>Chaetodon striatus</i>	Chaetodontidae	0.013333
	<i>Chromis cyanea</i>	Pomacentridae	0.016393
	<i>Chromis multilineata</i>	Pomacentridae	0.016667
	<i>Clepticus parrae</i>	Labridae	0.013333
	<i>Haemulon flavolineatum</i>	Haemulidae	0.013333
	<i>Haemulon macrostomum</i>	Haemulidae	0.016667
	<i>Halichoeres garnoti</i>	Labridae	0.017857
	<i>Halichoeres maculipinna</i>	Labridae	0.015625
	<i>Holacanthus tricolor</i>	Pomacanthidae	0.014286
	<i>Holocentrus rufus</i>	Holocentridae	0.010989
	<i>Lutjanus apodus</i>	Lutjanidae	0.014925
	<i>Lutjanus mahogoni</i>	Lutjanidae	0.013333
	<i>Microspathodon chrysurus</i>	Pomacentridae	0.012048

	<i>Mulloidichthys martinicus</i>	Mullidae	0.013333
	<i>Scarus iseri</i>	Scaridae	0.017241
	<i>Scarus taeniopterus</i>	Scaridae	0.010638
	<i>Sparisoma aurofrenatum</i>	Scaridae	0.016393
	<i>Sparisoma viride</i>	Scaridae	0.016129
	<i>Stegastes adustus</i>	Pomacentridae	0.021739
	<i>Stegastes leucostictus</i>	Pomacentridae	0.015385
	<i>Stegastes partitus</i>	Pomacentridae	0.02439
	<i>Stegastes planifrons</i>	Pomacentridae	0.021739
	<i>Thalassoma bifasciatum</i>	Labridae	0.016949
Abrolhos	<i>Abudefduf saxatilis</i>	Pomacentridae	0.047619
	<i>Acanthurus bahianus</i>	Acanthuridae	0.05
	<i>Acanthurus coeruleus</i>	Acanthuridae	0.05
	<i>Anisotremus virginicus</i>	Haemulidae	0.047619
	<i>Chaetodon striatus</i>	Chaetodontidae	0.047619
	<i>Cryptotomus roseus</i>	Scaridae	0.047619
	<i>Haemulon aurolineatum</i>	Haemulidae	0.047619
	<i>Haemulon plumieri</i>	Haemulidae	0.047619
	<i>Halichoeres poeyi</i>	Labridae	0.047619
	<i>Scarus zelindae</i>	Scaridae	0.047619
	<i>Sparisoma axillare</i>	Scaridae	0.047619
	<i>Stegastes fuscus</i>	Pomacentridae	0.090909
Rocas	<i>Abudefduf saxatilis</i>	Pomacentridae	0.032258
	<i>Acanthurus bahianus</i>	Acanthuridae	0.02381
	<i>Acanthurus chirurgus</i>	Acanthuridae	0.034483
	<i>Aluterus scriptus</i>	Monacanthidae	0.019608
	<i>Cephalopholis fulva</i>	Serranidae	0.032258
	<i>Chaetodon ocellatus</i>	Chaetodontidae	0.032258
	<i>Chromis multilineata</i>	Pomacentridae	0.032258
	<i>Holocentrus adscensionis</i>	Holocentridae	0.032258
	<i>Malacanthus plumieri</i>	Malacanthidae	0.026316
	<i>Melichthys niger</i>	Balistidae	0.032258

<i>Sparisoma amplum</i>	Scaridae	0.032258
<i>Sparisoma axillare</i>	Scaridae	0.032258
<i>Sparisoma frondosum</i>	Scaridae	0.032258
<i>Stegastes rocasensis</i>	Pomacentridae	0.055556
<i>Thalassoma noronhanum</i>	Labridae	0.037037

Figure 2. **Detailed agonistic networks for each study locality.** Network nodes represent species recorded interacting agonistically and colors represent their respective fish family.

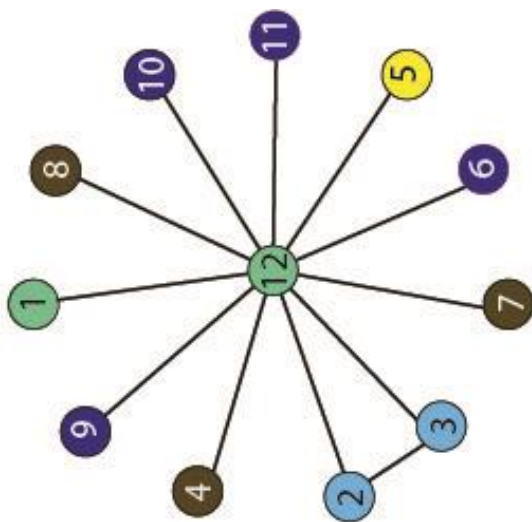


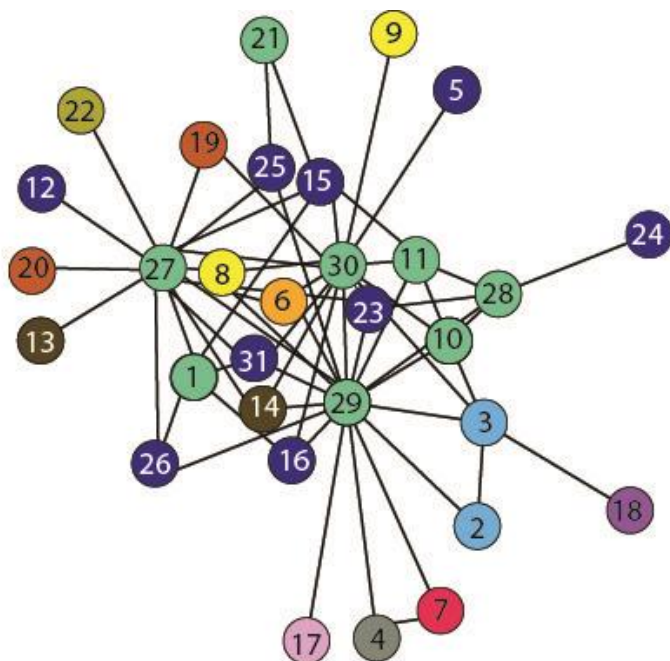
Rocas

- 1 - *Abudefduf saxatilis*
- 2 - *Acanthurus bahianus*
- 3 - *Acanthurus chirurgus*
- 4 - *Aluterus scriptus*
- 5 - *Cephalopholis fulva*
- 6 - *Chaetodon ocellatus*
- 7 - *Chromis multilineata*
- 8 - *Holocentrus adscensionis*
- 9 - *Malacanthus plumieri*
- 10 - *Melichthys niger*
- 11 - *Sparisoma amplum*
- 12 - *Sparisoma axillare*
- 13 - *Sparisoma frondosum*
- 14 - *Stegastes rocasensis*
- 15 - *Thalassoma noronhanum*

Abrolhos

- 1 - *Abudedefduf saxatilis*
- 2 - *Acanthurus bahianus*
- 3 - *Acanthurus coeruleus*
- 4 - *Anisotremus virginicus*
- 5 - *Chaetodon striatus*
- 6 - *Cryptotomus roseus*
- 7 - *Haemulon aurolineatum*
- 8 - *Haemulon plumieri*
- 9 - *Halichoeres poeyi*
- 10 - *Scarus zelindae*
- 11 - *Sparisoma axillare*
- 12 - *Stegastes fuscus*



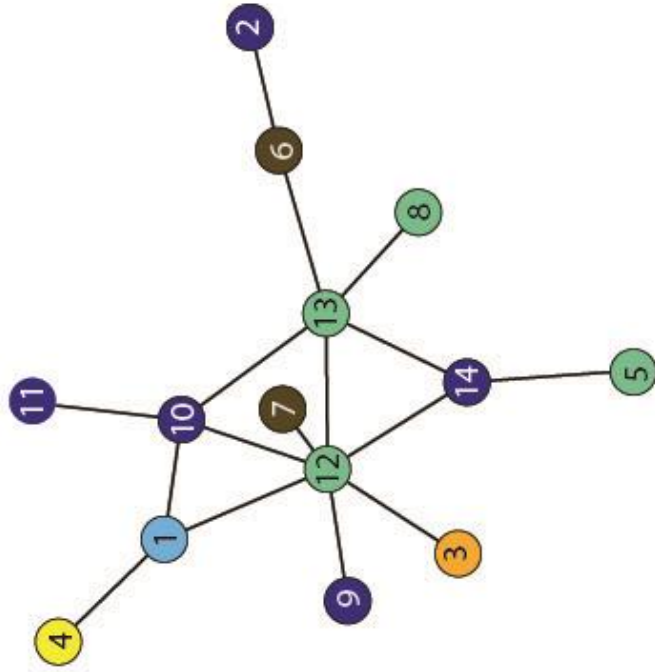


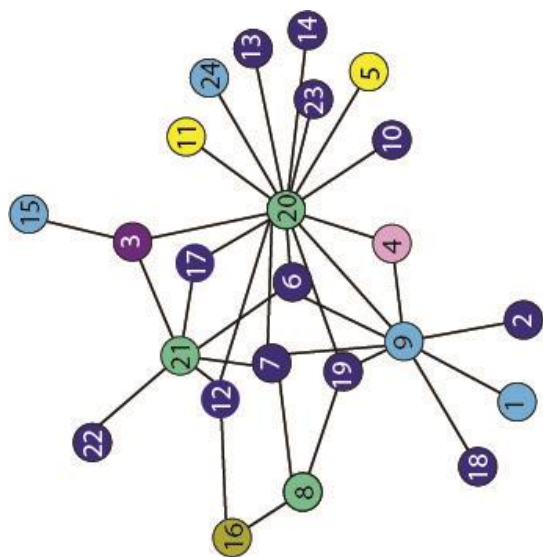
Curaçao

- | | |
|-------------------------------------|---------------------------------------|
| 1 - <i>Abudefduf saxatilis</i> | 19 - <i>Lutjanus apodus</i> |
| 2 - <i>Acanthurus coeruleus</i> | 20 - <i>Lutjanus mahogoni</i> |
| 3 - <i>Acanthurus tractus</i> | 21 - <i>Microspathodon chrysurus</i> |
| 4 - <i>Aulostomus maculatus</i> | 22 - <i>Mulloidichthys martinicus</i> |
| 5 - <i>Bodianus rufus</i> | 23 - <i>Scarus iseri</i> |
| 6 - <i>Canthigaster rostrata</i> | 24 - <i>Scarus taeniopterus</i> |
| 7 - <i>Cephalopholis cruentata</i> | 25 - <i>Sparisoma aurofrenatum</i> |
| 8 - <i>Chaetodon capistratus</i> | 26 - <i>Sparisoma viride</i> |
| 9 - <i>Chaetodon striatus</i> | 27 - <i>Stegastes adustus</i> |
| 10 - <i>Chromis cyanea</i> | 28 - <i>Stegastes leucostictus</i> |
| 11 - <i>Chromis multilineata</i> | 29 - <i>Stegastes partitus</i> |
| 12 - <i>Clepticus parrae</i> | 30 - <i>Stegastes planifrons</i> |
| 13 - <i>Haemulon flavolineatum</i> | 31 - <i>Thalassoma bifasciatum</i> |
| 14 - <i>Haemulon macrostomum</i> | |
| 15 - <i>Halichoeres gamoti</i> | |
| 16 - <i>Halichoeres maculipinna</i> | |
| 17 - <i>Holacanthus tricolor</i> | |
| 18 - <i>Holocentrus rufus</i> | |

Yucatán

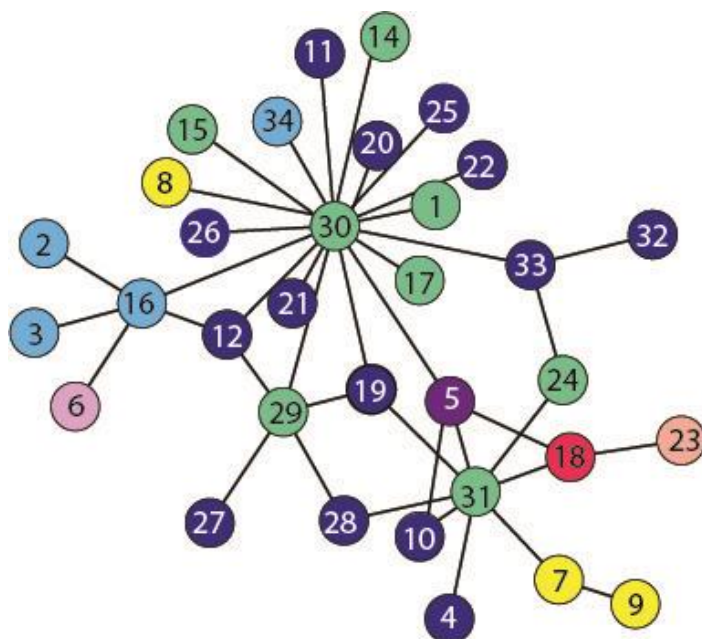
- 1 - *Acanthurus coeruleus*
- 2 - *Bodianus rufus*
- 3 - *Canthigaster rostrata*
- 4 - *Chaetodon striatus*
- 5 - *Chromis cyanea*
- 6 - *Haemulon parra*
- 7 - *Haemulon sciurus*
- 8 - *Microspathodon chrysurus*
- 9 - *Scarus taeniopterus*
- 10 - *Sparisoma aurofrenatum*
- 11 - *Sparisoma chrysopterum*
- 12 - *Stegastes adustus*
- 13 - *Stegastes partitus*
- 14 - *Thalassoma bifasciatum*





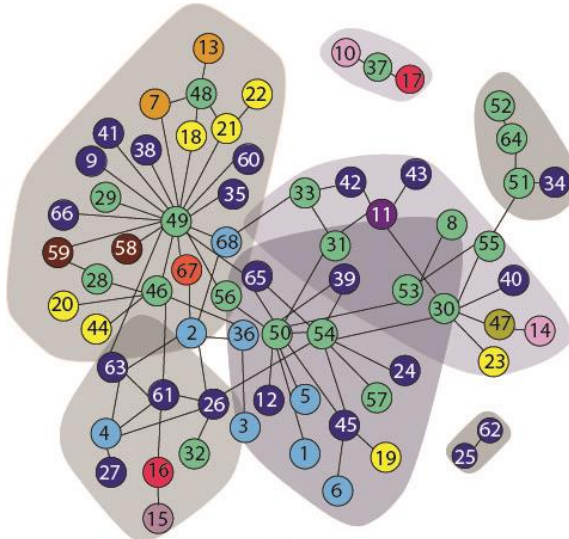
Moorea

- 1 - *Acanthurus triostegus*
- 2 - *Aspidontus dussumieri*
- 3 - *Balistapus undulatus*
- 4 - *Centropyge flavissima*
- 5 - *Chaetodon citrinellus*
- 6 - *Chellinus fasciatus*
- 7 - *Chlorurus spilurus*
- 8 - *Chrysiptera leucopoma*
- 9 - *Ctenochaetus striatus*
- 10 - *Epibulus insidiator*
- 11 - *Forcipiger longirostris*
- 12 - *Gomphosus varius*
- 13 - *Halichoeres hortulanus*
- 14 - *Halichoeres trimaculatus*
- 15 - *Naso lituratus*
- 16 - *Parupeneus multifasciatus*
- 17 - *Scarus oviceps*
- 18 - *Scarus prasiognathos*
- 19 - *Scarus psittacus*
- 20 - *Stegastes nigricans*
- 21 - *Stegastes punctatus*
- 22 - *Stethojulis bandanensis*
- 23 - *Thalassoma hardwicke*
- 24 - *Zebrasoma scopas*



Fiji

- | | |
|------------------------------------|--------------------------------------|
| 1 - <i>Abudefduf sexfasciatus</i> | 18 - <i>Epinephelus merra</i> |
| 2 - <i>Acanthurus auranticavus</i> | 19 - <i>Halichoeres trimaculatus</i> |
| 3 - <i>Acanthurus thompsoni</i> | 20 - <i>Labroides bicolor</i> |
| 4 - <i>Anampses neoguinaicus</i> | 21 - <i>Labropsis australis</i> |
| 5 - <i>Balistapus undulatus</i> | 22 - <i>Oxycheilinus digramma</i> |
| 6 - <i>Centropyge bispinosa</i> | 23 - <i>Parapercis hexophtalma</i> |
| 7 - <i>Chaetodon citrinellus</i> | 24 - <i>Pomacentrus spilotoceps</i> |
| 8 - <i>Chaetodon ephippium</i> | 25 - <i>Scarus chameleon</i> |
| 9 - <i>Chaetodon pelewensis</i> | 26 - <i>Scarus dimidiatus</i> |
| 10 - <i>Cheilinus chlorourus</i> | 27 - <i>Scarus globiceps</i> |
| 11 - <i>Chlorurus bleekeri</i> | 28 - <i>Scarus prasiognathos</i> |
| 12 - <i>Chlorurus spilurus</i> | 29 - <i>Stegastes albifasciatus</i> |
| 13 - <i>Choerodon anchorago</i> | 30 - <i>Stegastes nigricans</i> |
| 14 - <i>Chromis margaritifer</i> | 31 - <i>Stegastes punctatus</i> |
| 15 - <i>Chrysiptera taupou</i> | 32 - <i>Stethojulis bandanensis</i> |
| 16 - <i>Ctenochaetus striatus</i> | 33 - <i>Thalassoma hardwicke</i> |
| 17 - <i>Dascyllus aruanus</i> | 34 - <i>Zebrasoma scopas</i> |



Bali

- | | |
|---|---|
| 1 - <i>Acanthurus grammoptilus</i> | 35 - <i>Coris gaimard</i> |
| 2 - <i>Acanthurus lineatus</i> | 36 - <i>Ctenochaetus striatus</i> |
| 3 - <i>Acanthurus mata</i> | 37 - <i>Dascyllus trimaculatus</i> |
| 4 - <i>Acanthurus nigricans</i> | 38 - <i>Epibulus insidiator</i> |
| 5 - <i>Acanthurus nigricauda</i> | 39 - <i>Gomphosus varius</i> |
| 6 - <i>Acanthurus tristis</i> | 40 - <i>Halichoeres hortulanus</i> |
| 7 - <i>Amanses scopas</i> | 41 - <i>Halichoeres trimaculatus</i> |
| 8 - <i>Amphiprion melanopus</i> | 42 - <i>Hemigymnus fasciatus</i> |
| 9 - <i>Anampses melanurus</i> | 43 - <i>Hemigymnus melapterus</i> |
| 10 - <i>Apolemichthys trimaculatus</i> | 44 - <i>Heniochus varius</i> |
| 11 - <i>Balistapus undulatus</i> | 45 - <i>Labroides dimidiatus</i> |
| 12 - <i>Bodianus mesothorax</i> | 46 - <i>Neoglyphidodon melas</i> |
| 13 - <i>Cantherhines dumerilii</i> | 47 - <i>Parupeneus multifasciatus</i> |
| 14 - <i>Centropyge tibicen</i> | 48 - <i>Plectroglyphidodon dickii</i> |
| 15 - <i>Centropyge vrolikii</i> | 49 - <i>Plectroglyphidodon lacrymatus</i> |
| 16 - <i>Cephalopholis argus</i> | 50 - <i>Pomacentrus adelus</i> |
| 17 - <i>Cephalopholis cyanostigma</i> | 51 - <i>Pomacentrus amboinensis</i> |
| 18 - <i>Chaetodon kleinii</i> | 52 - <i>Pomacentrus auroventris</i> |
| 19 - <i>Chaetodon lineolatus</i> | 53 - <i>Pomacentrus bankanensis</i> |
| 20 - <i>Chaetodon melannotus</i> | 54 - <i>Pomacentrus burroughi</i> |
| 21 - <i>Chaetodon trifascialis</i> | 55 - <i>Pomacentrus coelestis</i> |
| 22 - <i>Chaetodon trifasciatus</i> | 56 - <i>Pomacentrus lepidogenys</i> |
| 23 - <i>Chaetodon ulietensis</i> | 57 - <i>Pomacentrus moluccensis</i> |
| 24 - <i>Chlorurus bleekeri</i> | 58 - <i>Pseudanthias dispar</i> |
| 25 - <i>Chlorurus capistroides</i> | 59 - <i>Pseudanthias huchtii</i> |
| 26 - <i>Chlorurus sordidus</i> | 60 - <i>Pteragogus enneacanthus</i> |
| 27 - <i>Chlorurus strongylocephalus</i> | 61 - <i>Scarus niger</i> |
| 28 - <i>Chromis atripes</i> | 62 - <i>Scarus oviceps</i> |
| 29 - <i>Chromis margaritifer</i> | 63 - <i>Scarus psittacus</i> |
| 30 - <i>Chromis opercularis</i> | 64 - <i>Stegastes nigricans</i> |
| 31 - <i>Chromis ternatensis</i> | 65 - <i>Thalassoma hardwicke</i> |
| 32 - <i>Chromis viridis</i> | 66 - <i>Thalassoma lunare</i> |
| 33 - <i>Chromis weberi</i> | 67 - <i>Zanclus cornutus</i> |
| 34 - <i>Cirrhilabrus exquisitus</i> | 68 - <i>Zembrasoma scopas</i> |

CONCLUSÃO GERAL

No presente estudo demonstramos que a diversidade de espécies em escala regional pode promover o estabelecimento de um grande número de espécies em comunidades locais de peixes recifais. O aumento da complexidade e heterogeneidade de hábitat, promovido pelo gradiente de riqueza de corais, pode ser um dos principais fatores locais responsáveis pela sustentação da grande variedade de espécies encontradas em escalas espaciais reduzidas. A variedade de recursos promovida pelo hábitat potencialmente explica os altos valores beta diversidade e acumulação de espécies em comunidades locais mais ricas regionalmente, porém não explica a fraca relação entre a riqueza regional e o reduzido número de espécies que disputam recursos semelhantes em pequenas escalas espaciais. No entanto, o restrito número de espécies que interagem agonisticamente em escala local e a similaridade na estrutura e composição taxonômica das redes agonísticas regionais sugerem que atributos intrínsecos das espécies, especialmente limite de distribuição e dieta, são os principais candidatos para explicar o padrão macroecológico da estrutura de interações agonísticas.

Portanto, as comunidades de peixes recifais são, de fato, fortemente influenciadas por processos de larga escala e regem sobre a estruturação das mesmas. Nosso estudo, porém, atingiu escalas espaciais capazes de detectar a influência de fatores locais sobre a distribuição e comportamento de espécies que competem diretamente por mesmos recursos. Por fim, o fato de comunidades locais suportarem um número de espécies proporcional à riqueza regional, mas uma pequena fração demonstrar comportamento agonístico, reforça a abordagem de questões sobre restrições energéticas e teorias ecológicas envolvendo partição de nicho nos ecossistemas capazes de suportar alta biodiversidade.