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PADRÕES GLOBAIS DE CO-OCORRÊNCIA E INTERAÇÕES AGONÍSTICAS EM DONZELINHAS (POMACENTRIDAE)

Santa Maria, RS
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Trabalho de Dissertação apresentado ao Programa de Pós-Graduação em Biodiversidade Animal, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para a obtenção do título de Mestre em Ciências Biológicas – Área Biodiversidade Animal.

Orientadora: Profª. Drª. Mariana Bender Gomes

Santa Maria, RS
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RESUMO

PADRÕES GLOBAIS DE CO-OCORRÊNCIA E INTERAÇÕES AGONÍSTICAS EM DONZELINHAS (POMACENTRIDAE)

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Os recifes de coral retêm a maior biodiversidade marinha e sustentam uma grande variedade de espécies de peixes que interagem de várias maneiras. As donzelas estão entre os peixes de recife mais conspícuos, e são notáveis por seu comportamento territorial e agressivo, o que muitas vezes leva à dominância de competidores e baixa probabilidade de coexistência entre espécies de donzelas. No entanto, o grau em que o comportamento territorial das donzelas influencia os padrões de co-ocorrência e interações agonísticas é desconhecido. Também não se sabe como as características biológicas e a distância filogenética estão relacionadas às interações agonísticas da família Pomacentridae e se essas características podem explicar melhor os padrões de distribuição das castanhetas. Elucidamos esses aspectos usando um conjunto de dados global de oito locais representando um gradiente de riqueza de espécies e parentesco filogenético entre peixes. Para entender os direcionadores das interações agonísticas utilizamos uma Análise de Caminho e para entender a estrutura da interação agonística e quais eram as espécies centrais em cada sítio. Nossos resultados mostraram que o principal fator de co-ocorrência de donzelinhas foi a distância filogenética (espécies mais distantes co-ocorrem com mais frequência) (P= 0.55), enquanto as interações agonísticas foram impulsionadas principalmente pela coocorrência de castanhetas (P = 0.74). Além disso, as donzelinhas do gênero *Stegastes* foram as espécies centrais na rede de interações agonísticas em seis dos oito sítios de nosso estudo, representando seu comportamento territorial e elevada frequência de interações. Nosso estudo ajuda a aprimorar nosso conhecimento sobre a relação entre co-ocorrência e interações agonísticas e compreender a estrutura de interações agonísticas da família Pomacentridae, somando-se ao que já se sabe sobre o papel dessas espécies no ecossistema recifal

Palavras-chave: Comportamento territorial. Interações ecológicas. Co-ocorrência. Distância filogenética.

ABSTRACT

GLOBAL PATTERNS OF CO-OCCURRENCE AND AGONISTIC INTERACTIONS IN DAMSELFISHES (POMACENTRIDAE)

AUTHOR: Rafaella Nunes Palma de Freitas

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Coral reefs retain the greatest marine biodiversity, and sustain a wide variety of fish species that interact in multiple ways. Damselfishes are amongst the most conspicuous reef fish, and are notable for their territorial and aggressive behavior, which often leads to competitor dominance and low coexistence probability between damselfish species. However, the degree to which the territorial behavior of damselfishes influences patterns of co-occurrence and agonistic interactions is unknown. It is also unknown how biological traits and phylogenetic distance are related to the agonistic interactions of the Pomacentridae family and if these traits can explain the distribution patterns of damselfishes better. We elucidate these aspects using a global dataset of eight sites representing a gradient of species richness and phylogenetic relatedness between fish. To understand the drivers of agonistic interactions we used a Path Analysis and to understand the agonistic interaction's structure and which were the central species in each site we used the out-degree centrality metric. Our results showed that the main driver of co-occurrence of damselfishes was the phylogenetic distance (most distant species co-occur more frequently) (P= 0.55), while the agonistic interactions were driven mainly by the co-occurrence of damselfishes (P= 0.74). Besides this, the damselfishes from the *Stegastes* genus were the central species in the agonistic interactions network in six of the eight sites of our study, representing their territorial behavior and elevated interactions frequency. Our study helps to improve our knowledge about the relationship between co-occurrence and agonistic interactions and to understand the structure of agonistic interactions of the Pomacentridae family, adding to what is already known about these species' role in the reef ecosystem.

Keywords: Territorial behavior. Ecological interactions. Co-occurrence. Phylogenetic distance

SUMÁRIO

INTRODUÇÃO

Os padrões de distribuição e a co-ocorrência entre espécies vem sido estudados há muito tempo e é considerado um tema desafiador na ecologia (Diamond e Gilpin 1982; Gaston 2000, Gotelli et al. 2010). A co-ocorrência de espécies é representada em padrões, cada padrão é uma maneira diferente de medir a frequência de duas ou mais espécies que co-ocorrem em uma estrutura espacial (MacKenzie et al. 2004; Horner-Devine et al. 2007). Sabe-se que alguns fatores estão influenciando os padrões de co-ocorrência, como a competição por recursos e atributos biológicos como dieta e abundância das espécies (Cavender-Bares et al. 2009; Kamilar and Ledogar 2011; Shukla et al. 2022; Vazquez et al. 2009). Além da co-ocorrência, o papel das interações intraespecíficas e interespecíficas (e.g. territorialidade) na estruturação das comunidades é bem documentado na escala local (Fontoura et al. 2020; Nunes et al. 2023; *unpublished article*). Estas interações acontecem ao longo de todos os grupos de animais e plantas nos ambientes terrestres e marinhos, existe uma grande gama de diferentes interações, como interações alimentares, agonísticas, de limpeza, polinização, parasitismo, entre outras (Bawa 1990; Caves 2021; Combes 2001). Entretanto, estudos macroecológicos, ou em ampla escala, sobre este tema ainda são escassos (Gotelli et al. 2010). Nos ecossistemas recifais, espécies de peixes são caracterizadas pelos mais diversos tipos de interações, como interações alimentares, de limpeza e agonísticas (Cantor et al. 2018; Inagaki et al; 2019; Quimbayo et al. 2017). O estudo da influência de atributos biológicos é necessário para desvendar como essas comunidades estão estruturadas através dos oceanos, e contribuir para o entendimento de como o comportamento das espécies rege o funcionamento do ambiente marinho.

Interações agonísticas estão entre os tipos de interação mais estudados em diversos grupos taxonômicos ao longo da árvore da vida, incluindo invertebrados, aves, mamíferos e peixes (Ayres-Peres et al. 2011; Bastian et al. 2008; Fowler-Finn et al. 2006; Labra et al. 2007; Senar et al. 1989). Estes estudos revelam que as interações agonísticas envolvem principalmente a competição por recursos ou reprodução, e que atributos como categoria trófica ou dieta podem levar espécies a interagir agonisticamente, uma vez que isto implica na competição por recursos (Fontoura et al. 2020). Muitas vezes, atributos biológicos - como categoria trófica, tamanho corporal e coloração - são conservados filogeneticamente (Cavender-Bares et al. 2009), e espécies mais próximas filogeneticamente tendem a apresentar atributos biológicos similares entre si (Floeter et al. 2018). Dessa forma, espécies aparentadas possuem maior probabilidade de interagir em disputas por recursos como alimento, parceiro(a) e território (Floeter et al. 2018). Enquanto estudos na escala local revelam que interações agonísticas são moldadas por fatores relacionados à competição por recursos ou reprodução, estudos na escala regional podem demonstrar como estas interações são moldadas por fatores que variam em ampla escala, como gradientes de riqueza e de temperatura (Fontoura et al. 2020; Gerber et al. 2008; Thorp 1978).

Nos ecossistemas recifais, as donzelas territoriais da família Pomacentridae são um ótimo modelo para o estudo de interações agonísticas, uma vez que são, em sua maioria, espécies herbívoras e mantêm territórios onde cultivam uma “fazenda” de algas para consumo próprio (Lobel 1980). Estes territórios são defendidos através de um comportamento agressivo, conhecido como comportamento agonístico (Draud e

Itzkowitz. 1995, Robertson. 1984) Estudos revelam a importância destas espécies na estruturação e resiliência dos ecossistemas recifais, ao consumir, “cultivar” e “selecionar” algas de sua preferência em seus territórios, as donzelinhas contribuem para a transferência de energia e nutrientes no sistema recifal (Klumpp et al. 1987). Além disso, ao defender seu território, incrementam a quantidade de algas e micro invertebrados na escala do habitat (Hixon e Brostoff 1983). Dessa forma, as espécies de donzelinhas são consideradas chave na composição de espécies e estrutura dos recifes (Ferreira et al. 1998). O comportamento territorial e a sobreposição na utilização de recursos por espécies herbívoro-territoriais permitem inferir que a tolerância à co-ocorrência com outras espécies de donzelas territoriais deve ser limitada (Medeiros et al. 2010). Ainda, é possível que haja uma tendência para que espécies territoriais co-ocorram apenas (ou mais frequentemente) com espécies não-territoriais, para que não haja constante conflito entre as espécies (Gaboriau et al. 2018). Todavia, quando espécies territoriais co-ocorrem, é provável que uma espécie seja dominante em relação à outra (Waldner e Robertson 1980). Outra possibilidade é de que a ocorrência com outras donzelas territoriais resulte em a maiores frequências de interações agonísticas (Hourigan 1986). Apesar de estudos recentes revelarem os padrões de interações agonísticas entre peixes recifais, ao longo de um amplo gradiente de riqueza de espécies (Fontoura et al. 2020), a influência da co-ocorrência sobre as interações agonísticas entre espécies ainda é desconhecida, sobretudo em comunidades sujeitas a diferentes *pools* de riqueza regional de espécies.

O funcionamento e a estruturação dos ecossistemas recifais depende das interações entre espécies, como interações peixe-bentos (Tebbett et al. 2020). Por serem consideradas espécies-chave, as donzelas são essenciais para a estruturação do ecossistema recifal (Klumpp et al. 1987, Fontoura et al. 2020). Entretanto, a influência do parentesco, do comportamento (territorialidade) e de atributos biológicos (como dieta e posição na coluna d'água) nos padrões de co-ocorrência de espécies da família Pomacentridae ainda é desconhecida. Além disso, não existem informações a respeito da relação entre a co-ocorrência e as interações entre indivíduos de mesma espécie ou espécies diferentes, e se os padrões de associação entre co-ocorrência e interações se mantêm ao longo de um gradiente de riqueza de espécies. Neste contexto, nosso objetivo principal foi investigar os principais fatores associados à co-ocorrência e interações agonísticas entre espécies da família Pomacentridae (donzelas) ao longo de um gradiente de riqueza, desvendando a influência de atributos biológicos, atributos comportamentais e grau de parentesco (sobre ocorrências e interações). Buscamos responder: a co-ocorrência necessariamente resulta na interação entre pares de espécies? Fatores como relação filogenética, tipo de comportamento territorial, dieta e abundância local influenciam a co-ocorrência ou as interações entre pares de espécies? Esperamos que a co-ocorrência e interações agonísticas entre espécies possam ser moldadas por estes fatores de formas alternativas: (a) comportamento territorial: neste cenário, pares de espécies territoriais co-ocorrem em menor frequência, mas quando co-ocorrem, interagem mais frequentemente do que pares de donzelas não-territoriais; (b) atributos biológicos: sob este cenário, espécies com características semelhantes, como dieta, tamanho corporal e profundidade habitada, co-ocorrem em menor frequência para evitar a competição local e sobreposição espacial, e, por outro lado, interagem com maior frequência por terem que competir pelos mesmos recursos, como espaço e alimentos; (c) relação filogenética: espécies mais próximas filogeneticamente tendem a não co-ocorrer, a, como forma de evitar a competição; entretanto, em co-ocorrência, estas espécies interagem agonisticamente; (d) *feedbacks* entre co-ocorrência e interações: co-ocorrência e interações agonísticas entre pares de espécies são correlacionadas, sendo que a co-ocorrência nos recifes permite a presença interações, da mesma forma, é possível que as interações estruturem a distribuição e co-ocorrência de indivíduos no espaço.

Estrutura da Dissertação

Esta dissertação está estruturada em formato *Research Article*, conforme as normas da revista *Marine Biology.*

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Co-occurrence and agonistic interactions patterns in the Pomacentridae family across the world's oceans

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Abstract

Coral reefs retain the greatest marine biodiversity, and sustain a wide variety of fish species that interact in multiple ways. Damselfishes are amongst the most conspicuous reef fish, and are notable for their territorial and aggressive behavior, which often leads to competitor dominance and low coexistence probability between damselfish species. However, the degree to which the territorial behavior of damselfishes influences patterns of co-occurrence and agonistic interactions is unknown. It is also unknown how biological traits and phylogenetic distance are related to the agonistic interactions of the Pomacentridae family and if these traits can explain the distribution patterns of damselfishes better. We elucidate these aspects using a global dataset of eight sites representing a gradient of species richness and phylogenetic relatedness between fish. To understand the drivers of agonistic interactions we used a Path Analysis with a few possible predictor variables, such as: co-occurrence, species traits, phylogenetic distance, territorial behavior, abundance and local richness. To understand the agonistic interaction's structure and which were the central species in each site we used the out-degree centrality metric. Our results showed that the main driver of co-occurrence of damselfishes was the phylogenetic distance (most distant species co-occur more frequently) (PC= 0.55), while the agonistic interactions were driven mainly by the co-occurrence of damselfishes (PC= 0.74). Besides this, the damselfishes from the *Stegastes* genus were the central species in the agonistic interactions network in six of the eight sites of our study, representing their territorial behavior and elevated interactions frequency. Our study shows that agonistic interactions instead of exploitative competition, is the main driver of species co-occurrence

Keywords: Territorial behavior. Ecological interactions. Co-occurrence. Phylogenetic distance

Introduction

Understanding species occurrence and how it happens is a major interest in ecology and biogeography (Diamond & Gilpin 1982; Gaston 2000; Wiens & Donoghue 2004). Species co-occurrence can be used to measure the frequency of two or more species that co-occur among a spatial structure and how this happens (MacKenzie et al. 2004; Horner-Devine et al. 2007). Co-occurrence has been studied for a long time in ecology across scales (Diamond and Gilpin 1982). It is known that a few factors are driving the co-occurrence patterns to happen (Hartman et al. 2014). At the local scale, competition is known to have an effect in the co-occurrence, being caused by phylogenetic relatedness where competition might be stronger between related species (Darwin 1859) and richness where limited resources must be effectively shared among species in species-rich sites to avoid competitive exclusion (Kohli et al. 2018). Species biological traits are usually a proxy for competition shaping co-occurrence, since species with similar traits are participating in the same niche and sharing the same resources (Cavender-Bares et al. 2009). Diet is one of the main traits that is responsible to appoint the species distribution and community structuring (Kamilar and Ledogar 2011; Shukla et al. 2022). Additionally, since phylogenetically related species tend to share similar traits, relatedness could influence species co-occurrence patterns with species that are phylogenetically distant occurring more frequently than closely related ones (Winston. 1995). Adding to this view, there is the competitive exclusion principle, that states that two species with identical niches could not coexist, MacArthur and Lewis (1967) postulated the theory of limiting similarity, where it posits that there is a maximum level of similarity between competing species that will allow these species to coexist. Along with this previous theory, it is known that sister species that are sympatric will tend to co-occur less to minimize the likelihood of competitive exclusion (Brown and Wilson 1956; Darwin 1927; Slatkin 1980). Abundance is also known to influence species co-occurrence by affecting the strength of interactions (Vazquez et al. 2009). Besides this density-dependent relation, local richness can vary along a latitudinal gradient, i.e the tropical regions have a higher diversity of terrestrial and marine species, co-occurrence of species has a very close relationship with local richness, since localities or regions with more species (higher richness) influence the probability of species to co-occur (Prinzing et al. 2016). Co-occurrence of species make interactions possible, there is a wide range of interactions that can happen between individuals including trophic and agonistic interactions (Ayres-Peres et al. 2011; Fortin et al. 2005).

Agonistic interactions are a common type of interaction and represent the aggressive or dispute behavior that occurs between individuals that may be defending territories or partners (Scott and Fredericson 1951). These interactions can happen between individuals of the same or different species, the role of intraspecific and interspecific interactions in structuring communities is well documented at the local scale, but studies are still scarce at the global scale (Gotelli et al. 2010). At local and regional scales, studies have demonstrated how agonistic interactions occur across the Tree of Life. Agonistic interactions have been documented for groups of invertebrates, birds, lizards, mammals, fishes (Ayres-Peres et al. 2011; Bastian et al. 2008; Fowler-Finn et al. 2006; Labra et al. 2007; Radesäter et al. 1979; Senar et al. 1989). These studies reveal that these interactions mostly involve competition for either resource or reproduction. For instance, three groups of primates interact agonistically during the mating process with different aggression intensities (Thierry 1985). Besides competition associated with mating, agonistic interactions can also be influenced by local resource availability (Dyer and Rice. 1999; Neumann et al. 2022), demonstrating this, three scavenging bird species were studied and showed eleven types of agonistic interactions while competing for the organic waste in Ghana (Annorbah et al. 2012). Agonistic interactions can be driven by species biological traits, such as diet, since this leads to resource and territorial dispute, in some cases, these biological traits are conserved phylogenetically, meaning that phylogenetically close species that tend to have more similar traits can interact more frequently based in the dispute of territory and resource (Cavender-Bares et al. 2009; Dri et al. 2022). While local scale studies show that agonistic interactions are driven by factors related to competition of resource and reproduction, regional scale studies could demonstrate how these interactions are driven by different factors that are related to a different and wider scale, such as richness and temperature in a latitude and longitude gradient (Fontoura et al. 2020; Gerber et al. 2008; Thorp 1978).

Recently, Fontoura et al. (2020) showed that the structure of agonistic interactions in reef fishes varies along the richness gradient, presenting in richer places, a resource partitioning between species. When, in poorer places, there are few dominant species, which interact more frequently, presenting a hierarchical structure. Damselfishes (Pomacentridae family) are a good model to study agonistic interactions in coral reefs, since they are known for the territorial behavior (Hixon 1980; Menegatti et al. 2003). These species cultivate their own algae “farm” and are very eager to defend their territory, “chasing” the intruders away from their home (Hata and Ceccarelli 2016; Lobel 1980). This territorial behavior varies among species in its level of aggressiveness, being divided in three categories: intensive, intermediate and extensive (Hata and Kato. 2004; Emslie et al. 2012). While intensive damselfishes are more aggressive, the extensive damselfishes are less aggressive, this usually depends on the size of home-range these species have (Ceccarelli et al. 2001). As a consequence, the damselfishes are usually the first to interact agonistically in a reef, being central in agonistic interaction’s networks (Canterle et al. 2020; Fontoura et al. 2020). During the evolution of the family, the species converged into three different trophic groups: herbivores, planktivores and omnivores (McCord et al. 2021; Frederic et al. 2016). The different diets in the family allow the species to have a totally different niche, while the herbivore species are associated with benthos and have a small home-range where they are constantly defending their territory through agonistic interactions intra and interspecifically, the planktivores species inhabit the water column and are not territorial, having a bigger home-range and mobility. The evolution of the family is also related to the distribution in the macroecological scale, the species that inhabit the Indo-Pacific region are usually planktivores. According to Siqueira et al. (2021) ecological, evolutionary and geological drivers led to a high richness of planktivorous reef fish species in the Indo-Australian Archipelago (IAA). Among these drivers, the ecological niche allows these species to inhabit only the part in the water column where its resource is (Siqueira et al. 2020).

The relationship between co-occurrence and species interactions is still a matter of debate (Gao et al. 2022; Zhang et al. 2022). Peres-Neto (2004) showed that despite competitive interactions, freshwater fish species still co-occur in eastern Brazil, and recently the direct inference of species interactions from co-occurrence has been questioned (Blanchet et al. 2020). For example, environmental conditions influencing the distribution of two species could cause a co-occurrence signal that could be misinterpreted as ecological interactions (Blanchet et al. 2020). Yet it is still possible that co-occurring species interact, as it is the case of co-occurring territorial damselfishes, where there is dominance and hierarchy of species over the other (Waldner and Robertson, 1980). Thus, when they co-occur, due to their territorial behavior, damselfish species interact agonistically in an interspecific and intraspecific way (Draud and Itzkowitz. 1995, Robertson. 1984), causing a high frequency of agonistic interactions (Hourigan, 1986). When species with the same resource niche are co-occurring in a limited space, the species have a habitat partitioning system, especially the territorial ones, having a hierarchy (Fontoura et al. 2020). This niche partitioning has been shown to structure the ecological interactions networks in marine ecosystems, especially in species-rich communities (Galingo et al. 2021; Waldner and Robertson. 1980).

The functioning and structuring of reef ecosystems depend on species interactions (Tebbett et al. 2020). As they are considered key species, damsels are essential in reef ecosystem structuring (Klumpp et al. 1987; Fontoura et al. 2020). However, the influence of phylogenetic relatedness, behavioral (territoriality) and biological attributes on co-occurrence patterns of Pomacentridae species is still unknown, especially at a macroecological scale. Furthermore, there is limited information on the relationship between species co-occurrences and interaction patterns (but see Fontoura et al. 2020), and on whether patterns hold along gradients of species richness. Thus, our major aim was to investigate the major drivers of damselfish co-occurrence and agonistic interactions patterns along a species richness gradient, disentangling the relative roles of biological and behavioral traits, phylogenetic relatedness and agonistic interaction frequency. We expect that co-occurrence and agonistic interactions patterns could be driven by a few alternate variables, these being: (a) territorial behavior, in this scenario, pairs of territorial species would co-occur less frequently, but when co-occurring would interact more frequently than pairs of non-territorial damselfishes. (b) co-occurrence and agonistic interactions are correlated, having the co-occurrence driven the interactions, this scenario is intertwined with the last one, where when species co-occur that would suggest that they would interact more frequently, independently of the type of behavior. (c) biological traits, species with similar traits such as diet, size and depth will co-occur more frequently by having the same limited niche and would also interact more frequently by having to compete for the same resources, such as territory and food, this scenario lead us to the last alternative hypothesis that is correlated to this one. (d) phylogenetically close species would not co-occur frequently avoiding the competition, but when the co-occurrence happens, that would lead to agonistic interactions.

Materials and methods

Study area and data sampling

Fish community data used in this study corresponds to an extensive database of videoplots (see below) sampled across the world's oceans (Fontoura et al. 2020; Canterle et al. 2020) (Fig. 1). Data was obtained at eight reef sites distributed along a broad longitudinal gradient (34,000 km long), four of these sites are located at the Western Atlantic Ocean (two in Brazil: Abrolhos Archipelago and Rocas Atoll, and two in the Caribbean Sea: Curaçao Island and Yucatán in Mexico), one site in the Eastern Atlantic Ocean (Príncipe Island) and three sites in the Indo-Pacific Ocean (Bali, Fiji and Moorea).

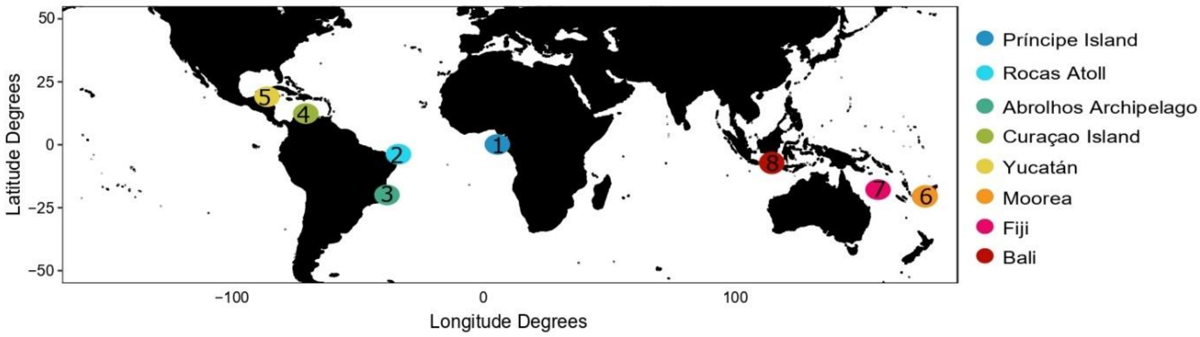

Figure 1. Map of studied reef sites organized along a species richness gradient, from Príncipe Island to Bali. Local species richness corresponds to Rocas Atoll, Abrolhos Archipelago, Príncipe Island, Curaçao Island, Yucatan Peninsula, Moorea, Fiji and Bali.

Fish were sampled using the remote underwater video (RUV) methodology, which consists of the use of cameras to record videos for spatial and behavioral monitoring of determined habitats, an alternative to the traditional Underwater Visual Census (UVC) technique (Mallet and Pelletier 2014). This approach avoids biases imposed by the divers' presence, and makes it possible to sample complex fish behaviors as agonistic and feeding interactions (Longo and Floeter 2012). In each location, we deployed 50 RUVs, with the exception of Príncipe Island where only 46 were sampled (Longo et al. 2014; Fontoura et al. 2020). Videos were sampled between 2 and 10 m depth. Each video frame had on average 17 minutes long, during which the camera (GoPro) focused on a 2x2 m area, delimited by the diver at the beginning of each video. Only the 10 central minutes of each video were analyzed to avoid the diver's influence in the first and final minutes of the video. For each underwater remote video, we recorded the total local species richness, co-occurrence, agonistic interactions and maximum abundance (MaxN) of fish species of the Pomacentridae family. Local species richness was simply the total number of species registered in each video during the delimited time and area. A fish co-occurrence was counted when two species were seen in the same video during the delimited time (10 minutes) and area (2m2) (Fontoura et al, 2020; Canterle et al, 2020). An agonistic interaction, the representation of fish territorial behavior, was counted every time a fish was observed chasing another fish individual, with no intention of predation (Canterle et al. 2020; Fontoura et al. 2020). The MaxN (maximum abundance) was measured counting the maximum number of individuals from each species at the same moment (single frame) of the video inside the delimited area (Canterle et al, 2020). For each sampling unit (2m2/10 minutes video recordings), we summed the co-occurrences between pairs of fish individuals, considering both interspecific and intraspecific interactions, as well as the agonistic interactions between individuals.

Biological and behavioral data for Pomacentridae species was either compiled from the literature or obtained from available databases. Territorial behavior classification for each species follows Cecarelli et al. (2001), which identified damselfishes as territorial or non-territorial. The territorial behavior represents the protection of a determined area, the reason damselfishes protect an area can be related to competition and/or reproduction, for example, herbivorous damselfishes from the genus *Stegastes* protect their 'farm' from possible intruder, other damselfishes such as the males from the *Microspathodon* genus guard the spawn eggs, in both cases, the territorial behavior is demonstrated by an agonistic interaction (Cecarelli et al. 2001). Thus, the interaction and co-occurrence behavioral groups were classified based on pairs of species combinations: (i) territorial-territorial: when both co-occurring or interacting species present territorial behavior, (ii) territorial-non territorial: when only one species of the co-occurring or interacting pair presents a territorial behavior and (iii) non territorial-non territorial: when both co-occurring or interacting species are not territorial. Biological traits data describe other relevant characteristics of damselfish species, and include reef association, size, mobility, activity, schooling, position in the water column and diet. This database was collected in the GASPAR Project (General Approach to Species-Abundance Relationships) and available in Mouillot et al. (2014). Fish were distribute into the trait categories the: (1) Reef association: either associated or not to reefs (i.e., stable substrates); (2) Size: 0–7 cm, 7.1–15 cm, 15.1–30 cm, 30.1–50 cm,50.1–80 cm, and>80 cm; (3) Mobility: sedentary (including territorial species), mobile within a reef, and mobile between reefs; (4) Period of activity: diurnal, both diurnal and nocturnal, and nocturnal; (5) Schooling: solitary, pairing, or living in small (3–20 individuals), medium (20–50 individuals), or large (>50 individuals) groups; (6) Vertical position in the water column: benthic, bentho-pelagic, and pelagic; and (7) Diet: herbivorous-detritivorous, macroalgal herbivorous, invertivorous targeting sessile invertebrates, invertivorous targeting mobile invertebrate, planktivorous, piscivorous and omnivorous. Finally, we used the most updated phylogeny of damselfishes (McCord et al. 2021) from which we calculated the phylogenetic distance between co-occurring and interacting Pomacentridae species. Our fish community database from video samples comprises 68 out of 345 Pomacentridae species in the phylogeny (McCord et al. 2021). The pairwise phylogenetic distance based on branch lengths connecting 68 damselfish species was extracted using the 'phylogenetic.phylo' function from the Ape package in R, where it calculates the pairwise distances using phylogeny branch lengths connecting species (Paradis E and Schliep K. 2019).

Network approaches

We used complex network graphs and metrics to describe patterns of co-occurrence and interactions among pairs of damselfish species along the richness gradient. Co-occurrence and agonistic interaction networks were represented in graphs where nodes represent pairs of co-occurring or interacting species, and links denote either their co-occurrence within the same videoplot, or, their agonistic interactions, also registered in videoplots. For agonistic interaction networks we measured the out-degree centrality metric, which represents the propensity of each species in the network to interact with other species (Ghosh & Lerman. 2011). The out-degree metric is based on the number of species that each species was registered interacting with, and higher values represent that the species has greater centrality and importance in the network. Out-degree values were obtained using the 'centr_degree' function from the Bipartite package (Dormann et al. 2008), and species' centrality value was represented in its node size; the larger the node, the greater its centrality in agonistic interaction networks. The agonistic interactions networks were direct, indicating which species initiated the interactions, this is represented in the network by an arrow. To plot both types of networks we used the 'graph_from_data_frame' function from the Igraph package (Csardi, 2006), with the number of interactions and co-occurrences represented by line thickness connecting nodes. A third network with the proportion of agonistic interactions relative to the total number of co-occurrences between pairs of species is available in Supplemental Material (Fig S2).

Ecological models

To test the null hypothesis, we used the C- score index (Stone and Roberts. 1990) and observed non-random patterns of reef fish species co-occurrence based on a matrix of presence and absence in the eight sites of our study by randomizing with 1,000 randomizations (Gotelli, 2000). The C - score quantifies the mean number of checkerboard units that can be produced for each pair of species, with the randomization, the result is the observed C - score to the average C - score generated by randomization. For this analysis, we used the function 'cooc_null_model' in the EcoSimR package (Gotelli et al. 2015) with the sim4 algorithm, this algorithm preserves differences among species in occurrence frequencies, but assumes differences among sites in suitability are proportional to observed species richness, which is important since we are working with a richness gradient macroecological scale. Also, sim4 is one of the three algorithms that have low probability of type I errors (Gotelli, 2000). In this analysis, if the C - score is larger than the average C - score produced from null distribution ($p < 0.05$), it means that there is a non-random pairwise species co-occurrence pattern that was not expected by chance, representing that there are no co-occurrence patterns between the damselfish's species, suggesting spatial segregation.

To identify the main drivers of agonistic interactions between damselfish we used a Linear regression. In this case, we regressed the observed number of agonistic interactions between each pair of species across all video-plots with five different variables: i) co-occurrence (the sum of the co-occurrences between each pair of damselfish species); ii) phylogenetic distance (phylogenetic distance between each interacting pair of species); iv) MaxN (mean maximum abundance for each interacting pair of species); and v) local richness (number of species from the Pomacentridae family registered in the video-plots for each site). The data for Linear regressions was organized in a single dataframe, containing pairs of interacting damselfish species across the eight reef sites as rows, and the predictor variables for each pair of species occurring in each site as columns, accordingly: behavior (1: when only one of the species was territorial and 2: when both species of the pair were territorial), mean maximum abundance for the interacting pair, number of realized agonistic interactions between each pair, number of co-occurrences, total damselfish richness for each site, phylogenetic distance between the pair of species and diet (sum of the categories in which the species fit in: 1 for herbivore, 2 for omnivore and 3 for planktivore). The Linear regressions were performed using the 'lm' function from the Stats R package (R Core Team. 2013). The assumptions of this model are four: the behavior of a dependent variable is explained by a linear, or curvilinear relationship between the dependent variable and the independent variables; the relationship between the dependent variable and any independent variable is linear or curvilinear; the independent variables do no depend on each other too; the errors are independent, normally distributed with mean zero and a constant variance.

To assess the relationship between co-occurrence and agonistic interactions, and help determine who are the direct or indirect drivers of both, we implemented a Path Analysis. In this model we measured the relative influence of species co-occurrence (co-occurrences for each pair across all videos), their phylogenetic and trait distances, their behavior, local abundances (MaxN) and local richness of damselfishes on the number of agonistic interactions between pairs of species across videoplots. We then contrasted this complete model with a simplified model in which co-occurrence was the response variable and the territorial behavior of damselfish species and their phylogenetic distance were predictor variables. We implemented this model using the 'cfa' function and plotted results using the 'semPaths' function from the Lavaan package (Rosseel 2012). All analyses were conducted using the R Studio software (RStudio Team. 2022).

Results

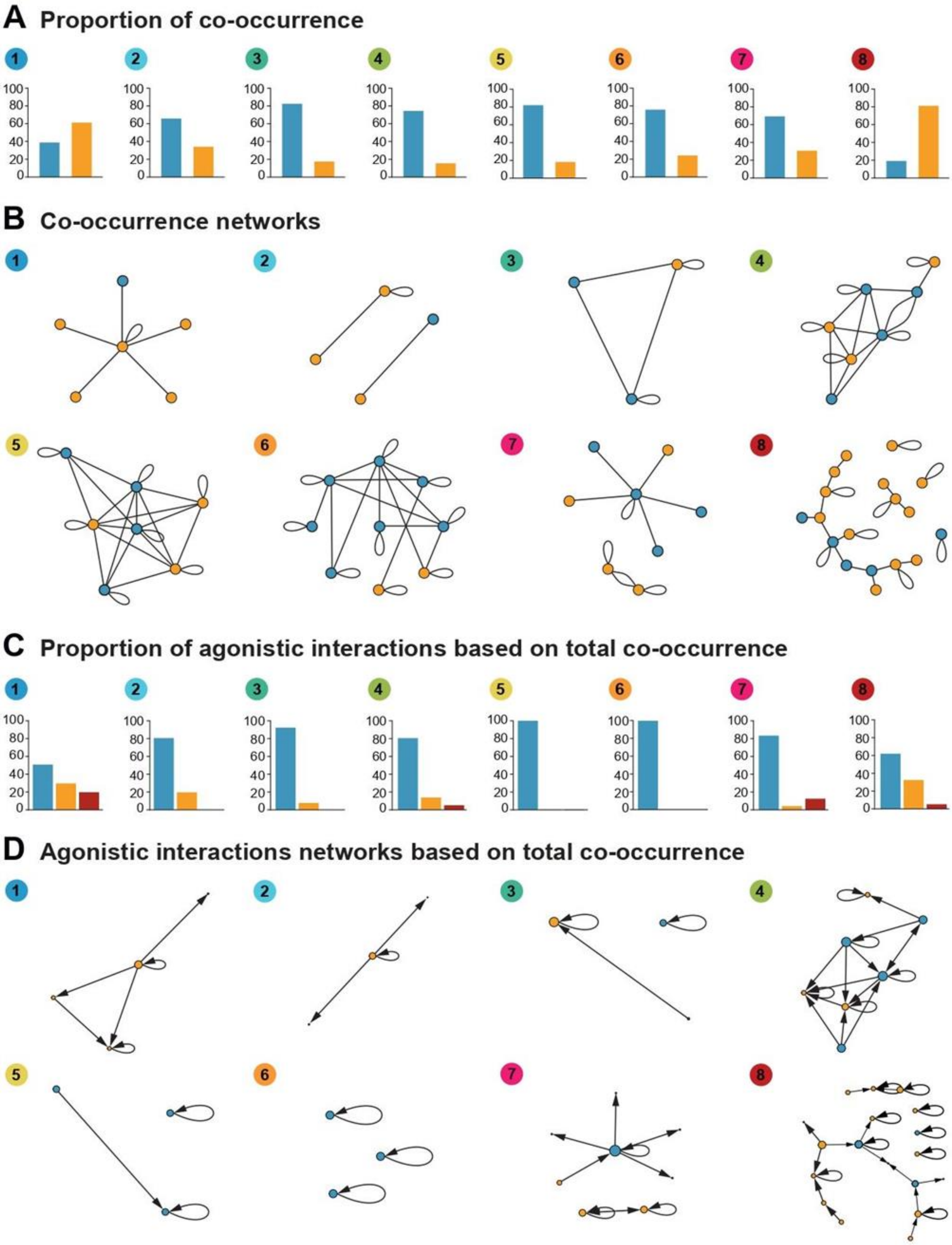

Figure 2.The proportion of co-occurrences between territorial (blue) and non-territorial (yellow) pairs of damselfish species (A) and co-occurrence networks where nodes represent pairs of co-occurring territorial (blue) and non-territorial (yellow) species. In (C), the proportion of agonistic interactions between territorial (blue) and non-territorial (yellow) and territorial-non-territorial (red) pairs of damselfish species, based in the total co-occurrence of pairs of damselfish species, between territorial (blue) and non-territorial (red) and territorial-non-

territorial (yellow) pairs of damselfish species. In (D) agonistic interactions networks with out-degree centrality metric, where node size denotes species' centrality in each network. Study sites are organised in an ascending order by local species richness: Príncipe Island, Rocas Atoll, Abrolhos Archipelago, Cruaçao Island, Yucatán Peninsula, Moorea, Fiji and Bali.

In total, 68 Pomacentridae species were registered in videoplots across the eight studied reef sites: The proportion of co-occurrences (Fig. 2A, 2B) was greater among territorial species in six out of the eight reef sites being greater for non-territorial species only in Bali and Príncipe Island. In these sites, the co-occurrences reached 81.1% and 61.2%, respectively. When considering the number of agonistic interactions relative to the total co-occurrence of fish pairs in each behavioral group (territorials, non-territorials and territorial-non-territorial), the greater proportions of agonistic interactions were performed by pairs of territorial species (Fig. 2C). The null model presented a low C – score index of 1.15, since the higher the C-score, the less co-occurrence between all of the species' pairs in the matrix and the result was close to 0, it means that the matrix of species is more segregated than aggregated. Also, the P-value ($P<0.001$) indicates that the co-occurrence pattern found is non-random (Fig. S2).

The out-degree centrality is representing the number of interactions that were realized by the species. In half of the interacting networks territorial damselfishes had the highest centrality values. In Bali and Rocas Atoll, non-territorial species were the ones starting most of the agonistic interactions, therefore being central (Fig. 2D). Species from the *Stegastes* genus represented the majority of agonistic interactions, the greater number of agonistic interactions along the eight sites were made by *Stegastes rocasensis*, an endemic of Rocas Atoll, where a total of 43 (75% of the total site interactions) interactions were registered. Another Brazilian endemic species, *Stegastes fuscus* performed a 76% of the agonistic interactions at Abrolhos Archipelago. In two sites of the Indo-Pacific region, Fiji and Moorea Island, the species *Stegastes nigricans* was responsible for 62% and 50%, respectively.

Different from what was expected, local richness did not have a positive nor significant influence in the number of damselfish agonistic interactions (Fig. 3A). Also, there was no relationship between species' maximum abundance and the number of agonistic interactions in video-plots (Fig 3B). In contrast, both the phylogenetic distance among pairs of individuals, and the co-occurrence of damselfishes influenced the number of agonistic interactions (Fig. 3C, D).

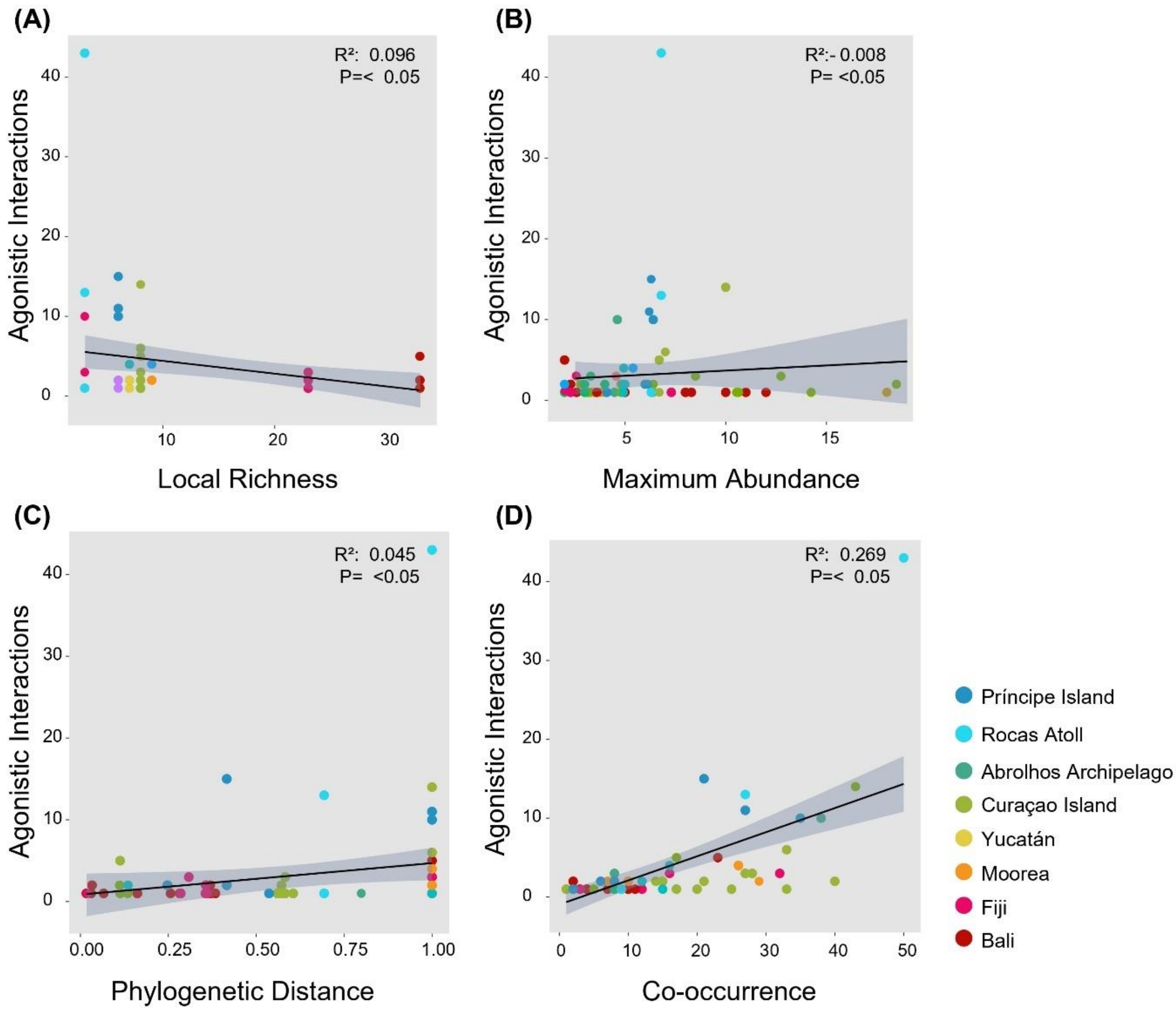

Figure 3. Linear regressions of damselfish agonistic interactions and: (a) site total damselfish richness; (b) maximum abundance of interacting species; (c) Phylogenetic distance between pairs of interacting species and (d) co-occurrence. Circles are color-coded to represent pairs of interacting damselfish species across 8 reef sites.

Path analysis models revealed that the co-occurrence of pairs of damselfish individuals is positively influenced by their phylogenetic distance (PC = 0.55) while agonistic interactions were positively influenced by the co-occurrence of damselfishes (PC = 0.74). Therefore, the phylogenetic distance among pairs of interacting individuals is indirectly influencing agonistic interactions by first driving their co-occurrence. In addition to the phylogenetic distance, the type of territorial behavior of damselfishes is also driving their co-occurrence (PC = 0.18). Also, the territorial behavior is directly influencing the agonistic interactions of damselfishes, but there is a weak relationship between both variables (PC = 0.07). Other tested variables, such as local richness (PC = 0.03) and maximum abundance (PC = -0.13) did not influence agonistic interactions.

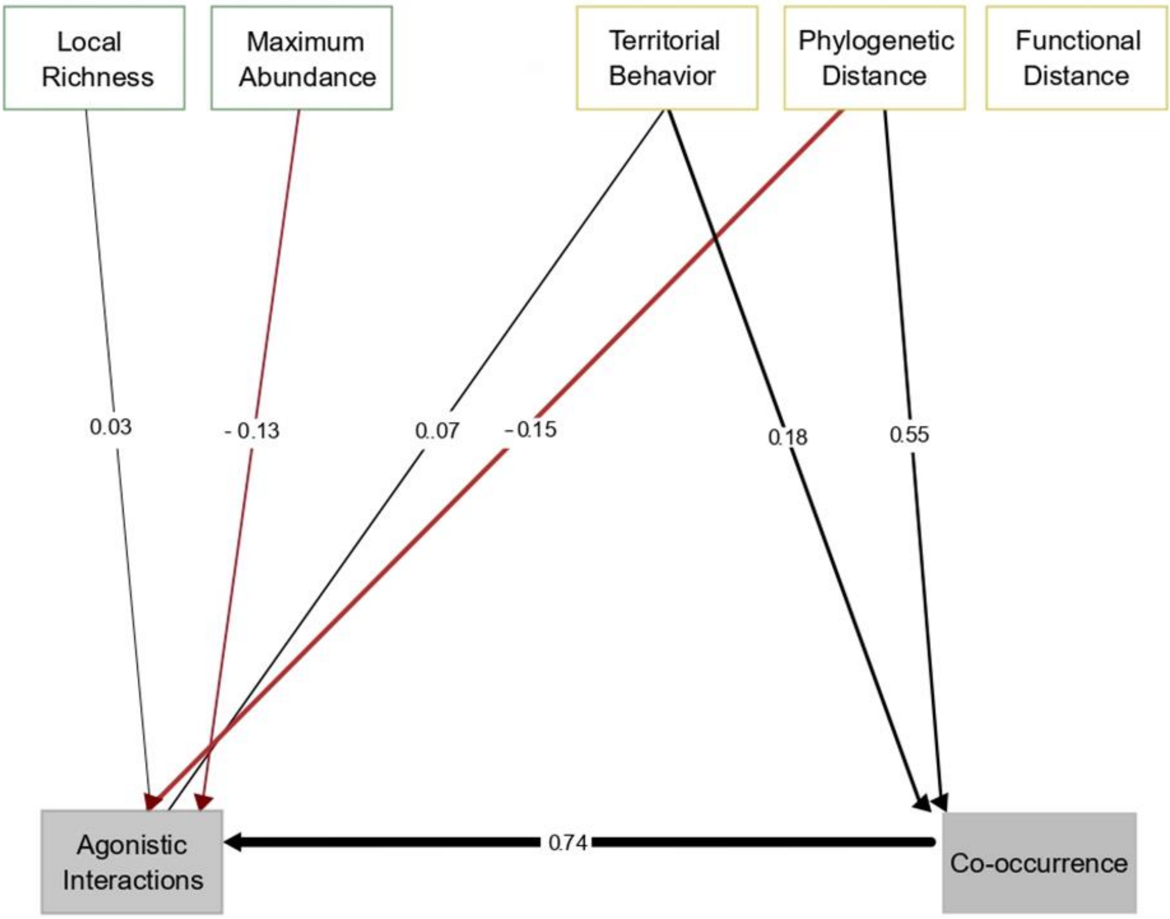

Figure 4. The drivers of agonistic interactions in reef damselfishes. Predictor variables of path analysis included the co-occurrence among damselfish individuals, their territorial behavior, maximum abundance, phylogenetic distance, local richness and functional distance. Line shading and thickness denote the strength of the standardized path coefficients, which are also shown. Line colors represent positive (black) or negative (red) relationships among pairs of variables.

Discussion

Our study revealed that territorial behavior did not influence damselfish co-occurrence across the species richness gradient. Nevertheless, damselfish territorial behavior influenced their agonistic interactions, with territorial species being central in agonistic interaction networks. While the phylogenetic distance of damselfishes positively influenced their co-occurrence, making the most distant species co-occur more frequently, it is fish co-occurrence that allows agonistic interactions in reef ecosystems, according to the Path analysis and Linear model performed. Our study is one of the few in macroecological scale to explore co-occurrence patterns along a species richness gradient, and its relationship with local scale interactions among individuals. It also considers the influence of different community parameters (species richness and local abundances) and species traits (biological traits, phylogenetic distance and territorial behavior) in such co-occurrence and interaction patterns. The damselfishes from the Pomacentridae family are the models of our study, these species, among other reef fish families, are fundamental to agonistic interactions taking place in reefs (Fontoura et al. 2020). Our findings reinforce the importance of damselfish species to agonistic interactions, and reveal that, in this case, co-occurrence is a suitable proxy of species interactions.

Our study revealed that pairs of territorial damselfish co-occur more frequently when compared to non-territorial pairs. Bali was an exception for this pattern, located in the Central Indo-Pacific region, the archipelago is known for its astonishing reef fish richness and abundance, being considered a marine hotspot (Bellwood et al. 2012; Bowen et al. 2013; Hughes et al. 2002; Roberts et al. 2002; Kulbicki et al. 2013). In Balinese reefs, non-territorial species co-occur more frequently than territorial pairs of individuals, this is possibly related to the high reef fish richness (~900 species) found in this region, which renders the occurrence of non-territorial species more frequent than that of poorer sites (Allen and Erdmann 2013). This is intertwined with another probable factor driving the co-occurrence of non-territorial damselfishes in Bali, i.e., fish position in the water column, since the majority of fish species inhabiting this region are pelagic or bentho-pelagic planktivores, and they are also the most abundant (Morais et al. 2021). In Príncipe Island, the other exception for this pattern, the frequent co-occurrence of non-territorial pairs of damselfishes is possibly explained by the very low species richness in local reefs (Floeter et al. 2008; Hachich et al. 2015), which limits the co-occurrence of species with other behavioral types. Since species such as territorial herbivore damselfishes are site-attached species, habitat specialization and its consequential competition are factors aligned to their patterns of distribution and co-occurrence (Chaves et al. 2012).

In plant-animal mutualistic networks, co-occurrence is predicted by species' trait-matching and neutral processes, where species' local abundances influence co-occurrence patterns by chance (Vazquez et al. 2009). In our study, the abundance of Pomacentridae species in video-plots was not related to their co-occurrence. This was also observed for the Chaetodontidae family in a global-scale study using underwater visual census data for 23 different reef localities (Nunes et al. 2020). The species co-occurrence patterns not resulting from a density-dependent process may be related to the influence of other factors that are driving the co-occurrence of damselfishes, such as phylogenetic distance (Gajdzik, 2016). While phylogenetic distance did not influence the co-occurrence of butterflyfishes (Nunes et al. 2020), it did influence the co-occurrence of damselfishes, this pattern where phylogenetically distant species co-occur more frequently was already observed in innumerous studies (Krasnov et al. 2014). Apparently, the phylogenetic distance among Pomacentridae species indirectly influences agonistic interactions by driving species co-occurrence in reef ecosystems. Species phylogenetically close tend to have similar traits, including diet or behavior, in the case of damselfishes, in the case of damselfishes, territorial herbivore species are closer, this would 'make us think' that the closer species would interact more. But looking from the co-occurrence and energy cost perspective, the species with too much similarity would avoid co-occurring to avoid competition, this probably explains why more distant species co-occur and interact more than close related species (Proaches et al. 2008).

While behavior was not a strong driver of agonistic interactions across reef sites, territorial damselfishes exhibited the highest proportion of interacting pairs when co-occurring. This was expected since whenever territorial damselfishes inhabit the same place, their natural behavior is to defend their territory from possible intruders or competitors (Gibson et al. 2001). It is therefore also reasonable to expect that territorial species would lead and interact more frequently with other fish individuals, being central in interaction networks. In the Pomacentridae family, territorial herbivores from the *Stegastes* genus are generally central in agonistic interaction networks (Da Silva-

Pinto et al. 2020). In Curaçao Island, Nunes et al. (2023; unpublished article) identified three *Stegastes* species as central in agonistic networks when investigating the entire reef fish community (Nunes et al. 2023). The pair of species that realized the highest proportion of agonistic interactions was *Stegastes rocasensis*, an endemic species from Rocas Atoll, this may have happened because *S. rocasensis* is the only territorial species of the Pomacentridae family inhabiting the Rocas Atoll, the other two species from the family that occur in the site are not territorial. In the other sites the agonistic interactions were also performed majorly intraspecifically (Table S1), according to Chesson (2000), intraspecific interactions have to occur in a higher rate than interspecific interactions, so coexistence can be maintained. A few studies showed that whenever damselfishes co-occur intraspecifically, there is a change from the territorial behavior to a dominance hierarchy system, while when two species that have a similar habitat specialization, for example when two species from the *Stegastes* genus co-occur, one of the species is going to co-occur less abundantly and interact less than the other (Doherty. 2012).

Among the countless and diverse life forms in coral reefs, the Pomacentridae family represents a diversity of species with remarkable importance to reef interactions, largely influencing local nutrient and energy flows (Chase et al. 2020). Our study fills an important knowledge gap on animal ecology, attesting that, there is a positive relationship between co-occurrence and agonistic interactions, for Pomacentridae reef fish, co-occurrence represents species' interactions. Also, our results showed that the co-occurrence of damselfishes is driven by phylogenetic distance, with the most distant species co-occurring more frequently and consequently interacting more. Thus, the study helps to improve our knowledge of important ecological processes in the

Pomacentridae family. Besides that, our study is one of the few to explore co-occurrence patterns along a species richness gradient, and its relationship with local scale interactions among individuals. Also, studying phylogenetic distance and its influence in co-occurrence in a macroecological scale is an innovative field in ecology.

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Supplementary material

Table S1. List with pairs of species that co-occurred and interactions the most in each one of the eight sites of the study

Local	Spp1	Spp2	Co-occurrence	Spp1	Spp2	Interactions
Abrolhos	*Stegastes fuscus*	*Stegastes fuscus*	38	*Stegastes fuscus*	*Stegastes fuscus*	10
Bali	*Chromis margatifer*	*Chromis margatifer*	23	*Chromis margatifer*	*Chromis margatifer*	5
Curaçao	*Stegastes partitus*	*Stegastes partitus*	43	*Stegastes partitus*	*Stegastes partitus*	14
Fiji	*Stegastes nigricans*	*Stegastes nigricans*	32	*Stegastes nigricans*	*Stegastes nigricans*	3
Mexico	*Stegastes partitus*	*Stegastes partitus*	29	*Chromis cyanea*	*Chromis cyanea*	4
Moorea	*Stegastes nigricans*	*Stegastes nigricans*	26	*Stegastes nigricans*	*Stegastes nigricans*	4
Príncipe	*Chromis multilineata*	*Chromis multilineata*	35	*Stegastes imbricatus*	*Chromis multilineata*	15
Rocas	*Stegastes rocasensis*	*Stegastes rocasensis*	50	*Stegastes rocasensis*	*Stegastes rocasensis*	43

Table S2. Path Analysis results.

	Estimate	Std.Err	Z-value	P(>|z|)	Std.lv	Std.all
Interactions						
Co-occurrence	0.369	0.054	6.838	0.000	0.369	0.733
Behavior	0.397	0.740	0.537	0.591	0.397	0.054
Maximum Abundance	-0.230	0.155	-1.479	0.139	-0.230	-0.135

Phylogenetic Distance	-2.174	1.765	-1.231	0.218	-2.174	-0.133
Richness	0.019	0.051	0.372	0.710	0.019	0.038
Co-occurrence						
Behavior	2.901	1.432	2.026	0.043	2.901	0.199
Phylogenetic Distance	17.710	3.183	5.565	0.000	17.710	0.547

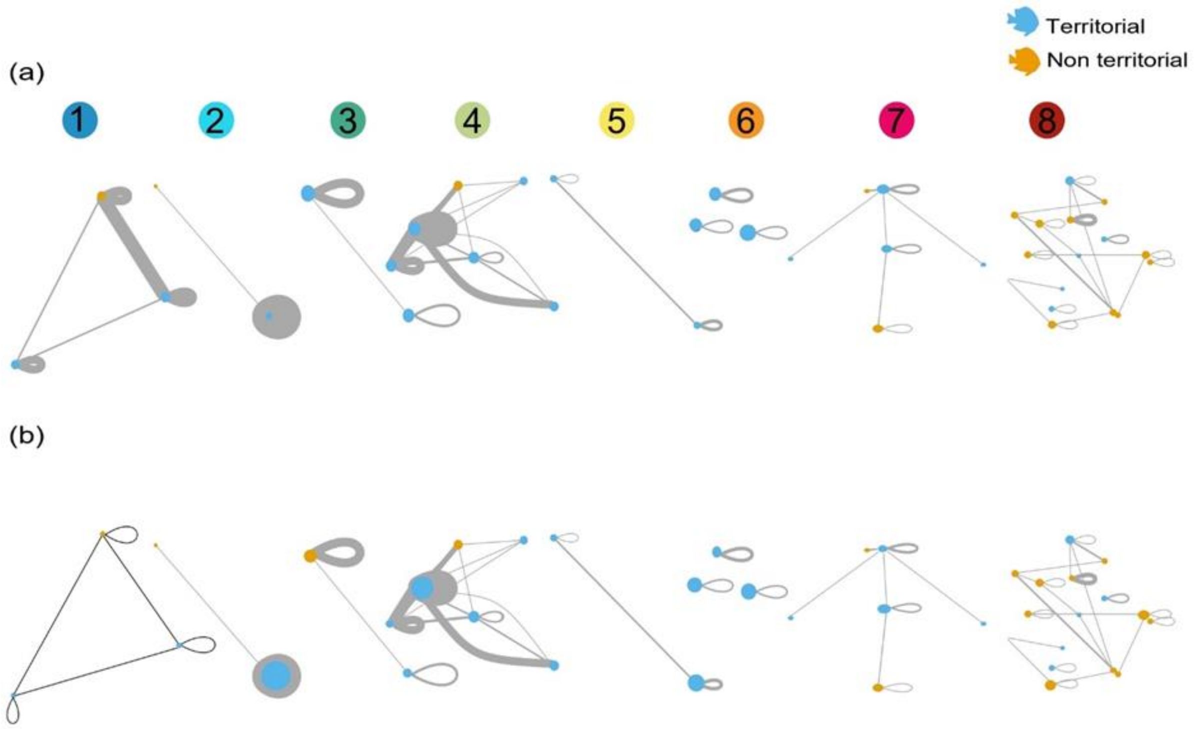

Fig S1. Agonistic interactions network: In A) network with out-degree centrality, the size of the circles is indicating how central the species is in the network, by how many interactions that species realised, the link between the pairs of species is indicating its interaction, the width of the link is demonstrating how many interactions happened between the pair. in B) the circle is indicating the species maximum abundance (MaxN) and the width of the link is indicating the number of interactions between the pair. In both networks the colours represent the behavior, blue circles represent territorial species, while yellow circles represent non- territorial species

Table S3. List with all species and the seven traits used: Reef association, size, mobility, activity, schooling, position in the water column and diet.

Spp	Reef associated	Size	Mobility	Activity	Schooling	Position	Diet
Abudefduf hoefleri	1	3	2	1	3	2	OM
Abudefduf saxatilis	1	3	2	1	3	2	OM
Abudefduf septemfasciatus	1	3	1	1	4	2	OM
Abudefduf sexfasciatus	1	3	1	1	4	2	PK
Abudefduf sordidus	1	3	1	1	4	2	OM
Abudefduf taurus	1	3	2	1	3	2	OM
Abudefduf vaigiensis	1	3	1	1	4	2	PK
Amphiprion melanopus	1	2	1	1	3	1	PK
Chromis atripectoralis	1	2	1	1	5	2	PK
Chromis atripes	1	2	1	1	4	2	PK
Chromis caudalis	1	2	1	1	4	2	PK
Chromis chrysura	1	2	1	1	4	2	PK
Chromis cinerascens	1	2	1	1	4	2	PK
Chromis cyanea	1	3	2	1	4	3	PK
Chromis margaritifer	1	2	1	1	4	2	PK
Chromis multilineata	1	3	2	1	5	3	PK
Chromis opercularis	1	3	1	1	4	2	PK
Chromis ternatensis	1	2	1	1	4	2	PK
Chromis viridis	1	2	1	1	5	2	PK
Chromis weberi	1	2	1	1	4	2	PK
Chromis xanthura	1	3	1	1	5	2	PK
Chrysiptera biocellata	1	2	1	1	3	1	OM
Chrysiptera brownriggii	1	2	1	1	3	1	OM
Chrysiptera taupou	1	2	1	1	3	1	OM
Chrysiptera unimaculata	1	2	1	1	3	1	OM
Dascyllus aruanus	1	2	1	1	4	1	PK
Dascyllus auripinnis	1	2	1	1	4	1	PK
Dascyllus carneus	1	2	1	1	4	1	PK
Dascyllus reticulatus	1	2	1	1	4	1	PK
Dascyllus trimaculatus	1	2	1	1	3	1	PK
Microspathodon chrysurus	1	3	1	1	1	2	HD
Microspathodon frontatus	1	3	1	1	1	2	HD
Neoglyphidodon crossi	1	2	1	1	3	1	OM
Neoglyphidodon melas	1	3	1	1	1	1	OM
Plectroglyphidodon dickii	1	2	1	1	1	1	OM
Plectroglyphidodon lacrymatus	1	2	1	1	1	1	OM
Pomacentrus adelus	1	2	1	1	3	1	HD

Pomacentrus amboinensis	1	2	1	1	4	1	OM
Pomacentrus auriventris	1	1	1	1	3	1	PK
Pomacentrus bankanensis	1	2	1	1	3	1	OM
Pomacentrus brachialis	1	2	1	1	4	2	PK
Pomacentrus burroughi	1	2	1	1	3	1	OM
Pomacentrus chrysurus	1	2	1	1	3	1	OM
Pomacentrus coelestis	1	2	1	1	4	1	OM
Pomacentrus imitator	1	2	1	1	4	1	PK
Pomacentrus lepidogenys	1	2	1	1	3	1	PK
Pomacentrus moluccensis	1	2	1	1	4	1	OM
Pomacentrus philippinus	1	2	1	1	4	2	PK
Pomacentrus similis	1	2	1	1	3	1	PK
Pomacentrus simsiang	1	2	1	1	3	1	OM
Pomacentrus spilotoceps	1	2	1	1	3	1	OM
Stegastes adustus	1	3	1	1	1	2	HD
Stegastes albifasciatus	1	2	1	1	3	1	HD
Stegastes fasciolatus	1	3	1	1	3	1	HD
Stegastes fuscus	1	2	1	1	1	2	HD
Stegastes imbricatus	1	2	1	1	1	2	HD
Stegastes leucostictus	1	2	1	1	1	2	HD
Stegastes lividus	1	2	1	1	4	1	HD
Stegastes nigricans	1	2	1	1	4	1	HD
Stegastes partitus	1	2	1	1	1	2	OM
Stegastes pictus	1	2	1	1	1	2	OM
Stegastes planifrons	1	2	1	1	1	2	HD
Stegastes punctatus	1	2	1	1	4	1	HD
Stegastes rocasensis	1	2	1	1	1	2	HD
Stegastes variabilis	1	2	1	1	1	2	HD

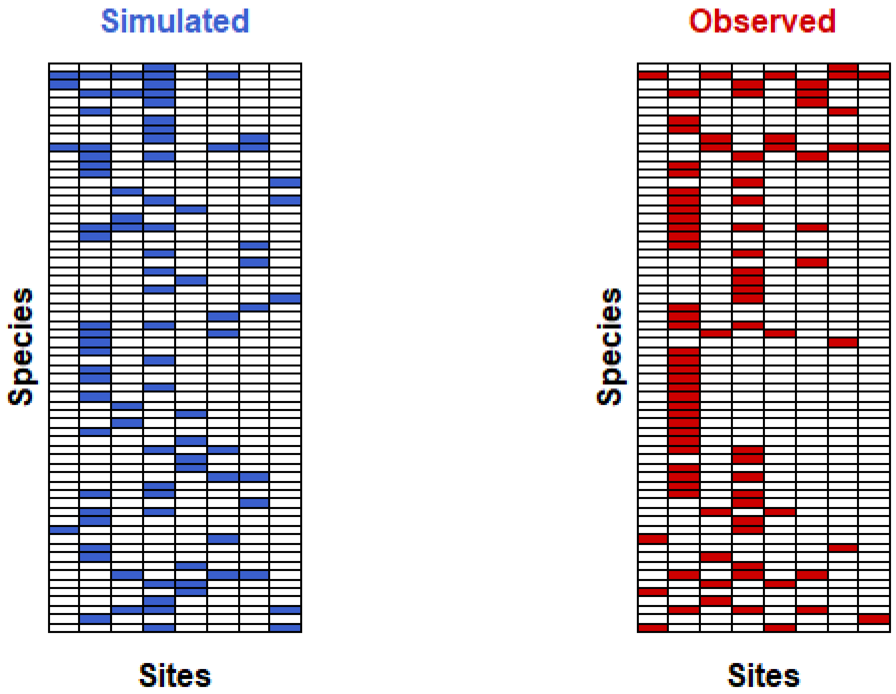

Fig S2. Co-occurrence patterns of distribution resulted from the null model. Each column is representing one of the eight sites studied, while the lines are representing the species. The blue matrix is representing the simulated pattern of co-occurrence by the randomization and the red matrix is representing the observed co-occurrence.

Table S4. Mean number of agonistic interactions for each of the eight sites studied.

Site	Mean interactions
Abrolhos	4.6
Bali	1.3
Curacao	4.5
Fiji	1.4
Mexico	2.6
Moorea	2.6
Principe	7.1
Rocas	19