REPORT

Endemic species dominate reef fish interaction networks on two isolated oceanic islands

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Abstract Ecological interactions are found across ecosystems, facilitating comparison among systems with distinct species composition. The balance of positive and agonistic interactions among species may be sensitive to variation in the diversity and abundance of species in a community. We studied marine interaction networks among reef fishes on two oceanic islands characterized by high rates of endemism and restricted population connectivity: Rapa Nui (Easter Island) and Robinson Crusoe Island (Juan Fernandez Archipelago). Specifically, we examined whether the type and strength of behavioral interactions varied between these two isolated fish assemblages, how the relative proportions of agonistic and positive interactions compare, and which are the most important interacting species in each system. Combining detailed interaction records using standardized remote underwater video and visual censuses, we observed: (a) Rapa Nui contains 50% more fish species but half the fish densities than Robinson Crusoe, (b) despite these differences, the total number of interactions and proportion of all potentially interacting species were similar between the two oceanic islands; (c) the species that occupied the greatest proportion of all potential interactions in each community were endemic to their respective islands; (d) the relative frequency of positive and agonistic interactions varied, with more agonistic interactions in the more speciose reef system (Rapa Nui) and more positive interactions where fish densities were higher (Robinson Crusoe); and lastly (e) the relative abundance of each species predicted the interaction strength and the number of interactions across all reef fish species. It is of particular importance to understand the role of endemic species and processes affecting reef fish ecological networks on oceanic islands given the multiple anthropogenic threats to these isolated and vulnerable ecosystems.

Keywords Coral reefs · Temperate reefs · Biotic interactions · Reef fishes · Endemics · Endemism

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Introduction

Ecological interactions play an important role in resource partitioning, both delimiting ecological niches and expanding the availability of resources used for others (Bay et al. 2001; Kane et al. 2009; Inagaki et al. 2019). Interaction webs provide a useful tool for understanding ecological and evolutionary processes since they summarize the behavior of a large portion of co-occurring species in a

community (Quimbayo et al. 2018a; Fontoura et al. 2020; Nunes et al. 2020). Interaction webs are composed of specific relationships that fall into two broad categories: trophic and nontrophic interactions (see Kéfi et al. 2015). Although trophic interactions such as predator–prey dynamics have historically been the focus of ecological study (Elton and Nicholson 1942), more recent attention on nontrophic interactions has revealed ecosystem-wide impacts of both agonistic and positive behaviors. Agonistic interactions such as territorial chasing emerge when the same local resources (e.g., food, territory, shelter) are disputed by conspecific and heterospecific competitors (Fontoura et al. 2020). It has been suggested that these interactions promote co-occurrence through resource partitioning and by the occupancy patterns of different species in a community (Robinson and Terborgh 1995; Robertson 1996; Peiman and Robinson 2010; Bonin et al. 2015; Fontoura et al. 2020). In contrast, positive interactions, such as the biogenic habitat created by foundation species (Angelini et al. 2011), play a crucial role in enhancing biodiversity by providing access to otherwise unavailable resources, ameliorating physical stress and predation risk (Bertness and Callaway 1994) and avoiding competitive exclusion (Gross 2008).

Comparison among interaction webs across communities has revealed ecological functions that tend to arise despite independent evolutionary origins (Fontoura et al. 2020). For instance, in the Galapagos Islands, giant tortoises break up vegetation and maintain corridors through the understory, providing navigable routes for other large vertebrates, feeding opportunities for insectivores, and altering competitive dynamics among understory plants (Gibbs et al. 2010). This is a similar function to that occupied by elephants in sub-Saharan Africa or bison in North America (Valeix et al. 2011). Other common interactions such as kleptoparasitism (theft of resources already acquired–Hamilton and Dill 2003) and cleaning behavior (removal of parasites and dead skin—Bshary and Grutter 2002) are nearly ubiquitous across Earth's ecosystems. At the same time, unique interactions carried out by endemic species with special morphological or behavioral traits are also common, especially in highly isolated locations (Friedlander et al. 2020; Quimbayo et al. 2018a, 2018b). It remains unknown to what degree the development of ecological interactions in unique circumstances is deterministic, following common interaction patterns according to universal ecological niche space, versus stochastic, generating novel interactions according to the species pool and environmental conditions unique to each location.

Reef fish communities on isolated oceanic islands serve as a model system to explore ecological interactions not seen in other places (e.g., Sazima et al. 2007; Narvaez et al. 2015; Morais et al. 2017). Oceanic islands harbor reef fish assemblages that are characteristically low in diversity but high in endemism and with restricted population connectivity, all of which simplify the study of the ecological interactions that operate within reef ecosystems (Allen 2008; Morais et al. 2017; Titus et al. 2017). In particular, nonconsumptive interactions such as cleaning behavior and territorial chasing provide a compelling measure of the balance between agonistic and positive interactions across biological and environmental gradients. Assembling these interactions for an entire ecological community requires effort and observations, and the conclusions that can be drawn are limited in terms of effects on organismal benefits (i.e., fitness, reproductive success, growth) for interacting species. However, combining detailed interaction records with network theory provides an integrated estimate of the type, strength, and complexity of these interactions.

Oceanic islands offer an excellent natural laboratory to compare the influence of fish richness and abundance as well as oceanographic temperature and productivity on the strength, frequency, and network structure of agonistic and positive interactions between and within species. Specifically, we tested the hypothesis that communities with higher species richness and lower productivity (and likely lower food availability) are prone to more agonistic interactions and fewer positive interactions among interacting species due to potential redundancy in trophic requirements and greater competition for fewer dietary resources. To achieve this, we asked the following questions: (1) are ecological interactions more frequent in more speciose fish assemblages? (2) is the frequency of biotic interactions between reef fishes predicted by the abundance of individuals? (3) do the relative proportions of agonistic and positive interactions vary with species richness and abundance of individuals? and, lastly (4) which are the most important interacting species in each community? To answer these questions, we conducted qualitative and quantitative analyses of ecological interactions in reef fish assemblages on two isolated oceanic islands off the coast of Chile: Rapa Nui (Easter Island) and Robinson Crusoe Island (Juan Fernandez Archipelago).

Materials and methods

Study area and design

Rapa Nui (Easter Island, 27° S) is the most remote inhabited island in the Pacific Ocean, located 3700 km from Chile and 2100 km east of the Pitcairn Islands (Wieters et al. 2014; Delrieu-Trottin et al. 2019). The island has a total area of 166 km^2 and is surrounded by a subtropical coral reef dominated by the corals *Porites lobata* and *Pocillopora verrucosa,* with a low presence of turf

macroalgae and patches of heavily grazed crustose coralline algae that cover the benthos (Wieters et al. 2014; Delrieu-Trottin et al. 2019). The fish fauna is primarily derived from the Indo-Pacific region, comprising both tropical and subtropical fish lineages, and is considered the island with the lowest fish diversity of the region (139 shore fish species) (Randall and Cea 2011). Due to its isolation, 32% of marine fishes are endemic to this island (Randall and Cea 2011; Cowman et al. 2017; Delrieu-Trottin et al. 2019). In contrast, Robinson Crusoe is part of a group of three isolated volcanic islands known as the Juan Fernández Archipelago (33° S), 650 km off the coast of mainland Chile (Pérez-Matus et al. 2014). The habitat of the subtidal temperate rocky reef that surrounds the island of 47.9 km^2 in area is dominated by a community of turfing and leathery macroalgae (e.g., *Padina fernandeziana*, *Colpomenia sinuosa* and *Dictyota kunthii)* and a high cover of vermetid worms (*Serpulorbis sp.*), which comprise more than 90% of benthic cover interspersed with rhodolith beds (Ramírez et al. 2013; Macaya et al. 2015). The fish community derives from both the Indo-Pacific Region and South Eastern Pacific continent and is composed of 41 species with 70% endemism (Friedlander et al. 2016; Cowman et al. 2017).

On each island, we selected four study sites, 5 km apart from each other (Fig. 1a) and dominated by similar habitat types (Fig. 1b, c). We conducted our fieldwork during the austral summer of 2016 and 2018 in Robinson Crusoe and during the austral summer of 2017 and 2018 in Rapa Nui.

At each site (Fig. 1a), two areas of approximately 400 m^2 were selected for the study, one at 3–10 m depth and another at 15–20 m. We monitored fish interactions of the entire assemblage using remote underwater video recordings (RUVs, single GoPro hero models 3–5 placed on a weighted tripod, ESM Fig. A1). Using two RUVs placed over the substrate and separated at least by 15 m so the field of view did not overlap, we recorded sequences of 15 min each of different areas of the reef at multiple times. To standardize the monitoring area, a graduated 2 m piece of PVC tube was placed in front of each camera demarcating an area of 2 m^2 as per Longo and Floeter (2012) and Longo et al. (2018). To homogenize the field of view area, the lens of the camera was positioned so that the lower half of the frame corresponded to the substrate and the upper half of the water column (ESM Fig. A2). For subsequent analyses, the first and last 2 min of recording were discarded, thus eliminating the possible influence of diver presence on fish behavior.

To understand how the relative proportions of agonistic and positive interactions could vary with species richness and abundance of individuals in each system, we implemented an Underwater Visual Census (UVC) to estimate the total species richness and abundance of individuals in each fish assemblage. For this method, six 25 × 4 m transects (100 m^2 each) spaced every 50 m were carried out at the same depth range. One diver would swim along the transect counting and estimating the size of each fish in observation sessions of 25 min per transect (this included the time registering ecological interactions). To minimize double counting in schools with more than 20 individuals, the diver recorded only individuals that were swimming showing their left side in the view of the diver (following previous sampling protocols in these locations; see Peréz-Matus et al. 2014; Wieters et al. 2014). To minimize potential diver error, the same diver conducted all surveys. Abundance was expressed as numerical density in number of individuals per m^2 (ind · m^{-2}). Additionally, in situ monitoring of fish interactions was recorded opportunistically while diving for UVC to supplement the RUV recordings with the use of direct observations and underwater photography.

Finally, we classified each fish into one of five trophic groups (herbivore, invertivore, piscivore, planktivore and omnivore) according to Ramírez et al. (2013) and Pérez-Matus et al. (2014) for fishes of Robinson Crusoe, and Wieters et al. (2014) for Rapa Nui.

Ecological interactions

In reef fishes, agonistic interactions are expressed as aggressive behaviors between individuals, indicative of interference competition for a resource (e.g., territory, feeding areas, refuge and resting sites; Peiman and Robinson 2010; Kindinger 2016; Fontoura et al. 2020). Nonconsumptive agonistic interactions were defined as one fish chasing another fish eliciting an escape in the absence of behaviors associated with predation or mutilating predation (scale and mucus eating) (Robertson 1996; Canterle et al. 2020; Fontoura et al. 2020; Nunes et al. 2020). Behaviors were considered predatory and thus excluded based on relative body size and trophic position of interacting species, or the observation of bites or attempted bites targeting tissues instead of obvious agonistic chases (see Nunes et al. 2020). We counted chases and display events to quantify agonistic interactions as a proxy of inter- and intra-specific competition for disputed resources (Robertson 1996; Canterle et al. 2020; Fontoura et al. 2020; Nunes et al. 2020) (Fig. 2a).

We classified two different types of interactions among reef fishes as positive: symbiotic cleaning interactions, in which one fish removes parasites and dead skin from another (Losey and Margules 1974; Quimbayo et al. 2018a, 2018b) (Fig. 2e, f), and nuclear–follower feeding group interactions, in which one species or group of "follower" species follows a different, usually larger "nuclear" species and accesses food resources dislodged or otherwise
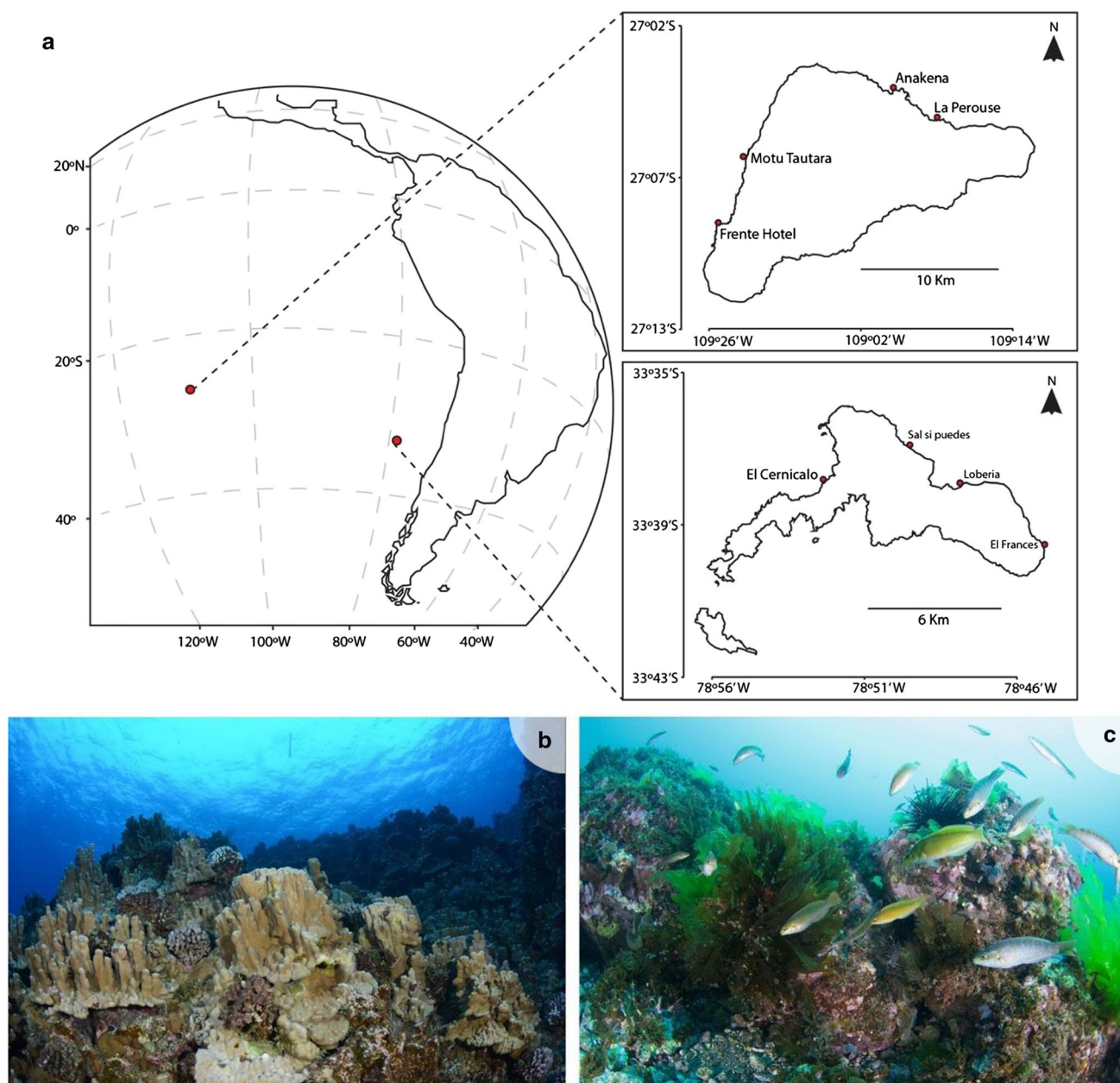
Fig. 1 a Map showing the location of the two study islands in the Pacific Ocean and the location of the survey sites around each island. Photograph depicting **b** typical community of Rapa Nui island with the most abundant coral species *Porites lobata* and *Pocillopora verrucosa* that dominate the rock substrate and **c** reefs of Robinson Crusoe island dominated by turf algae and rhodoliths

made available by the actions of the nuclear species (Sazima et al. 2007; Teresa et al. 2014; Sabino et al. 2017) (Fig. 2b, d).

To quantify the frequency of occurrence of cleaning interactions, one independent interaction event was considered when one cleaner species performed a physical contact (i.e., bite, tactile stimulation) on the body of a client in a determinate period, initiated by the first physical contact and ending when the cleaner left (Floeter et al. 2007; Quimbayo et al. 2018b). If the same cleaner

individual performed the interaction with the same client but separated in time and space, these were considered independent events (see Morais et al. 2017).

For nuclear–follower interactions, a single interaction event was considered to be when one or more individuals of the same species followed one or more individuals of a different species that was foraging in the same space and time, regardless of the number of followers observed for that event. Species and life stages of fish with a size less than 10 cm of total length (e.g., gobies and juvenile
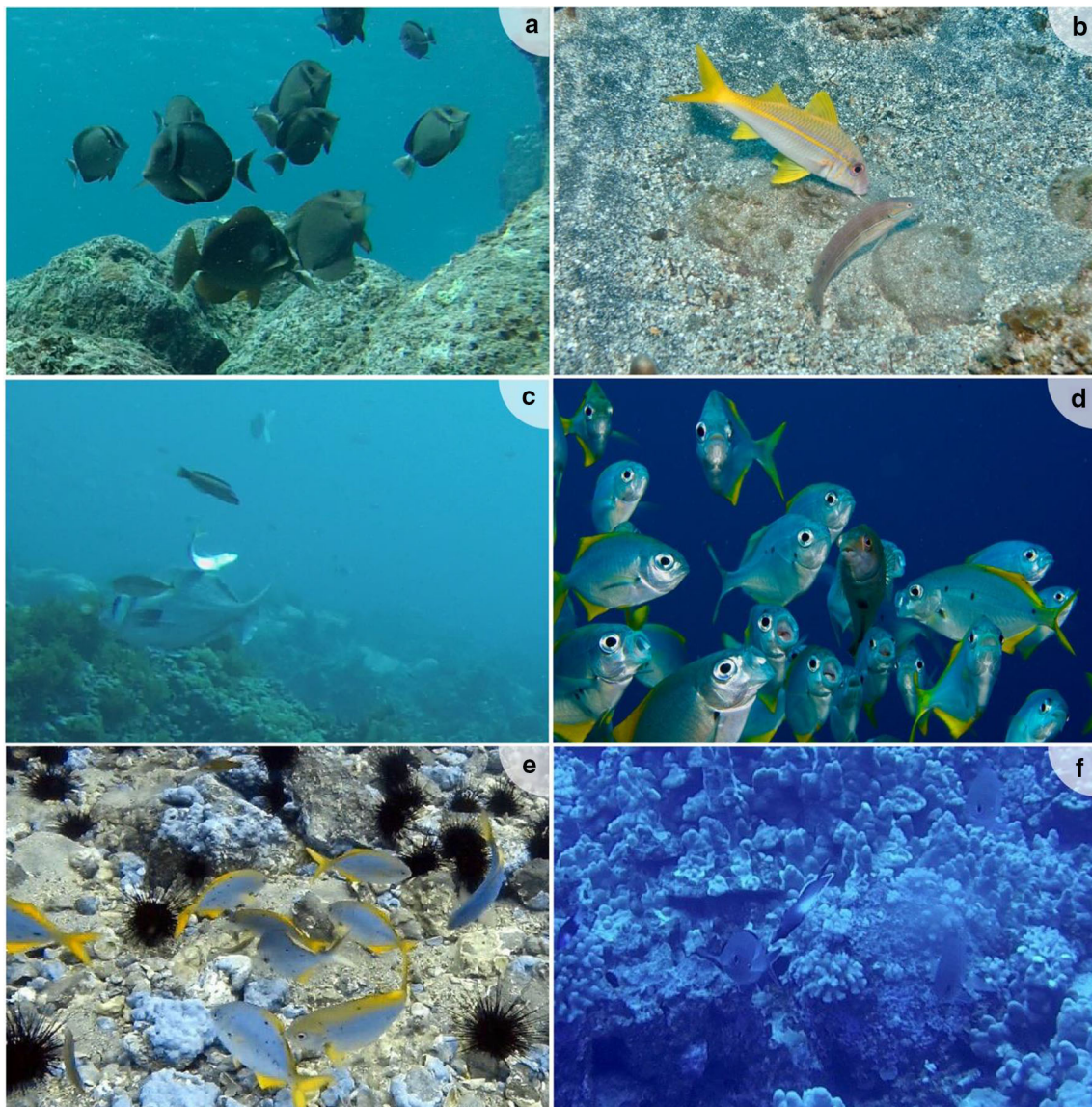
Fig. 2 Diversity of biotic interactions recorded for each reef fish assemblage. **a** dominance hierarchies by *Acanthurus leucopareius*, which display a dark coloration while aggressively chasing other members of the shoal during foraging. **b** foraging group consisting of the nuclear species *Mulloidichthys vanicolensis* followed by *Coris. debueni*. **c** juveniles of *Pseudocaranx chilensis* swim closely to *Nemadactylus gayi*, where after a previous touch, they quickly proceed to self-groom on the client's body. **d** a group of juveniles of *Scorpis chilensis* following *Malapterus reticulatus* with the mouth constantly open, waiting to grab discarded food. **e** cleaning station on substrate covered by calcareous algae: adult of pampanito *S. chilensis* swims near the substrate posing while *Malapterus reticulatus* inspects their body surface. **f** "tipi tipi uri" *Chaetodon litus* inspecting the body surface of a posing damselfish "mamata" *Chromis randalli*

wrasses) were not considered in the study because of possible misidentification due to the similarity between species.

We estimated the frequency of occurrence of each interaction in the reef fish assemblage observed as an index of interaction strength (see Morais et al. 2017; Nunes et al. 2020). As seen in other mutualistic interactions (e.g., plant–pollinator), the frequency of interaction between two species is considered a good quantitative proxy for interaction strength in large assemblages (see Vazquez et al. 2005; Melián et al. 2009; Novella-Fernandez et al. 2019 for details). We classified and counted each independent event (i.e., encounter between individuals), identifying the transmitter individual and species (actively performing the action), the type of interaction observed (see Table 1), and the receiver individual and species (which actively or passively receives the action). The total length (cm) of each fish was also estimated from field and RUV observations. Finally, an index was obtained of the number interactions per m^2 per hour of monitoring, standardized to the time of

Table 1 Description of the reef fish assemblages of Robinson Crusoe and Rapa Nui

	Robinson Crusoe	Rapa Nui
Number (S) and proportion of species involved (%)	12 (44.4%)	20 (47.5%)
Proportion of endemic species involved (%)	83.3%	45%
Total interaction frequency (N° int event · m^{-2} h^{-1-1})	5.76	4.39
Agonistic interaction frequency (N° int event · m^{-2} h^{-1})	2.62	3.76
Positive interaction frequency (N° int event · m^{-2} h^{-1})	3.14	0.04
Overall Network link density (L/S)	1.8	1.6
Agonistic Network link density (L/S)	1.3	1.5
Positive Network link density (L/S)	1.4	0.9
Overall Network Connectance (L/S^2)	0.15	0.08
Agonistic Network Connectance (L/S^2)	0.15	0.11
Positive Network Connectance (L/S^2)	0.17	0.09

Number (S) and proportion (%) of interacting species from the total reef fish assemblages. Proportion of endemic species involved is the ratio between number of endemic species involved and total species involved. Total interaction frequency is the number of interaction event observed per m^2 per hour (separated into agonistic and positive interaction frequency). Overall network link density is the mean number of biotic interactions per node (separated into agonistic and positive network link density). Overall network connectance: proportion of realized links in the overall networks (separated in agonistic and positive network connectance)

monitoring during which both species co-occurred (estimated by UVC and RUVs).

Data analyses

We used generalized linear models (GLM) to test for differences in the numerical density and richness of the fish assemblages (estimated by UVC) between Rapa Nui and Robinson Crusoe. Due to the nature of the responses variable (counts), we specified Poisson distribution errors with a log-link function to contrast the two islands.

We explored the structure of the ecological networks of Rapa Nui and Robinson Crusoe fish assemblages to study how cohesive and stable each fish community is in terms of their potential agonistic and positive interactions. In order to accomplish this, we assessed the overall interaction network of each island separately. These networks represent a combination of two subnetworks, the agonistic network, which represents aggressive interactions, and the positive network, which represents cleaning and nuclear–follower interactions. In order to understand how network structure varies between islands, we analyzed agonistic and positive interactions both together and separately. We measured the following topological metrics of each overall network and subnetwork: number of species (S), number of links (L), link density (L/S), and directed connectance (L/S^2). Connectance represents the proportion of all potential links among species that are actually realized (Martinez 1991). In our case, this represents how cohesive and stable each assemblage is (Thébault and Fontaine 2010) in terms of the frequency of agonistic and positive interactions of each island. Each network summarizes all of the directed/weighted social interactions, represented as links, between co-occurring species, represented as nodes. The position of the nodes within the network is random.

In order to determine the relative importance of each species within each network and subnetwork, and to find the key species of each assemblage in terms of their overall influence on agonistic and positive interactions, we measured two node (species) metrics: total degree centrality (C_D), which represents the number of interactions established by a node and quantifies the immediate influence of one species on all other interacting species (Delmas et al. 2017), and total interaction strength (IS), which represents the total frequency of each interaction for each species, following previous works (e.g., Delmas et al. 2017; Martín González et al. 2010; Puche et al. 2020).

Finally, in order to investigate the potential linear relationship between interaction strength, degree centrality (C_D), and species abundance within each assemblage, we used a linear regression with 95% confidential intervals over model predictions. We performed one-tailed analysis with a significance level of 0.05. The degree centrality (C_D), interaction strength and fish density of each species were log transformed to improve normality and homoscedasticity. We carried out this analysis using the package "igraph" and "ggpubr" function in R software version 3.2.4 (R Core Team 2017).

Results

A total of 692 min of video for Rapa Nui and 869 min for Robinson Crusoe were successfully obtained by the RUVs (63 video recordings for Rapa Nui and 79 video recordings for Robinson Crusoe), and 7200 min of underwater observations during UVC (48 replicate transects) were completed at each island. The two methods were complementary in registering ecological interactions, though due to the greater temporal coverage, RUVs registered 1.8 times more interactions than direct visual observations (ESM Table A1). Fish species richness across transects was significantly greater on average at Rapa Nui (mean 20.56 ± 3.01 SD) (GLM, z-value = 5.08, $p < 0.001$) compared to Robinson Crusoe (mean 13.13 ± 3.14 SD). The total number of species registered was 40 in Rapa Nui and 27 in Robinson Crusoe. Conversely, fish density was two times greater on average at Robinson Crusoe (mean 2.44 ± 0.87 SD ind $\cdot$ m^{-2}) (GLM, z-value = -2.08, $p < 0.05$) than Rapa Nui (mean 1.17 ± 0.35 SD ind $\cdot$ m^{-2}).

Ecological interactions at Rapa Nui

We observed 20 species involved in at least one of the interactions studied, which accounts for 47.5% of all reef fish species observed (Table 1), and 45% of the interacting species are endemic to Rapa Nui island. We recorded a total frequency of occurrence of 4.39 interactions $\cdot$ m^{-2} h^{-1}, but these were dominated by agonistic interactions (4.34 interactions $\cdot$ m^{-2} h^{-1}), with only 0.05 positive interactions $\cdot$ m^{-2} h^{-1} (Table 1; Fig. 3a). At Rapa Nui, 15 species were involved in agonistic interactions, of which 60% were benthic invertebrate feeders. Among them, primarily adult (> 15 cm) whitebar surgeonfish "ma 'ito" *A. leucopareius* (1.306 n° interactions $\cdot$ m^{-2} h^{-1}), butterflyfish "tipi tipi uri" *Chaetodon litus* (0.71 n° interactions $\cdot$ m^{-2} h^{-1}), south pacific gregory "kōtoti" *Stegastes fasciolatus* (0.708 n° interactions $\cdot$ m^{-2} h^{-1}), and glasseye "mata uira" *Heteropriacanthus cruentatus* (0.429 n° interactions $\cdot$ m^{-2} h^{-1}) were the most common species participating in aggressive chasing (Table 2, Fig. 3a).

Two species were recorded as cleaners at Rapa Nui, which are classified as sessile and mobile invertivores and both of which are known facultative cleaners: *Chaetodon litus* with a frequency of 0.022 n° interactions $\cdot$ m^{-2} h^{-1} (Fig. 2f), and the sunset wrasse "mōri vaihi" *Thalassoma lutescens*—mostly as juveniles, < 10 cm (0.015 n° interactions $\cdot$ m^{-2} h^{-1}) (Fig. 3a). Both species clean host fish alone or in groups of two or three near to the substrate. A total of six fish species were recorded as clients, most commonly the whitebar surgeonfish (0.013 n° interactions $\cdot$

m^{-2} h^{-1}) (Fig. 3a). The interaction was initiated by clients posing and waiting for the cleaning behavior of the cleaners. All cleaning interactions were reported in isolation, and no cleaning stations were recorded.

We recorded two nuclear–follower interactions, both with low frequency of interaction (< 0.01 n° interactions $\cdot$ m^{-2} h^{-1}): the foraging group of benthic mobile invertivorous fishes led by the nuclear species *Mulloidichthys vanicolensis* (yellowfin goatfish "a'avere") and followed by "teteme" *Coris debueni* (Fig. 2b) (one or two individuals) and juveniles (< 20 cm) of the carnivorous thick-lipped jack "po'opo'o" *Pseudocaranx cheilo* (no more than four individuals) (Fig. 3a), attracted to feeding on resources exposed by the disturbances of *M. vanicolensis*. This interaction occurs on sandy bottoms, mainly outside coral reefs.

Biotic interactions at Robinson Crusoe

We recorded 12 species participating in at least one of the interactions studied, which accounted for 44.4% of all species observed, 83.3% of which are endemic to Robinson Crusoe. We recorded a total frequency of occurrence of 5.76 interactions $\cdot$ m^{-2} h^{-1} (Table 1, Fig. 3b), with a more even distribution among agonistic interactions (2.62 interactions $\cdot$ m^{-2} h^{-1}), and positive interactions (3.14 interactions $\cdot$ m^{-2} h^{-1}) (Table 2; Fig. 3b). At Robinson Crusoe, seven species are involved in agonistic interactions, most commonly the Juan Fernandez "borracho" blenny *Scartichthys variolatus* (1.37 n° interactions $\cdot$ m^{-2} h^{-1}), followed by the carnivore serranid *Hypoplectrodes semicinctum* (0.636 n° interactions $\cdot$ m^{-2} h^{-1}), and the wrasse "vieja" *Malapterus reticulatus* (0.418 n° interactions $\cdot$ m^{-2} h^{-1}) (Table 2, Fig. 3b).

Two endemic species were recorded as cleaners at Robinson Crusoe island, both of which are classified as invertivores and facultative cleaners: the juveniles and adults of *Malapterus reticulatus,* with a frequency of 0.396 interactions $\cdot$ m^{-2} h^{-1} (Figs. 2e, 3b), and the wrasse "vieja gayi" *Pseudolabrus gayi,* with a similar cleaning interaction frequency (0.383 interactions $\cdot$ m^{-2} h^{-1}). Both wrasses were recorded cleaning other species, sometimes simultaneously, on cleaning stations. The cleaning stations were identified as being bounded by rocky areas (< 2 m^2) covered with rodolith algae, and were hotspots of activity including foraging, fish grooming (e.g., individuals are self-cleaning, brushing their body against the substrate, see Sachs 1988) and cleaning interactions (Fig. 2e). Four fish species were registered as clients, most commonly the Chilean sandpaperfish "lenguado" *Paratrachichthys fernandezianus* (0.176 interactions $\cdot$ m^{-2} h^{-1}) (Fig. 3b). Juveniles of *M. reticulatus* were observed cleaning adults
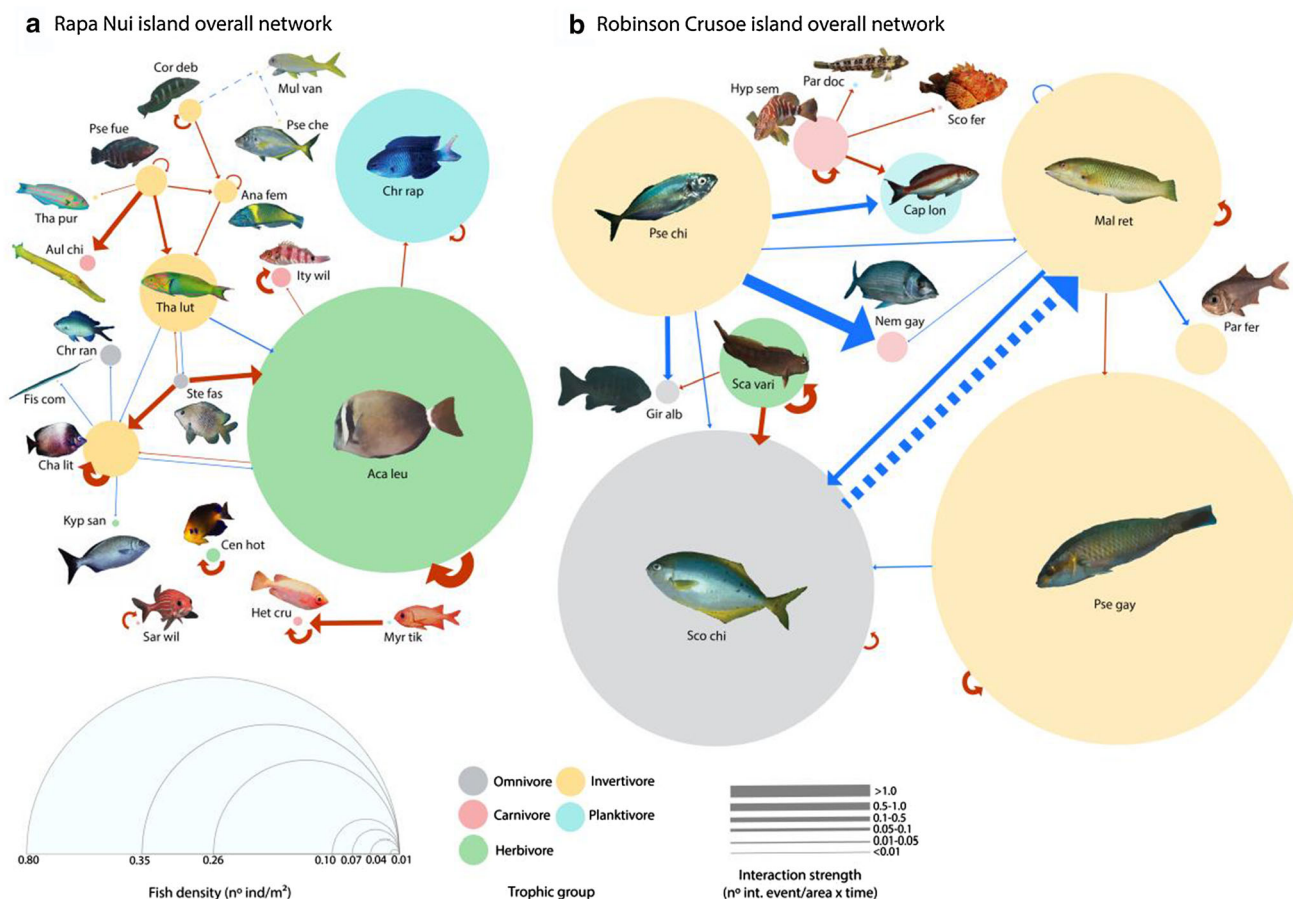
Fig. 3 Ecological interaction networks representing fish interactions at Rapa Nui island (**a**) and Robinson Crusoe island (**b**). The size of each node (circles corresponding to each species) indicates the mean density of each species in the community, and the color represents the trophic group. The thickness of the arrow indicates interaction strength. Agonistic interactions are in red and positive interaction are in blue, with solid arrows indicating cleaning interactions and segmented arrows indicating nuclear–follower interactions. Acronyms are used to abbreviate each species name and correspond to CODE in Table 2

of their own species. These interactions were initiated by clients who were posing and waiting for cleaners.

An unusual interaction was registered between juveniles of the carnivorous jack "jurel de Juan Fernandez" *Pseudocaranx chilensis* and five host species (Fig. 2c). Juveniles of *P. chilensis* swam near the host fish and performed a self-grooming behavior above the host, brushing their body fast against the back or side of the host dorsal fin and body multiple times. Juveniles of *P. chilensis* perform this interaction whether solitary or in groups of 3 or 4 individuals. In few occasions they also separated from the school to perform the interaction and then returned to the group. The various host species *G. albostriata*, *C. longimanus*, *S. chilensis* and *M. reticulatus* changed their behavior during the interaction, accelerating their swimming speed and trying to avoid physical contact with *P. chilensis*. However, large (> 25 cm in TL) individuals of the benthic invertivore morwong "breca de Juan Fernandez" *Nemadactylus gayi* stopped swimming when *P.*

chilensis posed riding the back of *N. gayi*, allowing the grooming behavior of *P. chilensis* (Fig. 2c).

One nuclear–follower association was recorded in Robinson Crusoe with a high frequency of interaction (1.047 interactions $\cdot$ m^{-2} h^{-1}): the foraging group was led by the invertivore *Malapterus reticulatus* and followed by a shoal of omnivore juveniles (< 15 cm, TL) of the sweep "pampanito" *Scorpis chilensis* (Fig. 2d), which were attracted and aggregated to feed from exposed food that crumbled out of the mouth of *M. reticulatus*. This foraging group often attracted more individuals of *S. chilensis*, leading to shoals of more than 40 individuals following a single *M. reticulatus*. Despite the number of followers, no behavioral alteration was observed in *M. reticulatus* (Fig. 3b).

Table 2 List of fish species involved in the biotic interactions recorded in Rapa Nui and Robinson Crusoe

Family	Species	CODE	Agonistic (N° int event/h*m^2)	Positive (N° int event/h*m^2)	Functional group	Endemism
Rapa Nui						
Acanthuridae	*Acanthurus leucopareius*	Aca leu	1.354	0.013	Herbivore	
Aulostomidae	*Aulostomus chinensis*	Aul chi	0.132		Piscivore	
Pomacanthidae	*Centropyge hotumatua*	Cen hot	0.293		Herbivore	RE
Chaetodontidae	*Chaetodon litus*	Cha lit	0.927	0.022	Invertivore	E
Pomacentridae	*Chrysiptera rapanui*	Chr rap	0.130		Planktivore	E
	Chromis randalli	Chr ran			Planktivore	E
	Stegastes fasciolatus	Ste fas	0.708		Omnivore	
Labridae	*Pseudolabrus fuentesi*	Pse fue	0.316		Invertivore	RE
	Anampses femininus	Ana fem	0.208		Invertivore	
	Coris debueni	Cor deb	0.138	0.005	Invertivore	E
	Thalassoma lutescens	Tha lut	0.141	0.015	Invertivore	
	Thalassoma purpureum	Tha pur	0.002		Invertivore	
Fistulariidae	*Fistularia commersonii*	Fis com		0.005	Piscivore	
Priacanthidae	*Heteropriacanthus cruentatus*	Het cru	0.429		Piscivore	
Cirrhitidae	*Itycirrhitus wilhelmi*	Ity wil	0.133		Piscivore	RE
Kyphosidae	*Kyphosus sandwicensis*	Kyp san		0.008	Herbivore	
Mullidae	*Mulloidichthys vanicolensis*	Mul van		0.011	Invertivore	
Holocentridae	*Myripristis tiki*	Myr tik	0.234		Planktivore	RE
	Sargocentron wilhelmi	Sar wil			Piscivore	E
Carangidae	*Pseudocaranx cheilo*	Pse che		0.006	Piscivore	
Robinson Crusoe						
Serranidae	*Caprodon longimanus*	Cap lon	0.142	0.238	Planktivore	
	Hypoplectrodes semicinctum	Hyp sem	0.636		Piscivore	
Girellidae	*Girella albostriata*	Gir alb	0.041	0.434	Omnivore	RE
Labridae	*Malapterus reticulatus*	Mal ret	0.418	1.479	Invertivore	RE
	Pseudolabrus gayi	Pse gay	0.383	0.021	Invertivore	RE
Cheilodactylidae	*Nemadactylus gayi*	Nem gay		1.348	Piscivore	RE
Pinguipedidae	*Parapercis dockinsi*	Par doc	0.119		Invertivore	E
Trachichthydae	*Paratrachichthys fernandezianus*	Par fer		0.176	Invertivore	RE
Carangidae	*Pseudocaranx chilensis*	Pse chi		2.089	Invertivore	RE
Blenniidae	*Scartichtys variolatus*	Sca var	1.370		Herbivore	RE
Scorpaenidae	*Scorpaena fernandeziana*	Sco fer	0.078		Piscivore	RE
Kyphosidae	*Scorpis chilensis*	Sco chi	0.522	1.248	Omnivore	RE

Species are listed in phylogenetic order (family). Agonistic and positive interaction rates are expressed as frequency of each interaction type in N° int event/h* m^2. Also shown are the functional feeding group and the level of endemism of each fish species (RE = Regional endemism; E = Local Endemism)

Interaction networks and subnetworks between Oceanic Islands

Link density (L/S) and connectance (L/S^2) were both higher in Robinson Crusoe than Rapa Nui fish assemblages (Table 1). This suggests that Robinson Crusoe has lower species richness than Rapa Nui but a higher proportion of all the potential interactions that the network can have.

There were more species performing agonistic interactions at Rapa Nui than at Robinson Crusoe (Fig. 3). The interaction network and both subnetworks of Robinson Crusoe presented higher connectance than in Rapa Nui (Table 1). At Robinson Crusoe, the positive subnetwork had slightly higher connectance than the agonistic subnetwork, while the contrary occurred in Rapa Nui (Table 1, ESM Fig. A3).

We found that both total interaction strength (Is) and degree centrality (C_D) for each species were linearly correlated with their abundance (Rapa Nui—IS: $F_{(1-18)} = 10.59$, $r^2 = 0.37$ $p = 0.004$, Fig. 4a; C_D: $F_{(1-18)} = 14.99$, $r^2 = 0.45$ $p < 0.001$, Fig. 4c; Robinson Crusoe—IS: $F_{(1-10)} = 16.17$, $r^2 = 0.62$, $p = 0.002$, Fig. 4b; C_D: $F_{(1-10)} = 7.83$, $r^2 = 0.44$, $p = 0.019$, Fig. 4d). We also observed a positive relationship between the IS and C_D of

each species at both Rapa Nui ($F_{(1-18)} = 26.52$, $r^2 = 0.60$, $p < 0.001$, Fig. 4e) and Robinson Crusoe ($F_{(1-18)} = 15.74$, $r^2 = 0.61$, $p < 0.001$, Fig. 4e). In Rapa Nui, we found a positive relationship between C_D and Ab and between Is and C_D in the agonistic subnetwork, and between Is and C_D in the positive subnetwork (ESM Fig. A4 and A5). In Robinson Crusoe, we found a positive relationship between Is and Ab and between Is and C_D in the agonistic
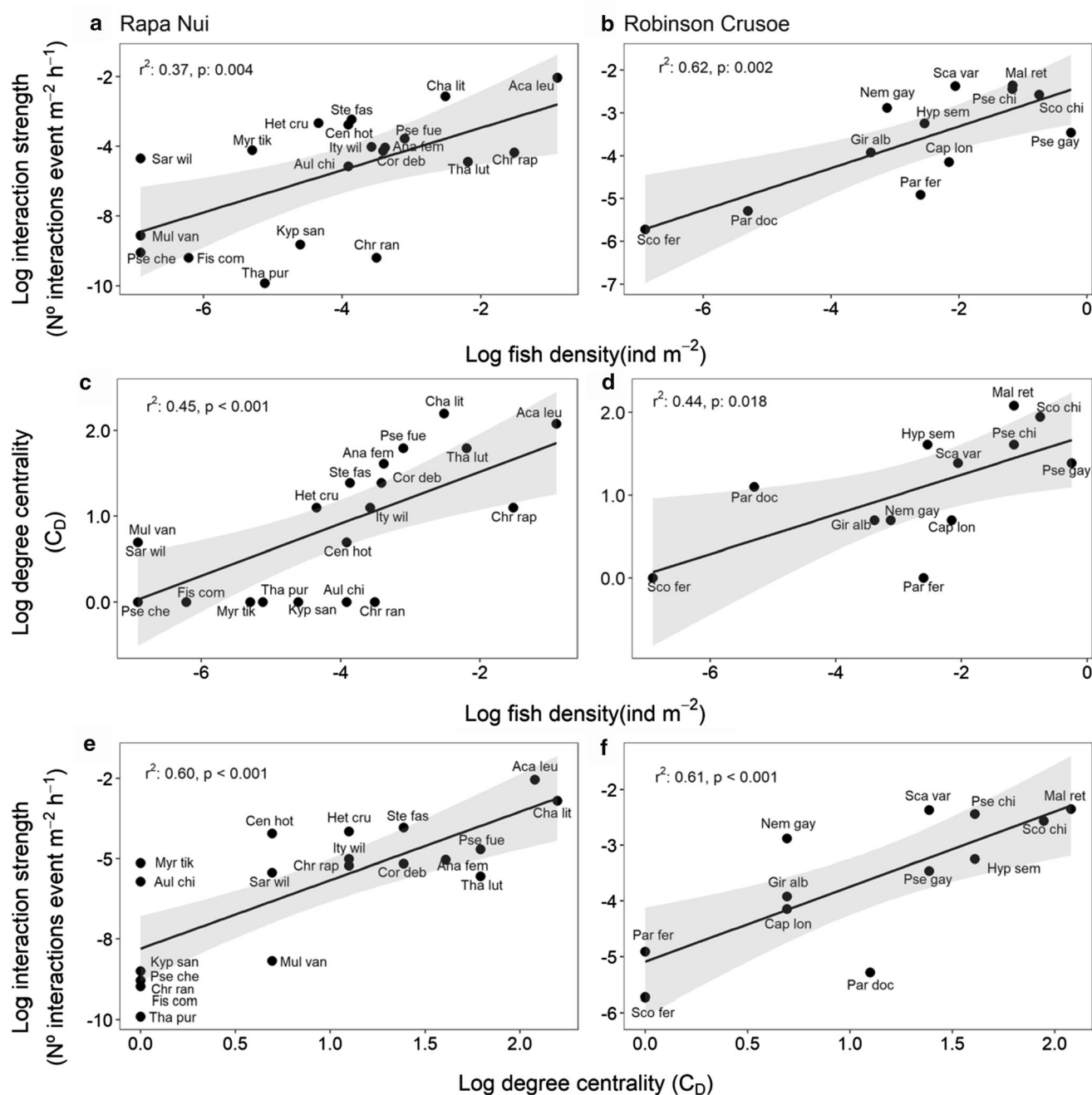

Fig. 4 Relationship between interaction strength and fish abundance in Rapa Nui (**a**) and Robinson Crusoe (**b**), degree centrality (C_D) and mean fish density in Rapa Nui (**c**) and Robinson Crusoe (**d**) and, interaction strength and degree centrality (C_D) in Rapa Nui (**e**) and Robinson Crusoe (**f**). Points represent the corresponding value for each fish species at each island. Acronyms are used to abbreviate each species name as described in CODE in Table 2. Lines represent the trendlines of the linear model and shaded areas represent the 95% CI

subnetwork, and between Is and C_D in the positive subnetwork (ESM Figs. A6 and A7).

Several species stood out in their disproportionate importance in ecological interactions, and the majority of these were endemic species. In Rapa Nui, the endemic butterflyfish *Chaetodon litus* was the most connected species (highest C_D) within the reef fish assemblage (ESM Table A2). In the agonistic subnetwork, *Acanthurus leucopareius* led the centrality measure (ESM Table A3), whereas *Chaetodon litus* led the ranking of the centrality measure in the positive subnetwork (ESM Table A4).

In Robinson Crusoe, the endemic wrasse *Malapterus reticulatus* led the rank of the most connected species (highest C_D) within the reef fish assemblage, following by the endemic *S. chilensis* (ESM Table A5). In the agonistic subnetwork, *Hypoplectrodes semisentum* was the most connected species (highest C_D), followed by *Scartichthys variolatus* (ESM Table A6). In the positive subnetwork, *M. reticulatus* was the most connected species (highest C_D), followed by *P. chilensis* (ESM Table A7).

Discussion

In our study, we observed a variety of complex and strong interactions among reef fish assemblages on two isolated oceanic islands. The majority of interactions observed were carried out by endemic species on both islands, and some of the behaviors reported here have never before been recorded for these species. We found that (a) Rapa Nui presented a higher species richness and low fish density, but higher frequency and number of agonistic interaction links than Robinson Crusoe; (b) despite differences between the two islands in species richness, the number of interaction links, and density of fish, the total frequency of interaction did not differ greatly; (c) the centrality parameters and interaction strength for each species were both correlated with the abundance of individuals; and (d) the proportion of all possible species participating in interactions was similar in both islands. Thus, our findings suggest that between these two low diversity systems, greater species richness does not necessarily present a greater frequency of social interactions in comparison with one with fewer species. In contrast, we found that link density and connectance were negatively associated with fish species richness and positively associated with fish abundance: since Robinson Crusoe has fewer species but greater fish abundance than Rapa Nui, the proportion of all possible interactions observed in the network is higher. This negative relationship between species richness and connectance may infer greater stability if the level of biotic interactions recorded here translate to ecosystem complexity (Rejmanek and Starý 1979; Valdovinos et al. 2009).

We found differences in the relative contribution of agonistic and positive subnetworks at Rapa Nui in comparison with Robinson Crusoe. Agonistic interaction dominated the interaction network at Rapa Nui, where we observed a higher frequency of aggressive behaviors. The predominance of agonistic interactions at Rapa Nui may be influenced by top-down processes such as fisheries, as well as bottom-up processes such as ecosystem productivity (Wilson et al. 2008; Montoya and Raffaelli 2010). Rapa Nui is located in one of the most hyper-oligotrophic marine regions in the world (Morel et al. 2010). Low productivity likely translates into a low food supply at Rapa Nui, which may lead to interference competition that can be expressed as aggression behavior (Robertson 1996; Bonin et al. 2015; Forrester 2015). In comparison, the rocky temperate reefs of the Juan Fernandez Archipelago are more productive with abundant algal and invertebrate food resources, which may reduce competition and the need for territorial aggression. In general, food supply of invertebrates in coral reefs can be rare, forcing invertivore fishes to search for food in soft-bottom areas adjacent to the reef. However, compared with other oligotrophic systems, Rapa Nui limited coverage of soft-bottom habitats, which translates into a restricted infaunal community (Gusmao et al. 2018). In addition, low cover of turf algae and macroalgae in Rapa Nui might limit the abundance of fish herbivores and invertivores (Wieters et al. 2014). This low food availability could augment competitive chases for limited resources (Bonin et al. 2015). Additionally, long-term overfishing in Rapa Nui has drastically reduced the abundance of high trophic level predators and herbivorous fishes (Friedlander et al. 2013; Castilla et al. 2014; Gaymer and Aburto 2020). Fishing effects are comparatively milder on Robinson Crusoe (Friedlander et al. 2013), but it is unclear how removal of fishery target species influences interaction networks. Previous work suggests that a moderate coexistence of multiple interaction types (i.e., agonistic and positive interactions) can stabilize a community, while a skewed composition is likely to destabilize communities (Mougi and Kondoh 2012; Kéfi et al. 2015, 2016). The higher relative importance of agonistic interactions at Rapa Nui could suggest this reef fish community is more vulnerable to perturbation than Robinson Crusoe.

Despite the differences between islands in the frequency of positive interactions, both islands showed few unique positive interactions. All cleaning interactions described here were performed by a few facultative cleaner species, and no dedicated cleaner species were encountered in either system. Cleaning is important for the maintenance of healthy fish communities (Narvaez et al. 2015), and yet this essential behavior is exhibited by very few species at both Rapa Nui and Robinson Crusoe, all of which are endemic and are among the most abundant species of each

assemblage. It is possible that the great abundance of facultative cleaners can fill the gap and maintain the health of the community. The extreme isolation of both islands could also explain the relative paucity of cleaner species (Narvaez et al. 2015). This is in accordance with other studies in remote subtropical and temperate ecosystems, which are characterized by the absence of dedicated cleaner fish and the presence of a few facultative cleaners (e.g., Morais et al. 2017; Narvaez et al. 2015). It is suggested that other nonfish species play an important role in cleaning (Becker and Grutter 2004; Quimbayo et al. 2014; Vaughan et al. 2017) but we did not record these interactions.

Understanding the physiological effects of ecological interactions on the interacting species, such as effects on stress, is crucial to classify an interaction as positive or negative for each species (Apprill 2020). Cleaning interactions have long been the subject of debate regarding the potential influence of this interaction on both cleaners and clients (Poulin and Grutter 2006; Vaughan et al. 2017). Some visual or tactile communication must be transmitted between cleaners and clients to initiate cleaning behavior (Losey and Margules 1974; Vaughan et al. 2017) and can be considered a positive social behavior itself (Soares et al. 2011). We recorded similar interactions in several species at both islands, except for the unusual interaction between the jack *P. chilensis* and the species *N. gayi, S. chilensis, M. reticulatus,* and *G. albostriata*. *P. chilensis* performs a self-grooming behavior using the body surface of these species, as is commonly observed when fish scrape themselves against hard substrates (Sachs 1988). We observed that most of the larger fish species hold a stationary swim, probably to receive the physical contact that the jack is performing. The high frequency of occurrence of this interaction (i.e., grooming) in the fish assemblage of Robinson Crusoe and the preference to perform this grooming behavior on fish instead of the benthic substrate suggests a strong relationship between *P. chilensis* and *N. gayi*, probably motivated to interact with each other such that both species reduce stress from the physical stimulation.

Another important positive interaction is that of nuclear–follower feeding groups. This kind of interaction can increase total feeding rates, foraging time and habitat availability for participating species, with potential effects on individual fitness, assemblage dynamics, and overall rates of energy transfer (Inagaki et al. 2019). The most common interaction on Robinson Crusoe is a nuclear–follower association occurring between two of the most abundant fish species, the feeding association between the wrasse *Malapterus reticulatus* and juvenile *Scorpis chilensis*. Ramirez et al. (2013) found that the diet of *S. chilensis* juveniles was more similar to that of *M. reticulatus* than with adults of *S. chilensis*, which feed mainly on

algae. We believe that the widespread and generalist feeding behavior of *M. reticulatus* could be so advantageous for young *S. chilensis* to easily obtain food that the distribution of the nuclear species could condition the distribution of the follower species, as evidenced by the large number of *S. chilensis* attracted to a single foraging *M. reticulatus*. Our observations of previously undescribed behavior underscore the immense capacity of remote islands to generate unique interactions between endemic species (Morais et al. 2017).

Quantitative assessment of species' roles within interaction networks is key to understanding the functioning of ecological communities (Jordán et al. 2008), especially in response to perturbations such as changes in primary productivity or commercial fishing, which could directly affect the abundance of interacting species (see Ávila-Thieme et al. 2021). Central species tend to be better connected and consequently are more likely to affect other species in the network when their abundance or distributions change (Gonzalez et al. 2010; Delmas et al. 2017; Cagua et al. 2019). In both systems, we found that few species were responsible for the majority of unique interactions observed (high degree centrality), most of which were endemic species. Few species can be responsible for key ecological interaction, even in species-rich communities (Hoey and Bellwood 2009), and our results show that different endemic species could be playing similar and important roles in the fish assemblages of Rapa Nui and Robinson Crusoe. It is unclear whether endemic species may influence ecologically important interactions differently than those of non-endemic congeners within an ecosystem (see Gorman et al. 2014). In oceanic isolated island, endemic species can be locally abundant and contribute greatly to the biodiversity of the community (Delrieu-Trottin et al. 2019; Friedlander et al. 2020). However, restricted geographic distribution and low gene flow make endemic species vulnerable to extinction, necessitating an understanding of the importance of novel interactions by endemic species for the conservation of oceanic island marine ecosystems.

Our study is the first to describe ecological interactions in agonistic and positive networks between fishes in the assemblages of Rapa Nui and Robinson Crusoe. In both islands, the majority of participating species are endemic, which highlights the importance of endemics in isolated oceanic islands (Friedlander et al. 2020). Further research could focus on evaluating the importance of these interactions within each assemblage and their effects on the fitness of participating species. In a recent study, Fontoura et al. (2020) found striking similarities of agonistic interactions across global variation in biodiversity patterns. Among reef fishes, these interactions are shown to be idiosyncratic among closely related and functionally

similar species (Fontoura et al. 2020). The integration of these different studies is important to understand the mechanisms underlying the structure of reef fish communities on isolated islands and the factors affecting interaction networks.

References

Allen GR (2008) Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. Aquat Conserv Mar Freshw Ecosyst 18:541–556

Angelini C, Altieri AH, Silliman BR, Bertness MD (2011) Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience 61:782–789

Apprill A (2020) The role of symbioses in the adaptation and stress responses of marine organisms. Ann Rev Mar Sci 12:291

Ávila-Thieme MI, Corcoran D, Pérez-Matus A, Wieters EA, Navarrete SA, Marquet PA, Valdovinos FS (2021) Alteration of coastal productivity and artisanal fisheries interact to affect a marine food-web. Sci Rep 11:1765

Bay LK, Jones GP, McCormick MI (2001) Habitat selection and aggression as determinants of spatial segregation among damselfish on a coral reef. Coral Reefs 20:289–298

Becker JH, Grutter AS (2004) Cleaner shrimp do clean. Coral Reefs 23:515–520

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193

Bonin MC, Boström-Einarsson L, Munday PL, Jones GP (2015) The prevalence and importance of competition among coral reef fishes. Annu Rev Ecol Evol Syst 46:169–190

Bshary R, Grutter AS (2002) Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. Anim Behav 63:547–555

Canterle AM, Nunes LT, Fontoura L, Maia HA, Floeter SR (2020) Reef microhabitats mediate fish feeding intensity and agonistic interactions at Príncipe Island Biosphere Reserve, Tropical Eastern Atlantic. Mar Ecol 00:e12609

Castilla JC, Yáñez E, Silva C, Fernández M (2014) A review and analysis of Easter Island's traditional and artisan fisheries. Lat Am J Aquat Res 42:690–702

Cagua EF, Wootton KL, Stouffer DB (2019) Keystoneness, centrality, and the structural controllability of ecological networks. J Ecology 107:1779–1790

Cowman PF, Parravicini V, Kulbicki M, Floeter SR (2017) The biogeography of tropical reef fishes: endemism and provinciality through time. Biol Rev 92:2112–2130

Delmas E, Brose U, Gravel D, Stouffer DB, Poisot T (2017) Simulations of biomass dynamics in community food webs. Methods Ecol Evol 8:881–886

Delrieu-Trottin E, Brosseau-Acquaviva L, Mona S, Neglia V, Giles EC, Rapu-Edmunds C, Saenz-Agudelo P (2019) Understanding the origin of the most isolated endemic reef fish fauna of the Indo-Pacific: Coral reef fishes of Rapa Nui. J Biogeogr 46:723–733

Elton C, Nicholson M. (1942). The Ten-Year Cycle in Numbers of the Lynx in Canada. J Anim Ecol 11: 215-244

Forrester GE (2015) Competition in reef fishes. Ecology of Fishes on Coral Reefs. Cambridge University Press 34–40

Fontoura L, Cantor M, Longo GO, Bender M, Bonaldo RM, Floeter SR (2020) The macroecology of reef fish agonistic behavior. Ecography 43:1278–1290

Floeter SR, Vázquez DP, Grutter AS (2007) The macroecology of marine cleaning mutualisms. J Anim Ecol 76:105–111

Friedlander AM, Ballesteros E, Beets J, Berkenpas E, Gaymer CF, Gorny M, Sala E (2013) Effects of isolation and fishing on the marine ecosystems of Easter Island and Salas y Gómez, Chile. Aquat Conserv 23:515–531

Friedlander AM, Ballesteros E, Caselle JE, Gaymer CF, Palma AT, Petit I, Varas E, Wilson AM, Sala E (2016) Marine biodiversity in Juan Fernández and Desventuradas islands, Chile: Global endemism hotspots. PLoS One 11: p.e0145059

Friedlander AM, Donovan MK, DeMartini EE, Bowen BW (2020) Dominance of endemics in the reef fish assemblages of the Hawaiian Archipelago. J Biogeogr 00:1–13

Gaymer CF, Aburto JA (2020) Conservation of Rapa Nui waters strongly supported by publications in Aquatic Conservation. Aquat Conserv 30: 1765–1769

Gibbs JP, Sterling EJ, Zabala FJ (2010) Giant tortoises as ecological engineers: a long-term quasi-experiment in the Galápagos Islands. Biotropica 42:208–214

González AMM, Dalsgaard B, Olesen JM (2010) Centrality measures and the importance of generalist species in pollination networks. Ecological Complexity 7:36–43

Gorman CE, Potts BM, Schweitzer JA, Bailey JK (2014) Shifts in species interactions due to the evolution of functional differences between endemics and non-endemics: An endemic syndrome hypothesis. PLoS One 9:e111190

Gross K (2008) Positive interactions among competitors can produce species-rich communities. Ecol Lett 11:929–936

Gusmao JB, Lee MR, MacDonald I, Ory NC, Sellanes J, Watling L, Thiel M (2018) No reef-associated gradient in the infaunal communities of Rapa Nui (Easter Island)–Are oceanic waves more important than reef predators?. Estuar Coast Shelf Sci 210: 123–131

Hamilton IM, Dill LM (2003) The use of territorial gardening versus kleptoparasitism by a subtropical reef fish (*Kyphosus cornelii*) is influenced by territory defendability. Behav Ecol 14:561–568

Hoey AS, Bellwood DR (2009) Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. Ecosystems 12:1316–1328.

Inagaki KY, Mendes TC, Quimbayo JP, Cantor M, Sazima I (2019) The structure of fish follower-feeding associations at three

oceanic islands in southwestern Atlantic. Environ Biol Fishes 103:1–11

Jordán F, Okey TA, Bauer B, Libralato S (2008) Identifying important species: linking structure and function in ecological networks. Ecol Modell 216:75–80

Kane CN, Brooks AJ, Holbrook SJ, Schmitt RJ (2009) The role of microhabitat preference and social organization in determining the spatial distribution of a coral reef fish. Environ Biol Fishes 84:1–10

Kéfi S, Berlow EL, Wieters EA, Joppa LN, Wood SA, Brose U, Navarrete SA (2015) Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores. Ecology 96:291–303

Kéfi S, Miele V, Wieters EA, Navarrete SA, Berlow EL (2016) How structured is the entangled bank? the surprisingly simple organization of multiplex ecological networks leads to increased persistence and resilience. PLOS Biol 14:e1002527

Kindinger TL (2016) Symmetrical effects of interspecific competition on congeneric coral-reef fishes. Mar Ecol Prog Ser 555:1–11

Longo GO, Floeter SR (2012) Comparison of remote video and diver's direct observations to quantify reef fishes feeding on benthos in coral and rocky reefs. J Fish Biol 81:1773–1780

Longo GO, Hay ME, Ferreira CE, Floeter SR (2018) Trophic interactions across 61 degrees of latitude in the Western Atlantic. Glob Ecol Biogeogr 28:107–117

Losey GS, Margules L (1974) Cleaning symbiosis provides a positive reinforcer for fish. Science 184:179–180

Macaya EC, Riosmena-Rodríguez R, Melzer RR, Meyer R, Försterra G, Häussermann V (2015) Rhodolith beds in the South-East Pacific. Mar Biodivers 45:153–154

Martinez ND (1991) Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. Ecol Monogr 61:367–392

Martín González AM, Dalsgaard B, Olesen JM (2010) Centrality measures and the importance of generalist species in pollination networks. Ecol. Complex 7:36–43

Melián CJ, Bascompte J, Jordano P, Křivan V (2009) Diversity in a complex ecological network with two interaction types. Oikos 118:122–130

Montoya JM, Raffaelli D (2010) Climate change, biotic interactions and ecosystem services. Proc R Soc Lond B Biol Sci 365:2013–2018

Morais RA, Brown J, Bedard S, Ferreira CEL, Floeter SR, Quimbayo JP, Rocha LA, Sazima I (2017) Mob rulers and part-time cleaners: Two reef fish associations at the isolated Ascension Island. J Mar Biol Assoc U K 97:799–811

Morel A, Claustre H, Gentili B (2010) The most oligotrophic subtropical zones of the global ocean: Similarities and differences in terms of chlorophyll and yellow substance. Biogeosciences 7:3139–3151

Mougi A, Kondoh M (2012) Diversity of interaction types and ecological community stability. Science 337:349–351

Narvaez P, Furtado M, Neto AI, Moniz I, Azevedo JMN, Soares MC (2015) Temperate facultative cleaner wrasses selectively remove ectoparasites from their client-fish in the Azores. Mar Ecol Prog Ser 540:217–226

Novella-Fernandez R, Rodrigo A, Arnan X, Bosch J (2019) Interaction strength in plant-pollinator networks: Are we using the right measure?. PLoS One 14:1–15

Nunes LT, Morais RA, Longo GO, Sabino J, Floeter SR (2020) Habitat and community structure modulate fish interactions in a neotropical clearwater river. Neotrop Ichthyol 8:e190127

Peiman KS, Robinson BW (2010) Ecology and evolution of resource-related heteroespecific aggression. Q Rev Biol 85:133–158

Pérez-Matus A, Ramirez F, Eddy TD, Cole R (2014) Subtidal reef fish and macrobenthic community structure at the temperate Juan Fernandez Archipelago, Chile. Lat Am J Aquat Res 42:814–826

Poulin R, Grutter AS (2006) Cleaning symbiosis: proximate and adaptive explanations. Bioscience 46:512–517

Puche E, Rojo C, Ramos-Jiliberto R, Rodrigo MA (2020) Structure and vulnerability of the multi-interaction network in macrophyte-dominated lakes. Oikos 129:35–48

Quimbayo JP, Floeter SR, Noguchi R, Rangel CA, Gasparini JL, Sampaio CLS, Ferreira CEL, Rocha LA (2014) Cleaning mutualism in Santa Luzia (Cape Verde Archipelago) and São Tomé Islands, Tropical Eastern Atlantic. Mar Biodivers Rec 5 e118:5

Quimbayo JP, Cantor M, Dias MS, Grutter AS, Gingins S, Becker JHA, Floeter SR (2018a) The global structure of marine cleaning mutualistic networks. Glob Ecol Biogeogr 27:1238–1250

Quimbayo JP, Schlickmann ORC, Floeter SR, Sazima I (2018b) Cleaning interactions at the southern limit of tropical reef fishes in the Western Atlantic. Environ Biol Fishes 101:1195–1204

Ramírez F, Pérez-Matus A, Eddy TD, Landaeta MF (2013) Trophic ecology of abundant reef fish in a remote oceanic island: coupling diet and feeding morphology at the Juan Fernandez Archipelago, Chile. J Mar Biol Assoc UK 93:1457–1469

Randall JE, Cea A (2011) Shore fishes of Easter Island. University of Hawai'i Press

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rejmanek M, Stary P (1979) Conectance in real biotic communities and critical values for stability of model ecosystems. Nature 280:311–313

Robertson DR (1996) Interspecific copetition controls abundance and habitat use of territorial caribbean damselfishes. Ecology 77:885–899

Robinson SK, Terborgh J (1995) Interspecific Aggression and Habitat Selection by Amazonian Birds. J Anim Ecol 64:1–11

Sabino J, Andrade LP, Sazima I, Teresa F, Floeter SR, Sazima C, Bonaldo RM (2017) Following fish feeding associations in marine and freshwater habitats. Mar Freshw Res 68:381–387

Sachs BD (1988) The Development of grooming and its expression in adult animals. Ann N Y Acad Sci 525:1–17

Sazima C, Krajewski JP, Bonaldo RM, Sazima I (2007) Nuclear-follower foraging associations of reef fishes and other animals at an oceanic archipelago. Environ Biol Fishes 80:351–361

Soares MC, Oliveira RF, Ros AFH, Grutter AS, Bshary R (2011) Tactile stimulation lowers stress in fish. Nat Commun 2:534–535

Teresa FB, Sazima C, Sazima I, Floeter SR (2014) Predictive factors of species composition of follower fishes in nuclear-follower feeding associations: a snapshot study. Neotrop Ichthyol 12:913–919

Thébault E, Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. Science 329:853–856

Titus BM, Palombit S, Daly M (2017) Endemic diversification in an isolated archipelago with few endemics: an example from a cleaner shrimp species complex in the Tropical Western Atlantic. Biol J Linn Soc 122:98–112

Valdovinos FS, Ramos-Jiliberto R, Flores JD, Espinoza C, López G (2009) Structure and dynamics of pollination networks: the role of alien plants. Oikos 118:1190–1200

Valeix M, Fritz H, Sabatier R, Murindagomo F, Cumming D, Duncan P (2011) Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. Biol Conserv 144: 902–912

Vaughan DB, Grutter AS, Costello MJ, Hutson KS (2017) Cleaner fishes and shrimp diversity and a re-evaluation of cleaning symbioses. Fish Fish 18:698–716

Vázquez DP, Morris WF, Jordano P (2005) Interaction frequency as a surrogate for the total effect of animal mutualists on plants. Ecol Lett 8:1088–1094

Wieters EA, Medrano A, Pérez-Matus A (2014) Functional community structure of shallow hard bottom communities at Easter Island (Rapa Nui). Lat Am J Aquat Res 42:827–844

Wilson SK, Fisher R, Pratchett MS, Graham NAJ, Dulvy NK, Turner RA, Cakacaka A, Polunin NVC, Rushton SP (2008). Exploitation and habitat degradation as agents of change within coral reef fish communities. Glob Chang Biol 14:2796–2809