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Research

The macroecology of reef fish agonistic behaviour

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Understanding the interplay between processes operating at large and small spatiotemporal scales in shaping biotic interactions remains challenging. Recent studies illustrate how phenotypic specialization, species life-history traits and/or resource partitioning recurrently underlie the structure of mutualistic interactions in terrestrial ecosystems along large latitudinal gradients of biodiversity. However, we know considerably less about how local processes interact with large-scale patterns of biodiversity in modulating biotic interactions in the marine realm. Considering agonistic behaviour as a proxy for contest competition, we empirically investigate whether the structure of reef fish agonistic interactions is conserved across a 34 000-km longitudinal gradient of biodiversity. By sampling coral reefs using standardized remote underwater video, we found recurrent patterns of fish agonistic behaviour in disparate communities distributed across five biogeographic provinces of the Pacific and Atlantic oceans. While the sheer number of species increases with regional richness, the number of aggressive disputes at the habitat scale is similar across communities. We then combined generalized linear models and network theory to reveal that, the emergent structure of local agonistic networks is not modular but instead recurrently display a nested structure, with a core of highly interactive site-attached herbivores of the Pomacentridae family. Therefore, despite the increase in the number of species involved in agonistic interactions toward speciose communities, the network structure is conserved along the longitudinal richness gradient because local disputes are mostly driven by closely-related, functionally-similar species. These findings suggest that evolutionary and local processes interact in modulating reef fish agonistic behaviour and that fine-scale niche-partitioning can structure the ecological networks in marine ecosystems.

Keywords: coral reefs, ecological interactions, ecological network, scaling, species richness, territoriality

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Introduction

Unravelling the interplay between spatial and temporal processes in shaping ecological communities is a persistent challenge in ecology. Evolutionary processes (e.g. speciation, extinction) and environmental filters strongly influence species diversity at large spatial scales (Mittelbach and Schemske 2015, Barneche et al. 2019), but we know considerably less about how they structure biotic interactions at finer spatial scales (but see Kortsch et al. 2019). Similarly, while intra- and interspecific biotic interactions taking place at such smaller scales can influence species distribution (Gotelli et al. 2010, Freestone et al. 2011, Belmaker et al. 2015), the extent to which they modulate niche partitioning in ecological communities, therefore shaping patterns that emerge across large spatial scales, is less clear (but see Pigot and Tobias 2012, Early and Keith 2019).

At large spatial scales, variation in biotic interactions is typically addressed along gradients of latitude and environmental conditions (Schemske et al. 2009, Schleuning et al. 2012, Kortsch et al. 2019, Longo et al. 2019). Latitudinal gradients mirror a well-known pattern in species diversity – the number of species increases in tropical ecosystems and towards lower latitudes. This diversity pattern has inspired the study of the structure of biotic interactions – particularly animal–plant mutualisms – among ecological communities at biogeographical scales (Schleuning et al. 2012, Martín-González et al. 2015, Dalsgaard et al. 2017). Collectively, these studies revealed that phenotypic specialization, species life-history traits (e.g. diet, home ranges) and resource partitioning are recurrent underlying drivers of the structural disparity of mutualistic networks along diversity gradients in terrestrial ecosystems. Whether such patterns of geographical variation hold true for biotic interactions in the marine realm are less known (but see Quimbayo et al. 2018, Longo et al. 2019). In the ocean, habitat conditions are less variable, resources are generally less predictable in time and space (Halley 1996), and the connectivity is such that there can be trophic interactions and energy flow between communities from distinct biogeographic regions (Albouy et al. 2019).

Reef fishes provide a good model to bridge this gap in how biotic interactions are structured along large biogeographical gradients in the ocean. This is a speciose taxonomic group distributed circumglobally in tropical and subtropical waters along a pronounced longitudinal diversity gradient (Kulbicki et al. 2013) that lacks the large temperature variations characteristic of latitudinal gradients. Across their large-scale distribution patterns (Bellwood and Hughes 2001, Kulbicki et al. 2013), reef fish ecological interactions are likely modulated by abiotic conditions (Longo et al. 2019) and the distribution of resources and risks experienced at finer scales (Robertson 1996, Freestone et al. 2011, Forrester 2015, Gil et al. 2017).

Coral reefs are productive systems that attract and support an impressive diversity of life, and can promote fierce local competition. Contest and scramble competition among reef fishes are conspicuous – since the same local resources (e.g. food, shelter) are used by many species, territorial disputes (Munday 2001) and agonistic behaviour are common (Blowes et al. 2013, Kerry and Bellwood 2015). Competition can be so prevalent that, by influencing individual growth, reproduction and mortality of reef fishes, it can modulate their abundance and distribution across coral reef habitats (Bonin et al. 2015). Combined, the effects of competition on abundance and survival of reef fish suggest that agonistic interactions may scale up to resource partitioning and therefore influence community structure. Richer coral reef regions can accommodate considerably higher diversity of reef fish at small spatial scales (Barneche et al. 2019) posing a unique opportunity for investigating whether the structure of agonistic interactions varies across a diversity gradient and its importance for mediating species coexistence. This growing body of evidence supporting the strength of local and regional processes shaping reef fish assemblages highlights the need to further explore the links between local biotic interactions, community structure and species distributions at large spatial scales (Pigot and Tobias 2012, Godsoe et al. 2015). Here, we investigate how local processes interact with large-scale patterns of biodiversity in structuring biotic interactions across reef fish communities.

We test the overarching hypothesis that the structure of agonistic interactions among reef fishes – a proxy for competitive disputes at finer spatial scales – varies along a large longitudinal gradient of biodiversity (see also Dalsgaard et al. 2011, 2013). First, we investigate whether the number of reef fish species that engage in agonistic interactions increases toward more speciose communities, given that regional species richness patterns widely influence species composition of local communities (Cornell and Harrison 2014). Second, we test whether the reef fish agonistic interactions along the biodiversity gradient were hierarchically structured – in which some species invest more in agonistic behaviour than others – or compartmentalized – in which agonism is contained within subsets of species – as found for other ecological networks (Sebastián-González et al. 2015, Quimbayo et al. 2018). We hypothesise that agonistic interactions are compartmentalized in species-rich communities suggesting resource partitioning, while a hierarchical structure is more pronounced in poorer communities, where fewer species dominate resource disputes. Finally, we investigate whether life-history traits and taxonomy influence the distribution of agonistic interactions among reef fish species across distinct biogeographical provinces. Agonistic fish behaviour can be modulated by trophic niche overlap, territorial behaviour and phylogenetic similarity (Peiman and Robinson 2010, Blowes et al. 2013). We thus expect reef fish that interact agonistically with many species to display traits related to narrow trophic niche and territoriality, such as feeding on defendable resources at the reef substrate and having small home ranges. By investigating potential regularities in agonistic interactions at biogeographic scales, our study contributes to the understanding of how local processes, such as resource use and niche-partitioning, may interact with evolutionary processes in modulating species coexistence in marine communities.

Material and methods

Study areas

We surveyed seven tropical reefs over a 34 000 km longitudinal gradient of biodiversity (Supplementary material Appendix 1 Table A1, A2): four at the Atlantic (Rocas Atoll, Abrolhos, Curaçao, Yucatán) and three at the Indo-Pacific Ocean (Moorea, Fiji, Bali). For the purposes of our study, each studied reefs was considered as a 'locality'. These localities were chosen because they span a pronounced longitudinal gradient of reef fish and coral species richness (Veron et al. 2009, Kulbicki et al. 2013), are distributed across two ocean basins and five distinct biogeographic provinces (sensu Kulbicki et al. 2013; Supplementary material Appendix 1 Table A1), and are similar in key environmental conditions, such as including biogenic reefs at similar annual mean sea surface temperature (27–29°C).

Data sampling design and effort

We designed a standardised study to record data on reef fish behaviour using Remote Underwater Video (RUV) sampling. We carried out the same sampling effort in all localities to control for possible influence of sampling on the relationships between agonistic behaviour and species richness across communities. Our standardised sampling effort (87.5 h of footage) consisted of 50 video samples per locality. A remote video sample consisted of a 15-min shot by a high-definition camera, fixed and focused over a 2 m^2 reef area previously chosen at random by a free diver (details in Longo and Floeter 2012, Longo et al. 2015; Supplementary material Appendix 1 Video A1). To encompass the local habitat heterogeneity, we sampled three different sheltered shallow reefs with depths between 2 and 10 m in each locality (Supplementary material Appendix 1 Table A2).

We identified all species and recorded all agonistic interaction events between them occurring in the central 10 min of each video sample (the first and last 2.5 min were discarded to remove any potential disturbance by the observers; Longo et al. 2015). We considered an agonistic interaction as a chasing event between individual fish (Supplementary material Appendix 1 Video A2) – a behaviour that is well-documented as representative of disputes for food resources, territory and/or mating opportunities (Robertson 1996, Kerry and Bellwood 2015). We focused on species larger than 5 cm in total length because identification of smaller individuals in remote video analysis can be unprecise (Longo and Floeter 2012).

To evaluate whether our standardized sampling effort was sufficient to represent the local species richness, we built sample-based rarefaction curves with 95% confidence intervals based on resampling techniques. This way, we evaluated how the total number of species, and the number of species engaged in agonistic behaviour, accumulates over increasing area in each locality (Coleman et al. 1982), by considering asymptotic curves as diagnostic of sufficient sampling effort (Coleman et al. 1982). Since differences in species richness across communities may require different effort to represent the local interactions (Kissling and Schleuning 2015, Dalsgaard et al. 2017), we further investigated whether the sampling effort was sufficient to represent the local agonistic interactions. To do so, we calculated the 'sampling completedness' of the agonistic behaviour in each locality by dividing the observed number of pairwise agonistic interactions by the estimated number of interactions (Chacoff et al. 2012), as approximated by the Chao estimator of asymptotic richness (Chao 1984). We considered high values of sampling completedness as an indication of representative sampling effort (Chacoff et al. 2012).

Reef fish species richness at multiple spatial scales

We estimated the reef fish species richness of the sampled biogenic reefs at three scales, defined as follows. The smallest scale considered was the 'habitat scale', at which richness was the number of reef fish species detected on each video sample of each locality (2 m^2). At the 'local scale', richness was the total number of species identified in all video samples of the locality, therefore comprising the total area of all 50 samples of each locality (100 m^2). At the 'regional scale', richness was taken from the comprehensive review by Kulbicki et al. (2013), where it was estimated as the total number of species recorded for each biogeographical province (Supplementary material Appendix 1 Table A1), through an exhaustive compilation of published lists of species at multiple sites within each province.

The locality richness – which ranged from 26 species at the poorest locality (Rocas Atoll) to 256 at the richest locality (Bali) – was double-checked with species checklists published for each locality. The strong positive relationship between the species richness estimated from Remote Underwater Video at the locality scale and the richness compiled for each province ($r^2 = 0.90$) indicated that species richness at the local scale was a reliable proxy of the 'regional pool' of species (Supplementary material Appendix 1 Fig. A1a). Our resampling analyses showed that the rarefaction curves for all localities, except Bali, tended to saturate with less than 50 video samples (Supplementary material Appendix 1 Fig. A2) which indicated that our sampling effort was sufficient and suitable to differentiate the number of species at the 'regional scale'. Further, there was higher species accumulation in localities with higher regional species richness, as shown by confidence intervals of rarefaction curves only overlapping between Curacao and Yucatán (Supplementary material Appendix 1 Fig. A2), which belong to the same biogeographic province and are known to have similar species richness (Kulbicki et al. 2013). In accordance to the downscaling spatial patterns (Bellwood and Hughes 2001, Caley and Schluter 2013), the habitat species richness showed a positive linear relationship with both the locality and regional richness (Supplementary material Appendix 1 Fig. A1b–c), which validates the spatial scales considered in this study.

Finally, we investigated whether the number of species that interacted agonistically followed the increase in species richness along the longitudinal gradient across multiple spatial scales. We fitted linear models to inspect the relationships between the species richness at regional scale and the species richness at the habitat ($2\,m^2$) and the local scales ($100\,m^2$). We then built sample-based rarefaction curves considering only the species engaged in agonistic behaviour to investigate whether their presence could be related to an increasingly sampled area in each locality (Coleman et al. 1982).

Agonistic interactions along the species richness gradient

We investigated the distribution of agonistic interactions among reef fishes across localities using the network formalism. For each locality, we combined the data from all 50 video samples to create an asymmetrical binary adjacency matrix in which elements $a_{ij} = 1$ represented the agonistic behaviour of reef fish species i towards the species j, $a_{ji} = 1$ the behaviour of j towards i, and $a_{ij} = a_{ji} = 0$ when species never interacted. These one-mode directed networks depicted species as nodes colour-coded by taxonomic families connected by links indicating the direction of the agonistic interaction (outward = actor, inward links = receptor). We considered the networks to be representative of the potential of agonistic behaviour at the regional scale because each network comprised the interactions among all species at the locality ($100\,m^2$), a scale at which the number of species is strongly correlated with that of the regional scale (Supplementary material Appendix 1 Fig. A1a). We then checked whether the intensity of agonistic behaviour was correlated with species co-occurrence at fine spatial scales by performing Mantel tests between the total number of agonistic interactions between pairs of species and their Jaccard similarity across video samples (Supplementary material Appendix 1 Table A3).

Next, we evaluated the within-community distribution of agonistic interactions and compared if and how the structure of the emergent agonistic networks varies with increasing reef fish richness along the species diversity gradient. To test for asymmetric distribution of interactions among fish species across localities, we used two metrics that describe generally competing structures – nestedness and modularity.

Nestedness describes a hierarchical interaction distribution, in which the interactions of the less connected nodes are proper subsets of the interactions of the more connected nodes (Bascompte et al. 2003). In our case, nestedness means some fish species interact agonistically with most of the within-community pool of species, while some species interact with fewer, predictable subsets of this pool. A nested agonistic network would contain a core of highly connected fish species that interacts with most of the network, along with more peripheral, less connected fish species that predominantly interact with the species in the core (Cantor et al. 2018). We measured nestedness for one-mode and directed networks (UNODF; Cantor et al. 2017) based on the overlap and decreasing fill of the adjacency matrix, as originally proposed for two-mode networks (Almeida-Neto et al. 2008).

Modularity describes a compartmentalized distribution of interactions among nodes (Newman 2006). In our case, modularity means there is some degree of specificity in the agonistic interactions, in which subsets of fish species tend to interact more often among themselves than with the rest of the local pool of species. A modular agonistic network would contain densely connected subsets of species indicating compartmentalization of the agonistic interactions among groups of species (Olesen et al. 2007). We measured modularity (Q; Newman 2006) to test for subsets of nodes with higher density of links within each other in comparison to the rest of the network using the walktrap algorithm (Pons and Latapy 2006).

To test the statistical significance of nestedness and modularity at each locality, we compared their empirical values with null benchmark distributions. We created benchmark distributions of nestedness and modularity using a null model that generated theoretical adjacency interaction matrices of same size (number of species) and connectance (proportion of the observed agonistic interactions) as the empirical locality networks. In the theoretical matrices, the probability of each matrix cell being occupied (i.e. contain an interaction between two nodes) was proportional to the row and column sums of the adjacency matrices of the empirical networks (null model 2 in Bascompte et al. 2003 adapted for one-mode networks by Cantor et al. 2017). We considered the empirical values of nestedness and modularity of each locality to be significant when they fell outside of the 95% confidence intervals of their respective benchmark distribution.

Finally, we built generalized linear models (GLMs) with Gaussian distribution to analyse whether nestedness and modularity vary along the longitudinal biodiversity gradient. In these models, we used null-model corrections of both network metrics as response variables and local richness (at $100\,m^2$ scale) as a predictor. We also build GLMs considering sampling completedness (Chacoff et al. 2012) as an additional predictor to control for potential sampling biases (Dalsgaard et al. 2017). We selected the most parsimonious GLMs for nestedness and for modularity as the ones with the lowest Akaike information criterion corrected for finite samples (AICc) and high support as given by the AICc weights (Burnham and Anderson 2002).

We applied null-model corrections to the network metrics prior building the GLMs because our agonistic networks had different sizes (i.e. different number of interacting species); by standardizing them, we allow for proper comparison of their nestedness and modularity values across localities (Sebastián-González et al. 2015). This standardization also corrected the observed metrics by fixing properties of the network that can be influenced by sampling (Schleuning et al. 2012). To do so, we quantified the differences between the observed and expected values of nestedness and modularity for each locality by calculating their *z*-scores as $Z = [(E - M_{\text{null}})/SD_{\text{null}}]$, where E was the empirical value of the network metric, M_{null} the mean value calculated from the ensemble of the 1000 theoretical networks, and SD_{null} their standard deviation (Sebastián-González et al. 2015, Dalsgaard et al. 2017). (We also considered a Δ-transformation of the network metrics, but they were highly correlated with, thus equivalent to, the z-transformation – UNODF: $\rho = 0.340$; Q: $r = 0.966$; see also Dalsgaard et al. 2017.)

The influence of biological traits on agonistic behaviour

To investigate the extent to which biological traits of reef fishes influenced the distribution of agonistic interactions along the richness gradient, we built linear mixed models (LMMs) in which we related the number of agonistic interactions performed by species of all localities to key descriptors of reef fish agonistic behaviour – taxonomic family, trophic groups and home range (Peiman and Robinson 2010, Blowes et al. 2013). We hypothesise that highly interactive fish species tend to have traits related to narrow trophic niche and territoriality, that is, phylogenetically close species living in small home ranges and feeding on defendable resources.

Since our study focuses on macroecological scale patterns, we classified fish species into broad functional groups. We considered five trophic groups based on their primary diets – herbivores, carnivores, omnivores, planktivores and invertebrate feeders (Froese and Pauly 2018) – and three categories of home range – site-attached (less than $5\,\text{m}^2$), low mobility (within reef) and mobile (between reefs) (Supplementary material Appendix 2 Table A1). While the oversimplification of species life-history traits can mask differences in species' niche (Bellwood et al. 2019), a broad trait classification allows for similar species from distinct biogeographical provinces to be aggregated, which has been proven effective in capturing patterns and singularities among reef assemblages worldwide (Mouillot et al. 2014, McWilliam et al. 2018).

We quantified the propensity of each species to interact agonistically by calculating the out-degree centrality in the locality networks as the sum of all outward links of a node. In our case, out-degree indicates the total number of other species each species was observed interacting with – species with many outward links (high out-degree centrality) had a high tendency to interact agonistically with other species, whereas those with few outward links (low out-degree centrality) had a lower tendency for agonistic behaviour. To visualize whether the distribution of links changed along the richness gradient, we compared the proportion of aggressive interactions by species in different network positions and of different life history traits. To identify species position within local networks, we calculated their normalized degrees as $dn_i = d_i/(s_l - 1)$, where d_i was the total number of links of species i relative to s_l, the network size (number of nodes) in locality l; then we classified those with high degree ($dn_i > \max(dn_l) \times 0.5$, where $\max(dn_l)$ is the maximum normalized degree of locality l) as being in the network 'core' and the ones with low degree ($dn_i < \max(dn_l) \times 0.5$) as being in the 'periphery' (Supplementary material Appendix 1 Fig. A3). We also used Cohen–Friendly plots to test observed and expected frequencies in contingency tables of agonistic interactions among network positions, trophic groups and home-range categories.

In the LMMs, fish species were the units of analysis, out-degree centrality was the dependent variable (log-transformed to improve model residuals), and taxonomic classification (family) and the two functional traits and their combination (trophic group and home range) were the independent variables. Independent variables were set as fixed factors, while locality was set as a random effect variable (i.e. random intercept model) to control for variation among localities. To account for the fact that some species were present in more than one locality, we build LMMs omitting the repeated species (11 out of 85) so to avoid non-independence of samples. We also build LMMs and fit to the entire dataset with all 85 species, considering or not taxonomic family as a random factor, to compare the best fitting models.

In all cases, we started by building a full LMM, then created nested LMMs by evaluating the significance of predictors with Likelihood Ratio Tests (LRT) and dropping the non-significant individual predictors ($p > 0.05$) based on differences in model fit (Zuur et al. 2007). In all models, we calculated the Variance Inflation Factor (VIF) to ensure the predictors were not correlated with each other (Zuur et al. 2010). We ranked all candidate models by the lowest Akaike information criterion corrected for finite samples (AICc) and evaluated their relative likelihoods using AICc weights (Burnham and Anderson 2002), considering a null model with only the intercept as a benchmark. The most parsimonious model was selected as the one with the lowest AICc. To measure the proportion of variation accounted by its fixed effects (i.e. how close the parsimonious model was to achieving the closest fit) we calculated the marginal pseudo-R^2 and compared it with the conditional R^2 to evaluate the influence of the random effect (locality) in explaining the propensity to interact agonistically (out-degree) (Nakagawa and Schielzeth 2013). Finally, we followed the protocol to validate the most parsimonious GLMs and LMMs by inspecting Q–Q plots and plots of residuals against fitted data and deviance residuals against predicted data (Bolker et al. 2009); we also simulate new data from the fitted model to further test for dispersion, uniformity and spatial and temporal autocorrelation (Hartig 2020). These and all other analyses were performed in R environment v3.0.3 (R Development Core Team) using packages 'vegan', 'lme4', 'DHARMa' (Hartig 2020), 'MuMin' (Bartoń 2018), 'igraph' (Csardi and Nepusz 2006) and 'UNODF' (Cantor et al. 2017).

Results

The number of agonistic reef fish species increases along the longitudinal richness gradient

We found that the total number of reef fish species that interact agonistically in each locality increased with the local species richness (Fig. 1a; $r^2 = 0.88$, $F_{1–5} = 47.03$, $p = 0.001$). However, the average number of interacting species at the habitat scale (2 m^2) did not (Fig. 1b, $r^2 = 0.06$, $F_{1–5} = 0.34$, $p = 0.58$). At this fine (100 m^2) scale, species co-occurrence correlated with the intensity of agonistic interactions (Supplementary material Appendix 1 Table A3). Accumulation curves of interacting species (Fig. 1c) showed a higher overlap in small areas (< 10 m^2). The curve of interacting species for the richest locality (Bali) differed from the other localities at the cumulative sampled area of 20 m^2, as opposed to the other localities in which accumulation curves tend to differentiate from each other at sampled areas of 100 m^2.

The structure of agonistic networks is conserved along the longitudinal richness gradient

The number of reef fish species engaged in agonistic behaviour increased with species richness along the longitudinal gradient (Fig. 1a–b; see also more nodes in the networks in Fig. 2a–b). The number of agonistic interactions per species – out-degree centrality – among distinct taxonomic families was greater in larger networks (Fig. 2c; Supplementary material Appendix 2 Table A1). As the number of species per family increased towards richer communities, a higher number of species within families engaged in agonistic behaviour (Fig. 2c).

All reef fish agonistic networks were roughly organized as star-like structures, in which one to three central species were more connected to several more peripheral species than among themselves, especially in speciose communities (Fig. 2b). In the networks of all localities, site-attached herbivores and/or the Pomacentridae family were mode central (Fig. 2b) suggesting that these species tend to initiate and/or engage more often in agonistic behaviour (i.e. higher out-degree values; Fig. 2c). Indeed, herbivores and site-attached species occupied the network core position more often than expected (Fig. 2d). Across all networks, the number of outward links were more often observed from the core to the peripheral species (Fig. 2e), suggesting that aggressive behaviour was generally directed toward species with different combination of functional traits.

The recurrent centralized, core-periphery network structure agreed with the tendency for nestedness and the lack of modularity. Overall, local agonistic networks were more nested than expected by chance (Fig. 3a), and did not contain cohesive groups of interacting species, as shown by modularity that was not different from the null expectancy (Fig. 3a; Supplementary material Appendix 2 Table A2). Despite a higher number of species engaged in agonistic behaviour in richer communities (Fig. 2b), neither nestedness nor modularity showed clear increasing trends along the species richness longitudinal gradient (Fig. 3b, d), even when controlling for sampling completedness of the networks (Supplementary material Appendix 2 Table A3, Fig. A1, A2). This suggested that the degree of nestedness in local agonistic interactions was conserved across biogeographical provinces.

Reef fish agonistic behaviour can be related to small ranging behaviour

The propensity of reef fish species to engage in agonistic interactions was broadly related to their trophic and ranging behaviour. The results from the linear models reinforced the central positions of herbivores and site-attached species in the agonistic networks (Fig. 2). The most parsimonious model described the number of agonistic interactions per fish species as a function of trophic and home range categories (Table 1; Supplementary material Appendix 2 Fig. A3). The combined explanatory power of trophic and home range categories (fixed terms) accounted for 42.3% (marginal R^2); it increased slightly to 45.6% when also considering the random effect (conditional R^2, Table 2), indicating that the

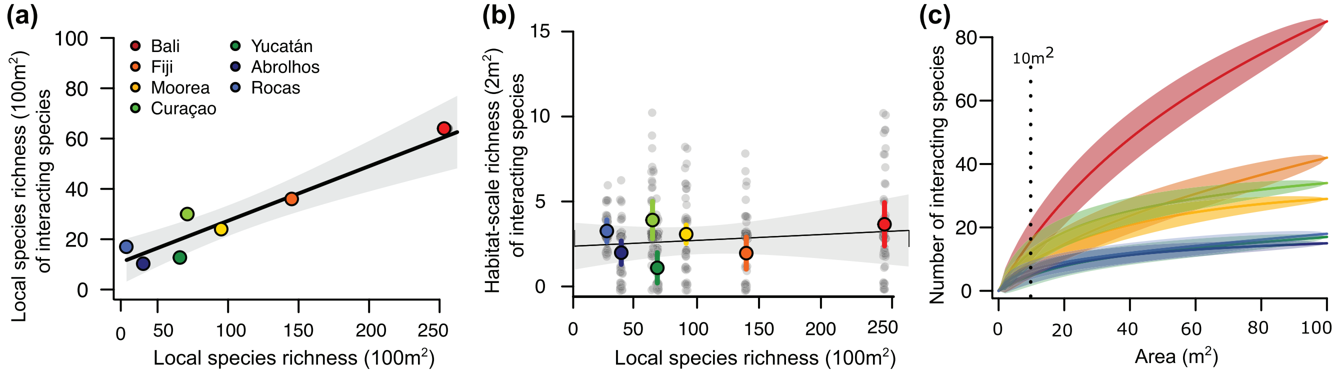

Figure 1. Spatial relationships between the number of reef fish species that engage in agonistic behaviour along a broad longitudinal gradient of species richness. (a) The total number of interacting reef fish species at each locality (100 m^2) increases with the local reef fish species richness. (b) The average number of interacting reef fish species (coloured circles) at the habitat scale (2 m^2) does not change with local richness (grey circles show the richness in each of the 50 video samples, at 100 m^2 scale). For the positive relationships between species richness at the habitat and local scales with richness at the regional scale, see Supplementary material Appendix 1 Fig. A1. (c) Accumulation curves of the number of species observed interacting agonistically within each locality over increasing sampled area. Shaded areas represent 95% confidence intervals of linear models (a, b) and accumulation curves (c).

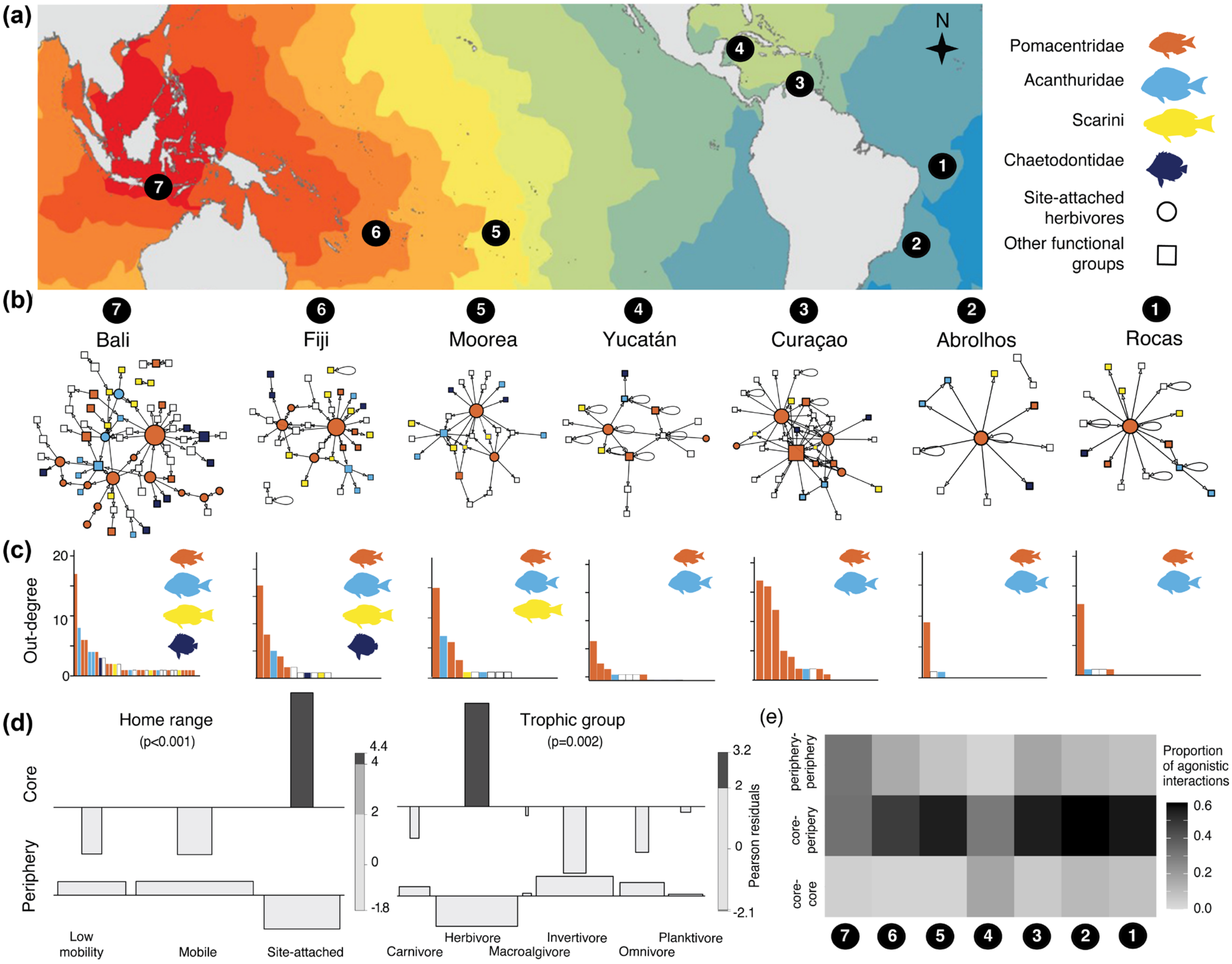

Figure 2. Reef fish agonistic networks along a large longitudinal species richness gradient. (a) The species richness gradient across biogeographical provinces, from high (red) to low (blue) number of reef fish species (Kulbicki et al. 2013), in which numbered circles indicate the localities where agonistic behaviour was sampled. (b) Reef fish agonistic networks, in which nodes representing species are linked by the direction of their agonistic behaviour (actor: outward, receiver: inward links). Node colours indicate taxonomic family; node shapes indicate trophic group (circle: site-attached herbivores; square: others); node sizes are proportional to out-degree centrality (i.e. sum of outward links). (c) Species ranks based on out-degree centrality, as a proxy for the tendency to behave agonistically toward others. Bars colours indicate taxonomic family. Fish icons representing the families common to all localities indicate whether a species from such families displayed agonistic behaviour toward other reef fish species in each locality. (d) Site-attached and herbivore species tended to occupy the network core position more often than expected due to high number of active aggressive events (out-degree), as shown by the high Pearson's residuals in the Cohen–Friendly plots (darker bars). The height of rectangles is proportional to Pearson's X^2, and the width is proportional to expected value. (e) Across localities, the proportions of outward links were higher between species of different network positions, and especially directed from the core to the peripheral species.

variation in agonistic interaction was not primarily driven by variation among localities. In particular, the most parsimonious model indicated that fish species known for having very small home ranges ($< 5\,m^2$) tended to engage more often in aggressive behaviour (significance of the home range category 'site-attached'; Table 2).

In addition, the model containing functional entities (combinations of trophic group and home range categories) received some, although less, support (ΔAICc < 2; Table 1). This model also pointed site-attached herbivores as the only functional entity to positively influence the propensity of species to interact agonistically (Supplementary material Appendix 2 Table A4). All other models with fish taxonomic family as explanatory variable were less plausible (ΔAICc > 2; Table 1). These results were robust to whether or not the 13% of the species present in more than one community were included; in all cases, the most parsimonious LMM only included trophic group and home range and pointed that site-attached fish species tend to be more aggressive (Supplementary material Appendix 2 Table A5–A7).

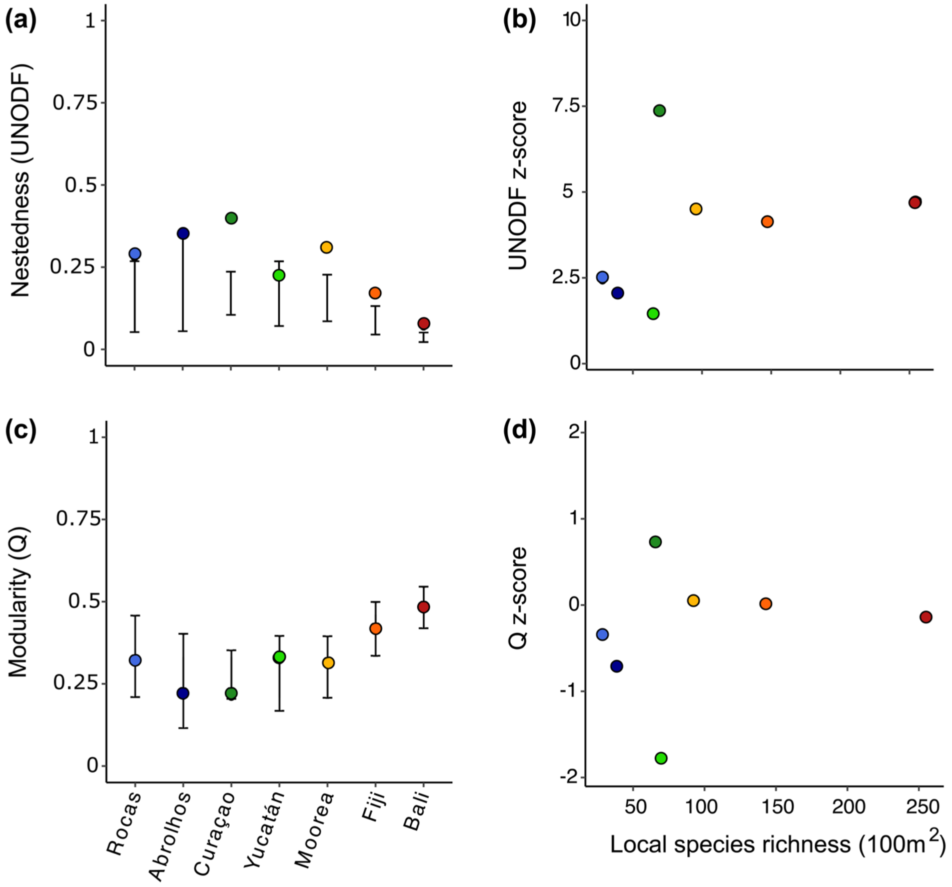

Figure 3. Reef fish richness and the structure of reef fish agonistic networks in seven tropical reef localities. (a, c) In all localities, agonistic networks were nested (UNODF) and not modular (Q). Empirical network values (coloured circles) were significant when outside of the 95% confidence interval generated by a null model (whiskers). (b, d) There was no clear linear relationship between local species richness (100 m^2) and the standardized nestedness (z-scored UNODF) and modularity (z-scored Q) of the agonistic networks, even when accounting for sampling completedness (Supplementary material Appendix 2 Table A3).

Table 1. Candidate linear mixed models for describing the number of agonistic interactions per reef fish species along the richness gradient as a function of their biological traits.

	Model	df	AICc	ΔAICc	wAICc	Marginal R^2	Conditional R^2
1	Agonistic interactions ~ Home range + Trophic group + (1|locality)	10	169.300	0.00	0.66	0.42	0.46
2	Agonistic interactions ~ Functional entity (Home range × Trophic group) + (1|locality)	13	170.600	1.31	0.34	0.44	0.49
null	Agonistic interactions ~ 1 + (1|locality)	3	189.700	20.44	0.00	0.00	0.08
3	Agonistic interactions ~ Taxonomic family + (1|locality)	18	194.40	24.88	0.00	0.29	0.31
4	Agonistic interactions ~ Home range + Trophic group + Family + (1|locality)	25	198.60	29.35	0.00	0.45	0.52
5	Agonistic interactions ~ Taxonomic family + Home range + Trophic group + Functional entity (Home range × Trophic group) + (1|locality)	26	199.00	29.70	0.00	0.47	0.54

Species traits (home range, trophic group, taxonomic family) are considered as fixed factors and locality as a random factor (1|locality). Null model contains only the intercept. Models are ranked by the lowest corrected Akaike's information criterion (AICc). The relative weight of evidence for each model is indicated by Akaike weight (wAICc). df = degrees of freedom. R^2 give the conditional and marginal coefficient of determination of the models.

Table 2. Estimated parameters of the most parsimonious linear mixed model (model 1, Table 1) describing the number of agonistic interactions among reef fishes in function of their home range and trophic group categories, considering locality as random variable.

	Estimate	SE	df	t-value	p-value
Intercept	0.39	0.35	59.02	1.10	0.26
Fixed effects					
Trophic group					
Herbivores	0.35	0.45	61.75	0.78	0.44
Macroalgivores	−0.06	0.82	61.77	−0.07	0.95
Invertivores	0.01	0.43	61.37	0.03	0.98
Omnivores	−0.15	0.45	61.37	−0.32	0.75
Planktivores	−0.53	0.48	61.34	−1.12	0.27
Home range					
Mobile	−0.38	0.28	60.84	−1.34	0.19
Site-attached*	0.74	0.30	61.99	2.47	0.02
Random effects	Variance	SE		Marginal	Conditional
Locality	0.02	0.15	Pseudo-R^2	0.42	0.46
Residual	0.46	0.68			

SE: standard error; df: degrees of freedom; t-value: test statistic; Pseudo-R^2 give the conditional and marginal coefficient of determination of the model; asterisk (*) denotes statistical significance, $p < 0.05$.

Discussion

Our study reveals similar patterns of fish agonistic behaviour in disparate tropical reef communities along a 34 000-km longitudinal gradient of marine biodiversity. First, we found that more reef fish species are involved in agonistic interactions at reef communities located within larger regional species pools – although at the habitat scale the number of aggressive disputes for food resources, territory and/or mating opportunities is similar across communities. Second, the reef fish agonistic networks recurrently display a nested, star-like structure with a core of highly connected site-attached herbivores of the Pomacentridae family. Finally, the overall incidence of agonistic behaviour along the gradient tends to be driven by fish species with restricted ranging behaviour. Taken together, our findings demonstrate that, despite the increase in the sheer number of species – and interactions – toward speciose communities, the emergent structure of the local agonistic interactions characterized by a core of closely-related and functionally-similar species is conserved along the longitudinal richness gradient. While local coexistence of fish species is modulated by processes operating at large scales (Barneche et al. 2019), our study reinforces that competitive interactions for local resources, and subsequent niche-partitioning, can also influence their spatial distribution at smaller spatial scales (Robertson 1996).

The higher number of fish species engaged in agonistic behaviour in species-rich communities reflects the regional patterns of biodiversity, highlighting a link between large-scale processes and the structure of reef fish assemblages. The two most species-rich studied localities – Bali and Fiji – harbour several fish species with singular ecological functions; however, the diversification within reef fish families and functional redundancy are also pronounced in these communities (Mouillot et al. 2014). We found that as the number of species within families and functional groups common to all localities increases towards richer communities, the total number of species that engage in aggressive behaviour also increases. This correlation suggests that, in highly diverse communities, a greater number of closely-related and functionally-similar species may compete for local resources (e.g. food, territory, shelter and/or mates), and that aggression mirrors contest competition (Blowes et al. 2013).

The remarkable difference in the number of reef fish species that engage in agonistic behaviour between the extremes of the diversity gradient – Bali and Rocas Atoll – reflects the contrasting evolutionary history of this taxonomic group in the Atlantic and Indo-Pacific Oceans (Cowman et al. 2017), which could contribute to the emergent regional patterns of interactions. While the Atlantic is known for its relatively small reef area, pronounced geographical barriers and depauperate reef fish diversity (Floeter et al. 2008), the much larger reef area in the Indo-Pacific has undergone a longer period of species accumulation and diversification (Bowen et al. 2013, Cowman et al. 2017). As species colonize such insular systems, the diversity of competing species may increase and their niche diverge over time (Mittelbach and Schemske 2015, Schluter 2000). However, the degree of speciation and/or morphological radiation can be dependent on the ecological opportunities created by habitat and local resource diversity (Losos 2010, Wagner et al. 2014). Niche and island biogeography theories suggest that habitat heterogeneity can be important for promoting and sustaining diversity in large systems that experience high immigration rates (Kadmon and Allouche 2007). During the evolutionary history of coral reef fishes, the Indo-Pacific region possibly held these three characteristics – large reef areas, high immigration rates (Bowen et al. 2013, Pellissier et al. 2014) and high habitat heterogeneity, promoted by the expansion of hermatypic corals that provided mosaics of microhabitats and new food resources. By contrast, in the Atlantic, isolation, smaller reef area and lower habitat heterogeneity may have reduced the diversity of coral reef fish. The synchronized diversification of small-bodied reef fishes and coral expansion in the Indo-Pacific (Bellwood et al. 2017), but not in the Atlantic, reinforces the hypothesis that environmental heterogeneity supports a wider niche and higher biological diversity than relatively uniform environments (Whittaker et al. 1973). Accordingly, taking coral diversity as a proxy of resource availability for reef fishes, it is plausible to suspect that the number of reef fish species engaged in agonistic disputes can encode the long history of evolutionary and ecological processes involved on community assembly across biogeographical regions.

While the sheer number of reef fish species within communities increases with local and regional species richness, we found that the number of species that engage in agonistic disputes at fine spatial scales does not. This lack of relationship reinforces that biotic interactions are scale-dependent and the effects of the negative interactions are better detected at fine scales (Araújo and Rozenfeld 2014). Moreover, these findings suggest that reef fish in species-rich communities only interact with a small proportion of the local species pool and/or that not all species co-occur in the same microhabitat. Although not modular, agonistic networks towards speciose communities, contained relatively fewer interactions among core species, suggesting that such highly interactive species may compete for similar resources and thus end up not overlapping as much in space. The 3-dimensional complexity and heterogeneity of reef habitats in more diverse regions could also facilitate such non-overlapping spatial distribution, supporting higher diversity of fish species that can engage in territorial disputes at small spatial scales (Eurich et al. 2018). As in terrestrial ecosystems, such fine niche partitioning can increase species coexistence at small scales in highly diverse communities (Albrecht and Gotelli 2001, Karger et al. 2015).

Along the broad longitudinal richness gradient, we found that reef fish agonistic networks are nested. Such hierarchical structure reveals a local core of species that are aggressive towards several other species, along with some species that only engage in agonistic behaviour with few species. In all agonistic networks, this core of species tended to be occupied by site-attached species, suggesting that fish with restricted home ranges have high propensity for agonistic behaviour, reflecting disputes for resources within the microhabitat. Site-attached species tend to be more aggressive due to the need to defend territories containing resources such as food, shelter, mates (Mitani and Rodman 1979). The availability, distribution and reliability of such resources can define when the benefits of the agonistic behaviour underpinning resource defence exceed its costs (Brown 1964). Therefore, reef fish species relying on resources that are unpredictable in time and space (e.g. mobile prey) are less likely to defend resources compared to those that survive on predictable, defendable resources (e.g. sessile prey, shelter; Grant 1993, Ceccarelli et al. 2001).

In trophic and mutualistic ecological networks, the conservation of species' functional roles across communities is strongly influenced by their evolutionary histories and can lead to similar network topologies across biogeographic regions (Rezende et al. 2007, Stouffer et al. 2012). The high frequency of agonistic interactions by Pomacentridae species along the longitudinal gradient further suggest a phylogenetic influence on life-history traits that underlies the propensity for agonistic behaviour. For instance, specialized cleaner fish species and specialized pollinator hummingbird species have both shown, independently, a phylogenetic signal – closely related species from different biogeographic regions structure local mutualistic interactions in similar ways (Sebastián-González et al. 2015, Quimbayo et al. 2018). Similarly, we found that closely-related damselfishes (Pomacentridae; Frédérich et al. 2013) are consistently among the highly agonistic species in coral reef communities.

The family Pomacentridae is the third largest reef fish family and is widely distributed across coral reefs (Ackerman and Bellwood 2000, Ferreira et al. 2004, Kulbicki et al. 2013). This speciose group is an example of convergent and iterative radiation in the ocean (Frédérich et al. 2013) with surprisingly low trophic diversification compared to other reef fish lineages (e.g. Labridae; Gajdzik et al. 2019). Several factors might have contributed to this repeated pattern of adaptive radiation among damselfishes, such as the presence of many potential competitors (e.g. Acanthuridae and Labridae) during the rise of the coral reefs ecosystems (Bellwood et al. 2017). Trophic diversity, although low, is strongly related with disparities in ecomorphological attributes of damselfishes (e.g. planktivores and benthic feeders exhibit dissimilarities in jaw morphology). However, morphology poorly predicts interspecific variation in aggressive behaviour and the ability to cultivate algae developed by a restricted number of species within this family (Frédérich et al. 2013). These damselfishes (mostly of Stegastinae subfamily) display both behaviours and form the core of agonistic networks across localities. Locally, these territorial damselfishes – also known as farmers – can influence the structure of benthos communities determining coral settlement, algal growth and feeding activity of other reef fish (Ceccarelli et al. 2001). Along with an epilithic algae matrix, damselfish territories may also trap detritus (Wilson et al. 2003) and create habitat for invertebrates, which can be much denser than outside the territories (Ferreira et al. 1998). Such nutrient-rich territories attract many opportunistic and mobile fish species to feed, thus reflecting the high aggressiveness observed. Farmer damselfishes illustrate how aggressiveness can be favoured in disputes for resources at microhabitats, given that engaging in agonistic behaviour might not be energetically costly for these species (Cleveland 1999). When combined with other key life-history traits – such as short generational time, small body size, small home range – the ability to defend territories could be related to the widespread distribution of this lineage of reef fish across biogeographic regions.

In conclusion, our results highlight how both evolutionary and local processes can interact and structure biotic interactions in marine communities across spatial scales. While the longitudinal gradient of reef fish richness, shaped by historical evolutionary processes, influences the sheer number of species involved in agonistic interactions, we show a recurrent structure of agonistic interactions across this gradient, in which local disputes for resources at the microhabitat are mostly driven by a core of closely-related, site-attached herbivores and likely sustained through niche partitioning. However, it remains largely unresolved how much of the reef fish behaviour can be a reminiscent evolutionary signal of widespread parapatric speciation in reef fishes (Rocha and Bowen 2008) and how much of it is driven by more immediate processes at the ecological scale, such as environmental conditions and resource availability (Bowen et al. 2013, Keith et al. 2018). Therefore, some of the challenges ahead include disentangling the effects of phylogeny and functional traits on agonistic behaviour at intermediate reef scales and/or among the smallest and speciose group of cryptobenthic fishes (< 5 cm, Brandl et al. 2018), while accounting for the abundance of fish species and quantifying the intensity of their interactions and the resources they compete for at the local scale. By revealing the contributions of ecological and evolutionary processes in driving reef fish behaviour, we gain a better understanding of the mechanisms that govern the dynamics of biotic interactions in marine communities across scales.

Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5mkkwh733> (Fontoura et al. 2020).

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Authors contributions – LF, MC, GOL, SFR conceived the idea; LF, GOL, RMB, SFR collected data; LF processed the raw data; LF and MC analysed the data; LF and MC wrote the original manuscript. All authors contributed with ideas, edits and comments toward the final manuscript. LF and MC contributed equally to this work. LF and MC share the co-first authorship.

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