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The global structure of marine cleaning mutualistic networks

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Abstract

Aim: We studied the underlying biotic and abiotic drivers of network patterns in marine cleaning mutualisms (species feeding upon ectoparasites and injured tissues of others) at large spatial scales.

Location: Eleven marine biogeographical provinces.

Time period: 1971–2018.

Major taxa studied: Reef fish and shrimps.

Methods: We combined field and literature data to test whether recurrent patterns in mutualistic networks (nestedness, modularity) describe the distributions of marine cleaning interactions. Nested network structures suggest that some cleaner species interact with many clients while the others clean fewer, predictable subsets of these clients; modular network structures suggest that cleaners and clients interact within defined, densely connected subsets of species. We used linear mixed models to evaluate whether the life-history traits of cleaners contribute to the emergence of these patterns locally and whether environmental and geographical factors influence the network structures.

Results: Marine cleaning networks were more nested than modular. Nestedness was prevalent in communities with dedicated cleaners (ones that feed exclusively by cleaning), whereas communities with only facultative cleaners (ones that clean opportunistically) were generally unstructured. Cleaner type and taxa were the only traits shaping networks, with dedicated fish cleaners contributing disproportionally more than facultative cleaners and shrimps to the emergence of nestedness. Although cleaner species seem concentrated around the tropics and biodiversity centres, we did not detect an influence of environmental and geographical factors on network structures.

Main conclusions: Dedicated species are key in shaping the structure of marine cleaning mutualistic networks. By relying exclusively on cleaning to feed, dedicated cleaners interact with most of the available clients and form the network core, whereas the opportunistic facultative species tend to clean the most common clients. We hypothesize that trophic niche variation and phenotypic specialization are major drivers of this asymmetry in marine mutualisms. Our study strengthens the links between biotic interactions at the community level and the distribution of species and specializations at larger spatial scales.

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KEYWORDS
cleaner–client, dedicated–facultative cleaners, ecological network, marine mutualism, modularity, nestedness, resource partitioning

1 | INTRODUCTION

Every species is involved in intricate webs of ecological interactions. A persistent challenge in ecology is to unravel the interplay between ecological and evolutionary processes shaping these interactions. Recent years have seen a surge in the study of the resultant ecological networks, aiming to disentangle the underlying drivers of their structure (e.g., Andreazzi, Thompson, & Guimarães, 2017; Bascompte, Jordano, Mélián, & Olesen, 2003; Fontaine et al., 2011) and reveal the implications of this structure for individual fitness, population structure and community dynamics (e.g., Bascompte & Jordano, 2007; Pascual & Dunne, 2006). Although the bulk of the work comes from studies at the local community scales, the latest research has been tackling the timely challenge of assessing general assembling principles of ecological networks at large spatial scales (e.g., Martín-González et al., 2015; Zanata et al., 2017). Mutualisms are at the forefront of this trend.

We can now appreciate how recurrent structural patterns of mutualistic networks vary at macroecological scales (e.g., Schleuning et al., 2012; Trøjelsgaard, Jordano, Carstensen, & Olesen, 2015) owing to the environment (e.g., Sebastián-González, Dalsgaard, Sandel, & Guimarães, 2015), phylogeny (e.g., Rezende, Lavabre, Guimarães, Jordano, & Bascompte, 2007) and the degree of phenotypic specialization of the interacting species (e.g., Bascompte & Jordano, 2007; Vázquez, Chacoff, & Cagnolo, 2009). However, most attention has been given to mutualisms in terrestrial environments, particularly animal–plant interactions describing pollination and seed dispersal. We know considerably less about animal–animal mutualisms in the ocean (but see Guimarães, Sazima, dos Reis, & Sazima, 2007; Ollerton, McCollin, Fautin, & Allen, 2007; Sazima, Guimarães, dos Reis, & Sazima, 2010; Thompson, Adam, Hultgren, & Thacker, 2013). For example, little is known about how marine mutualistic networks are structured at large spatial scales and whether such structures are explained by similar drivers to the terrestrial mutualisms.

In the marine environment, cleaning is a conspicuous mutualistic interaction, in which a cleaner species benefits from feeding upon ectoparasites and tissue from the body of another, client species (Côté, 2000). Cleaning mutualism can also influence local abundance and species diversity by promoting population and community health (e.g., Bshary, 2003; Waldie, Blomberg, Cheney, Goldizen, & Grutter, 2011). In tropical and subtropical waters, *c.* 259 species of two taxa (teleost fish and decapod crustaceans) engage in cleaning behaviour (Vaughan, Grutter, Costello, & Hutson, 2017). Some species do so only temporarily (during the juvenile stage) or opportunistically, and are hereafter called "facultative" cleaners; other species specialize in cleaning throughout their lifetime, hereafter called "dedicated" cleaners (Vaughan et al., 2017). Such varying degrees of specialization in cleaning, as well as the distribution of cleaning interactions, can provide insights into the fundamental and realized foraging niche of cleaner species within marine communities (Floeter, Vázquez, & Grutter, 2007; Sazima et al., 2010). Cleaning mutualisms are influenced by multiple characteristics of cleaners and clients, such as morphology, size, behaviour, trophic group and abundance (Baliga & Mehta, 2015; Cheney, Grutter, Blomberg, & Marshall, 2009; Floeter et al., 2007; Quimbayo, Dias, Schlickmann, & Mendes, 2017). Nevertheless, the contribution of such traits to shaping the mutualistic network at the community level remains poorly understood.

In the last decade, we began to understand that marine cleaning interactions can be distributed asymmetrically within a community because individual species show varying degrees of specialization in cleaning interactions (Barbu, Guinand, Bergmüller, Alvarez, & Bshary, 2011; Guimarães, Sazima, et al., 2007; Sazima et al., 2010). A notable resultof such heterogeneity is the so-called nested pattern, in which the interactions of low-connected species tend to be a subset of interactions of highly connected species (Bascompte et al., 2003; Guimarães, Sazima, et al., 2007). However, the previous studies were restricted in their geographical scope, leaving three crucial knowledge gaps: (a) How widespread these network patterns are at large spatial scales; (b) which main life-history traits explain the disproportionately high cleaning services of some species at the local scale; and (c) which, if any, environmental and geographical factors relate to the emergence of these network patterns. Therefore, it remains uncertain whether nestedness is a recurrent pattern in marine cleaning networks and, if so, the nature of the underlying drivers. Exploration of how the structure of local networks varies across communities globally can shed light into the ecological and evolutionary mechanisms of the phenotypic specializations of species (e.g., Martín-González et al., 2015; Schleuning et al., 2012; Zanata et al., 2017). Here, we compiled a comprehensive empirical dataset on cleaning interactions in 28 marine communities distributed across 11 marine biogeographical provinces world-wide, with three goals in mind.

First, we describe the structure of marine cleaning mutualistic networks on a large spatial scale. As observed in animal–plant mutualisms, we expected that cleaning networks can be either modular, in which interactions are compartmentalized into sets of cleaner and client species that interact more often with each other than with the rest (e.g., Olesen, Bascompte, Dupont, & Jordano, 2007; Zanata et al., 2017), or nested, in which interactions are hierarchically organized so that some cleaner species interact with many client species and others tend to interact with fewer, proper subsets of these clients (e.g., Bascompte et al., 2003; Guimarães, Sazima, et al., 2007).

Second, given that cleaner species differ in their efficiency to attract clients (e.g., Cheney et al., 2009), we sought to identify which, if any, life-history traits influence the distribution of cleaning interactions and so contribute to structure networks locally. Specifically, we tested whether the level of exclusivity to mutualism (i.e., whether cleaners are facultative or dedicated; see Guimarães, Rico-Gray, et al., 2007; Thompson et al., 2013) along with a range of other biological traits (taxa, advertising coloration, water column position, body and group size) are associated with the number of client species with which they interact. We hypothesize that networks are nested in the presence of cleaners (either fish or shrimp) that are specialized and efficient, such as those that are dedicated, small-bodied, coloured, form larger groups and dwell at the seafloor. These traits (or a combination thereof) could improve the cleaning service and the detection of clients by cleaners or vice versa (see also Cheney et al., 2009; Quimbayo, Dias, et al., 2017; Vaughan et al., 2017). Alternatively, we hypothesize that modular cleaning networks can emerge if there is resource-use partitioning amongst morphologically and/or behaviourally distinct cleaners. For instance, when fish and shrimp cleaners co-occur, shrimps may target clients associated with the seafloor (Quimbayo, Nunes, et al., 2017) that might not be the focus of fish cleaners in the water column. Finally, we test whether the structure of emergent marine cleaning networks varies at a macroecological scale, where environmental and geographical factors (sea temperature, primary productivity, isolation and distance from a centre of biodiversity) are associated with species turnover and the composition of marine communities and thus indirectly affect the biotic interactions therein (e.g., Pellissier et al., 2017). We hypothesize that cleaning networks can be nested in less-productive sites distant from their biodiversity centre, where there may be less clients available, and that networks can be modular in productive and connected sites where clients abound.

2 | MATERIALS AND METHODS

2.1 | Data sampling

We collected and compiled data on cleaning interactions amongst marine species from 28 marine communities in 11 marine biogeographical provinces (defined for reef fish fauna; see Kulbicki et al., 2013). These were the Caribbean, the Southwestern, Central, North and Eastern Atlantic, the Western Indian, the Central Indo-Pacific and the Southwestern, Central, Northeastern and Tropical Eastern Pacific (Figure 1 Supporting Information Tables S1 and S2). Out of the 28 sites, we empirically recorded cleaning interactions in seven of them (Curaçao, Fernando de Noronha, St Paul's Rocks, Trindade, Príncipe, Red Sea and Galápagos Islands) through direct observations during dedicated SCUBA dive surveys. We considered a cleaning interaction as the directed physical contact between individuals, involving bites from one species (cleaner) on another (client), which can result in the removal of ectoparasites, injured or dead tissue (such as skin and scales) and/or mucus (see Johnson & Ruben, 1988).

The rest of the data were from a systematic review of the literature. We first gathered all the studies cited in the comprehensive, recent reviews on marine cleaning interactions by Côté (2000) and Vaughan et al. (2017). Then, we used electronic databases and search engines (Web of Science, Scopus and Google Scholar) to look for primary studies and grey literature that provide cleaning interaction data as supplement or in tables and figures. We used combinations of the following search terms, in English, Portuguese and Spanish: cleaning interactions, marine cleaning mutualism, cleaning symbiosis, shrimp cleaners, fish cleaners, marine clients, facultative cleaners, obligate cleaners and dedicated cleaners. We considered only studies with more than a single cleaner species because we were interested in depicting the local cleaner–client network structure rather than acquiring a comprehensive description of cleaner species distribution. Finally, we minimized the potential effects of varying sampling effort across studies by focusing on the incidence, not the strength, of the cleaning interactions. That is, we converted all quantitative interactions into qualitative ones to focus only on the topologies of the network.

2.2 | Network structure

We described the mutualistic interactions between cleaner and client species in each site using binary two-mode networks (Boccaletti, Latora, Moreno, Chavez, & Hwang, 2006). A mutualistic network was defined by an adjacency matrix **M**, in which the element $m_{ij} = 1$ when the cleaner species i was empirically observed interacting with the client species j, and $m_{ij} = 0$ otherwise. In the network depiction, nodes representing cleaners were linked to nodes representing clients (Supporting Information Figure S1). We first calculated the connectance of all networks (Supporting Information Table S1) as the proportion of realized cleaning interactions given the total possible interactions (Boccaletti et al., 2006). Then, we evaluated the global structure of each local network using metrics that describe two common, and generally competing, structural patterns of mutualistic networks: nestedness and modularity.

Nestedness describes an asymmetric, hierarchical distribution of interactions amongst species (e.g., Bascompte et al., 2003); here it indicates that some marine species clean most of the client species available locally, whereas others tend to clean subsets of these clients (Guimarães, Sazima, et al., 2007). Modularity describes a compartmentalized distribution of interactions amongst species (e.g., Olesen et al., 2007); here it is indicative of the degree of specificity of the cleaner–client interactions (e.g., Martín-González et al., 2015), as a modular network would contain highly connected and almost non-overlapping subsets (modules) representing cleaner species interacting more often with a subset of the available pool of client species. We quantified nestedness with the metric *NODF* based on the concepts of overlap and decreasing fill of the adjacency matrix

(Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008). We quantified modularity with the metric Q that measures the difference between the observed fraction of links connecting species in the same module and the fraction expected by chance (Newman, 2006) using an algorithm modified for two-mode networks (Dormann & Strauss, 2013).

We assessed the significance of nestedness and modularity using a null model approach. We built null distributions of *NODF* and Q-values for each local network by randomizing their observed cleaning interactions for 1,000 iterations, while constraining the observed size (i.e., same number of cleaner and client species) and connectance. We used an algorithm that randomizes interactions amongst species based on the empirical observations (i.e., row and column sums; Bascompte et al., 2003). Each cell of the theoretical matrices had a probability of being filled that was proportional to the observed number of interactions of both cleaners and clients, defined as: $c_{ij} = \frac{1}{2}\left(\frac{P_i}{C} + \frac{P_j}{R}\right)$, where P_i = number of cleaners that interacted with the client i (row sums); P_j = number of client species cleaned by the cleaner j (column sums); C = number of cleaner species (columns); and R = number of client species (rows). The observed nested or modular structure of a local network was considered significant when its empirical *NODF* and Q-values, respectively, lay outside of the 95% confidence intervals of their corresponding null distributions. Finally, we used unpaired Student's t tests to compare network connectance and the cleaner : client ratio between communities with only facultative cleaners and communities also containing dedicated cleaners.

2.3 | Contribution of cleaner species to the network structure

To estimate the contribution of cleaner species to the network structure, we evaluated the influence of each species on the emergence of the nested and modular patterns. After controlling for local differences in the observed number of interactions across cleaner species, we defined whether the overall nestedness and modularity of the network were changed by the presence of each cleaner. For each species in a given network, we compared the *NODF* and the Q of the entire network with the *NODF* and Q-values, respectively, obtained by randomizing only the interactions of that target species (Saavedra, Stouffer, Uzzi, & Bascompte, 2011). To randomize the interactions of the target species, we used the same null model described above. The cleaner species i was deemed a strong contributor to nestedness or modularity when, respectively, the *NODF* and the Q-value of the network whose interactions of the species i were randomized were consistent and close to the *NODF* and Q of the original network. We calculated the *Z-scores* of *NODF* and Q to compare all individual cleaners of each network; positive *Z-scored NODF* and *Z-scored* Q of a given species indicated that it contributed to an increase in the nestedness and modularity of the entire network, respectively, whereas negative values indicate otherwise (Saavedra et al., 2011).

2.4 | Influence of biological traits of cleaners on local network structure

To assess the extent to which cleaner traits influence the structure of mutualistic networks, we used linear mixed models (LMMs) to relate their life-history traits to their individual nestedness and modularity contributions (see below). We considered the relationship between cleaning efficiency and behaviour, functional and morphological traits (Figure 1; Supporting Information Table S3) as follows:

1. Taxa (fish or shrimp): species of these taxonomic groups vary both morphologically (e.g., vertebrate vs. invertebrate) and in the types of clients they target (Côté, 2000).
2. Type of cleaner (dedicated or facultative): this trait indicates the level of dependence and/or specialization on cleaning interactions for feeding, given that dedicated cleaners depend exclusively on cleaning activities to obtain food, whereas facultative cleaners perform the activity opportunistically or only during juvenile stages (Vaughan et al., 2017).
3. Coloration (number of body colours): distinctive colours that contrast with the background are associated with conspicuousness and signalling of the status of the cleaner to clients (Cheney et al., 2009).
4. Body size (maximum total length reported in centimetres; Froese & Pauly, 2017): cleaners species of different sizes may target different clients (Baliga & Mehta, 2015; Côté, 2000; Floeter et al., 2007).
5. Water column position (bottom/medium/top): cleaners more associated with the bottom could have different clients available from cleaners that stay in medium and higher positions of the water column (Johnson & Ruben, 1988; Quimbayo, Nunes, et al., 2017).
6. Group size [solitary, pair, small (3–20), medium (20–50) or large (>50 individuals)]: the number of individual cleaners can influence the time and efficiency of their cleaning service, in which larger groups are typically quicker to clean a client than smaller groups (Côté, 2000).

2.5 | Influence of environmental and geographical factors on network structure

We used LMMs to evaluate whether environmental and geographical factors that influence local species composition could indirectly influence the structure (nestedness and modularity) of cleaning mutualistic networks (see Pellissier et al., 2017). To allow comparisons amongst localities, we standardized both the nestedness (*NODF*) and the modularity (Q) of each network as *Z-scores* (e.g., Sebástián-González et al., 2015): $Z = [(Observed - Mean_{null})/SD_{\mathrm{null}}]$, where *Observed* was the empirical values of *NODF* or Q of a given network, $Mean_{null}$ was the average *NODF* or Q values of all null model matrices, and SD_{null} was their standard deviation. We used the Bio-ORACLE

FIGURE 1 Mutualistic interactions between client and cleaner species. Illustrative examples of the six biological traits of cleaners considered: taxa (fish/shrimp), type (dedicated/facultative), coloration, body size, water column position (bottom to top) and group size. (a) *Elacatinus phthirophagus* cleaning the head of a great Barracuda (*Sphyraena barracuda*) off Fernando de Noronha archipelago. (b) White-striped shrimps (*Lysmata grabhami*) cleaning the mouth of a Brow Moray (*Gymnothorax unicolor*) off Ascension Island. (c) *Bodianus rufus* cleaning a black margate (*Anisotremus surinamensis*) off Fernando de Noronha archipelago. (d) *Thalassoma noronhanum* cleaning a squirrelfish (*Holocentrus adscensionis*) off Rocas Atoll. (e) *Labroides rubrolabiatus* cleaning the grouper *Cephalopholis argus* off Moorea Island. (f) *Bodianus insularis* cleaning a *Pomacanthus paru* off Ascension Island. Photographs by S. R. Floeter (a, c, e), J. P. Quimbayo (d) and J. Brown (b, f) [Colour figure can be viewed at wileyonlinelibrary.com]

database (Tyberghein et al., 2012) to obtain data for two environmental factors in each locality: annual mean sea surface temperature (in degrees Celsius) and primary productivity (mean surface clorophyll *a* concentration) estimated from satellite imaging. We then measured three geographical factors for each locality: latitude, isolation and distance from centres of biodiversity. Isolation was the minimum distance (in kilometres) from mainland (or the nearest reef when appropriate); and the distance from biodiversity centres was measured considering the Caribbean for the Atlantic localities (Floeter et al., 2008) and the Indo-Australian Archipelago (Kulbicki et al., 2013) for the rest.

2.6 | Construction and validation of linear models

We built LMMs with a Gaussian distribution for both biological traits and environmental/geographical factors. To analyse the biological traits, we combined data of all cleaner species (units of analysis) from all the 28 localities and built two LMMs, one whose dependent variable was the contribution of cleaner species to nestedness and another with the contribution of cleaner species to modularity. In both models, all the six life-history traits described above were independent variables (set as fixed factors), and localities were set as a random effect variable (i.e., random intercept model). To analyse the environmental and geographical factors, we combined data of all 28 localities (units of analysis) and built two other LMMs, one with *Z-scored NODF* and the other with *Z-scored* Q as dependent variables, all environmental and geographical factors as independent variables (set as continuous fixed factors) and the marine biogeographical provinces as random factors to control for variation between provinces. Additionally, we considered the number of cleaner species in each locality as a fixed factor to account for differences in the sampling effort between studies. We evaluated the significance of all predictors with likelihood ratio tests (LRTs), dropped non-significant ($p > 0.05$) individual predictors from the full model and calculated significant differences in model fit based on χ^2 distributions.

Before building LMMs, we examined potential collinearity amongst independent variables (predictors) using Pearson correlations, in which $r < 0.60$ was considered a cut-off for keeping predictors in the models (Supporting Information Figures S2 and S3). After the model fitting, we calculated the variance inflation factor (VIF) to ensure that predictors were not correlated with each other (the final model presents low multicollinearity, with VIF < 2; Tables 1 and 2). Based on geographical coordinates of each locality and model residuals, we estimated Moran's I index using the inverse of the Euclidean distance amongst localities as weights. Overall, Moran's I indicated no spatial autocorrelation in the model residuals (nestedness: $I = -0.007 \pm 0.018$, $p = 0.53$; modularity: $I = -0.03 \pm 0.018$, $p = 0.26$; Supporting Information Figures S4 and S5); therefore, it

TABLE 1 Effects of biological traits on the individual contribution of cleaner species to nestedness and modularity of mutualistic networks based on LMMs

	Nestedness contribution			Modularity contribution			
Biological traits	**Estimate**	**LTR**	***p*-value**	**Estimate**	**LTR**	***p*-value**	**VIF**
Taxa		4.42	0.04**		3.18	0.07*	1.68
Fish	0.49			1.09			
Shrimp	−0.35			1.67			
Cleaner type		17.26	< 0.01**		0.13	0.71	1.79
Facultative	0.88			1.2			
Dedicated	1.88			1.08			
Coloration	0.14	0.82	0.36	0.05	0.16	0.69	1.29
Body size	−0.02	1.81	0.18	−0.01	0.27	0.6	1.88
Water column position		3.19	0.2		0.58	0.64	1.9
Bottom	0.07			1.07			
Medium	0.08			1.35			
Top	0.62			1.27			
Group size		1.6	0.81		2.49	0.64	1.85
Large	0.42			1.34			
Medium	0.09			1.21			
Small	0.27			1.01			
Pair	0.49			1.15			
Solitary	0.50			1.38			
Sample size (n)	140			140			
Local variability (random effect SD)	0.5			0.61			
Model residual	1.04			1.55			

Note. Traits are considered as fixed factors and locality as a random factor. The variance inflation factor (VIF) is shown for individual predictors of both models. **p <0.05; *marginal significance (0.05 < p <0.10) estimated through likelihood ratio tests (LRTs). SD = Standard Deviation.

TABLE 2 Effects of environmental and geographical factors on the large-scale structure of marine cleaning mutualistic networks based on linear mixed-effect models

	Z-scored nestedness			*Z-scored* modularity			
Factors	**Estimate**	**LRT**	***p*-value**	**Estimate**	**LRT**	***p*-value**	**VIF**
Local cleaner richness	0.44	3.65	0.06	−0.15	0.81	0.37	1.12
Environmental							
Sea surface temperature	0.1	0.03	0.86	0.04	0.01	0.91	1.74
Primary productivity	−0.59	1.74	0.19	−0.02	0.004	0.95	1.06
Geographical							
Latitude	−0.02	0.97	0.32	−0.01	0.3	0.58	1.27
Isolation	−1.05	2.34	0.13	−0.57	1.4	0.23	2.45
Distance from biodiversity centre	0.81	2.43	0.12	0.32	0.8	0.37	1.4
Sample size (n)	28			28			
Marine biogeographical province variability (random effect SD)	0.0001			0.0001			
Model residual	6.32			0.32			

Note. LRT = likelihood ratio test. Marine biogeographical provinces were considered as a random factor, whereas local cleaner richness and all environmental and geographical variables were considered as fixed factors (sea surface temperature, primary productivity, latitude, isolation and distance from biodiversity centre). The variance inflation factor (VIF) is shown for individual predictors of both models.

was not necessary to use spatial models to control for this source of variation nor to correct the degrees of freedom of our models. All analyses were performed in the R environment, v. 3.2.4 (R Core Team, 2016).

3 | RESULTS

We recorded 480 client species and 85 cleaner species (Supporting Information Table S1), out of which 86% were facultative ($n = 62$ fish, $n = 11$ shrimps) and 14% were dedicated cleaners ($n = 9$ fish, $n = 3$ shrimps; Supporting Information Table S2). Our database comprised about a third of all marine cleaner species (Vaughan et al., 2017) and contained 50% of all species recognized as dedicated cleaners and 28% of the facultative cleaners (Supporting Information Table S4). Cleaner shrimps may be under-represented in the literature due to difficulties in observing such cryptic, crevice-living and often nocturnal organisms. There were more cleaner species sampled in the Atlantic ($n = 88$) than in the Pacific ($n = 46$) and Indian ($n = 6$) ocean basins (Figure 2a; Supporting Information Table S2).

The number of cleaners per locality did not show a latitudinal trend, yet observations were mostly in tropical waters (−20, +20° latitude; Figure 2b). Despite large variability, the number of cleaners per locality showed a slightly increasing trend towards eastern longitudes (Figure 2b). Dedicated cleaners were more commonly found in the Caribbean, Southwestern Atlantic and Central Pacific, whereas facultative cleaners were distributed more homogeneously across all marine biogeographical provinces (Figure 2b; Supporting Information Table S2). Nevertheless, we note that these distributions reflect the network sizes, not cleaner diversity *per se*; that is, the number of cleaners here indicate the species sampled in each network, which might reflect the number of studies carried out in each biogeographical province but does not necessarily represent their total cleaner species richness.

Half of the localities contained both dedicated and facultative cleaners ($n = 14$), and the other half contained only facultative cleaners ($n = 14$; Figure 2a; Supporting Information Figure S1). The ratio of cleaner species per client species was lower in localities with both types of cleaners than in facultative-only localities (Student's *t* test, $t = -5.536$, $df = 25.15$, $p < 0.001$; Figure 3a). However, the network connectance (the proportion of realized cleaning interactions) was similar between localities with and without dedicated cleaners ($t = 0.190$, $df = 23.64$, $p = 0.851$; Figure 3b; Supporting Information Table S1).

Overall, cleaning networks were more often nested (15 out 28 localities) than modular (5 out 28 localities; Figure 4; Supporting Information Figure S1), and these metrics showed no strong

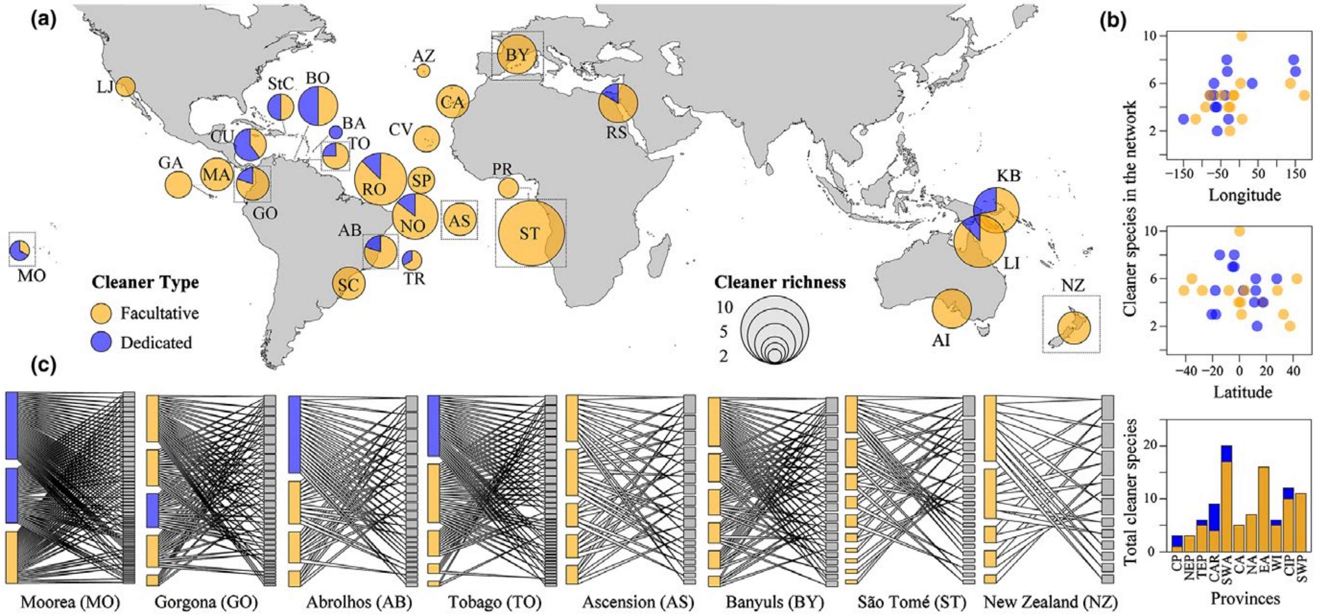

FIGURE 2 Distribution of marine cleaning mutualistic networks. (a) The 28 sampled localities, with pie charts representing the proportion of dedicated and facultative cleaner species and sizes proportional to the total richness of sampled cleaner species (full details in Supporting Information Table S1). (b) Distribution of number of cleaner species in the networks of localities along the longitudinal and latitudinal gradients (blue = localities with both dedicated and facultative; yellow = facultative only) and across marine biogeographical provinces (Central, Northeastern and Tropical Eastern Pacific; Caribbean, Southwestern, Central, North and Eastern Atlantic; Western Indian; Central Indo-Pacific and Southwestern Pacific; see Supporting Information Tables S1 and S2). (c) Representative cleaning networks of the localities (dashed boxes in the map) with both dedicated (blue) and facultative cleaners (yellow) and localities with only facultative cleaners. Cleaners are linked to client species (grey) by binary links whenever they were observed interacting. Cleaning networks of all localities are in Supporting Information Figure S1 [Colour figure can be viewed at wileyonlinelibrary.com]

latitudinal or longitudinal trends (Supporting Information Figure S6). Networks with dedicated cleaners had high *NODF* values, and most of them (79%) were more nested than expected by chance (Figure 4a). In contrast, most networks with only facultative cleaners were not nested (71%; Figure 4b). The opposite was found for modularity: facultative-only localities tended to have higher *Q*-values (Figure 4d) than localities with dedicated cleaners (Figure 4c), and we emphasize that most of the *Q*-values were not different from the null expectancy. Only three out of 28 localities were both nested and modular (all with dedicated cleaners; Figure 4).

Nested networks were characterized by a core of cleaners interacting with most clients, along with more peripheral cleaners interacting with the highly connected clients (Figure 2c). Dedicated cleaners were often, but not always, central species in the networks (Figure 2c; Supporting Information Figure S1). Cleaner type was the most important biological trait, followed by taxa, in explaining the positive contribution of cleaners to nestedness across all networks (Table 1). Dedicated cleaners showed significantly higher contributions to the emergence of nestedness than facultative cleaners (Figure 1 and Table 1; Supporting Information Table S3), whereas fish cleaners contributed more than shrimps (Table 1; Supporting Information Figure S7). All other traits (coloration, position in the water column, body and group sizes) did not significantly contribute to the emergence of nestedness (Table 1). Although shrimp cleaners contributed more than fish to the emergence of the few modular networks (marginally significant effect of taxa; Table 1; Supporting Information Figure S8), none of the other biological traits was related to the contribution of cleaners to modularity (Table 1). Finally, the emergence of nestedness and modularity was unrelated to both environmental (temperature and primary productivity) and geographical (latitude, isolation and distance from biodiversity centres) factors (Table 2).

4 | DISCUSSION

Our study reveals that the biological traits of species are key in structuring mutualisms in marine communities. At macroecological scales, marine cleaning mutualistic networks with dedicated cleaners repeatedly display a hierarchical, nested architecture, in contrast to the generally unstructured networks containing only facultative cleaners. Cleaner taxa play a minor role in structuring these networks, and the effects, if any, of environmental and geographical factors were not detected. Nestedness in cleaning interactions being mainly dependent on dedicated fish species implies that the level of interaction specificity drives the asymmetry of the distribution of biotic interactions, (Guimarães, Rico-Gray, et al., 2007; Thompson et al., 2013) at both local and large spatial scales.

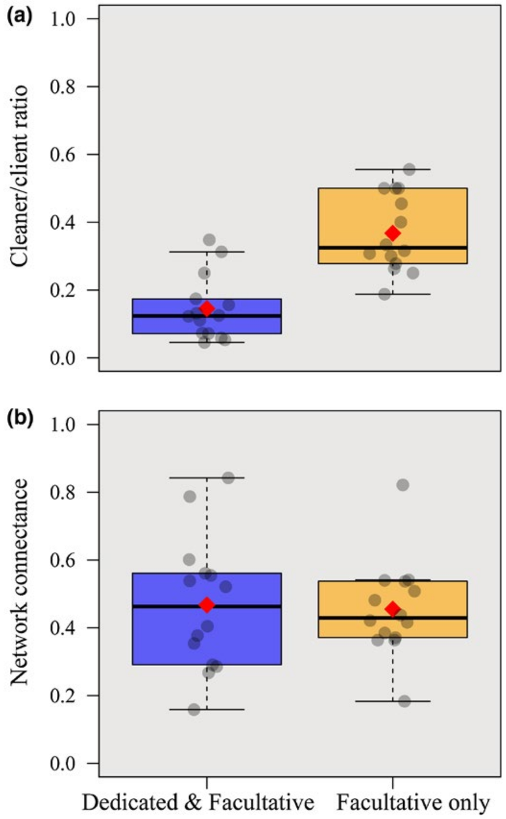

FIGURE 3 Proportion of species and mutualistic interactions in communities containing different cleaner types. (a) Number of sampled cleaner species per client species. (b) Network connectance in all mutualistic networks of ecological communities with dedicated and facultative cleaners ($n = 14$) and in localities with only facultative cleaners ($n = 14$). Network connectance is the proportion of realized links (observed cleaning interactions) given the possible number of interactions. Box plots indicate the median (horizontal line), mean (diamond), first and third quartiles (box), range of values excluding outliers (whiskers) and the observed data (grey circles) [Colour figure can be viewed at wileyonlinelibrary.com]

4.1 | Marine cleaning networks are more nested than modular

We detected non-random mutualistic interactions in marine communities around the world. Heterogeneity in local distributions of cleaning services reflects variation in the use of clients as food resources by cleaners. Modular networks suggest marked niche partitioning and specialization (e.g., Olesen et al., 2007), whereas nested networks suggest hierarchical niche overlap and varying degrees of generalization and specialization in mutualistic interactions (e.g., Guimarães, Sazima, et al., 2007). The lack of modularity in most of the cleaning networks indicates that specific groups of cleaners interacting with specific groups of clients are rare. Moreover, we found only a minor contribution of shrimps in promoting modular networks, suggesting that in some localities shrimps might use a slightly different set of clients from the fish cleaners, possibly resulting from the the nocturnal habits of shrimps and their preference for rock/reef crevices where clients are more limited. However, in most communities, shrimps share clients with cleaner fish of similar life history, such as small-bodied species that form small groups near the seafloor (e.g., Figure 1a; Johnson & Ruben, 1988; Quimbayo, Nunes, et al., 2017). Indeed, the typically nested cleaning networks imply that resource use amongst cleaners often overlaps in such a way that some cleaners interact with many clients and others interact only with predictable subsets of the most interactive clients.

4.2 | Dedicated mutualists shape marine cleaning networks

A key finding is that such nested cleaning networks primarily occurred in marine communities containing dedicated cleaners. The level of dependence between the interacting species can result in markedly different network structures, which is evident in intimate and non-intimate biological interactions. High-interaction intimacy networks, such as ant–myrmecophyte and gobies–shrimp symbioses, have high reciprocal specialization and are therefore highly compartmentalized (Blüthgen, Menzel, Hovestadt, Fiala, & Blüthgen, 2007; Guimarães, Rico-Gray, et al., 2007; Thompson et al., 2013). In contrast, low-interaction intimacy networks, such as seed dispersal and cleaning mutualisms, contain relatively loose interactions and therefore have overall low specificity and tend to be nested (e.g., Bascompte et al., 2003; Guimarães, Sazima, et al., 2007). Our study further suggests that the level of reliance on the interactions itself (i.e., being dedicated or not to it) can also influence the network structure and promote nestedness.

Dedicated species adopt cleaning as an exclusive foraging strategy, whereas facultative species are opportunists (Côté, 2000; Vaughan et al., 2017). Therefore, dedicated cleaners target most of the available clients, becoming highly connected species at the core of the network. In contrast, facultative cleaners exploit other food sources and may clean fewer clients as opportunities arise, for instance, clients that are common or use the same habitat. This asymmetry in foraging specificity leads to nestedness (Guimarães, Sazima, et al., 2007), which we found to be prominent in communities where dedicate and facultative cleaners co-occur. In localities with only facultative cleaners, their use of clients overlaps more because they clean when juveniles or when predation risk is low (Côté, 2000; Vaughan et al., 2017) and therefore eventually and sporadically interact with the entire pool of clients, hindering the emergence of nestedness.

Through behavioural and morphological adaptations, dedicated cleaners might be able to provide a better cleaning service, attract more clients, and thus take over a large part of the cleaning activities that might otherwise be performed by opportunistic facultative cleaners. The connectance of the networks with dedicated cleaners is very similar to the connectance of facultative-only networks, although in the latter the number of cleaners is higher. This suggests that few dedicated cleaners can clean similar proportions of clients cleaned by many facultative species (i.e., the cleaning service is more

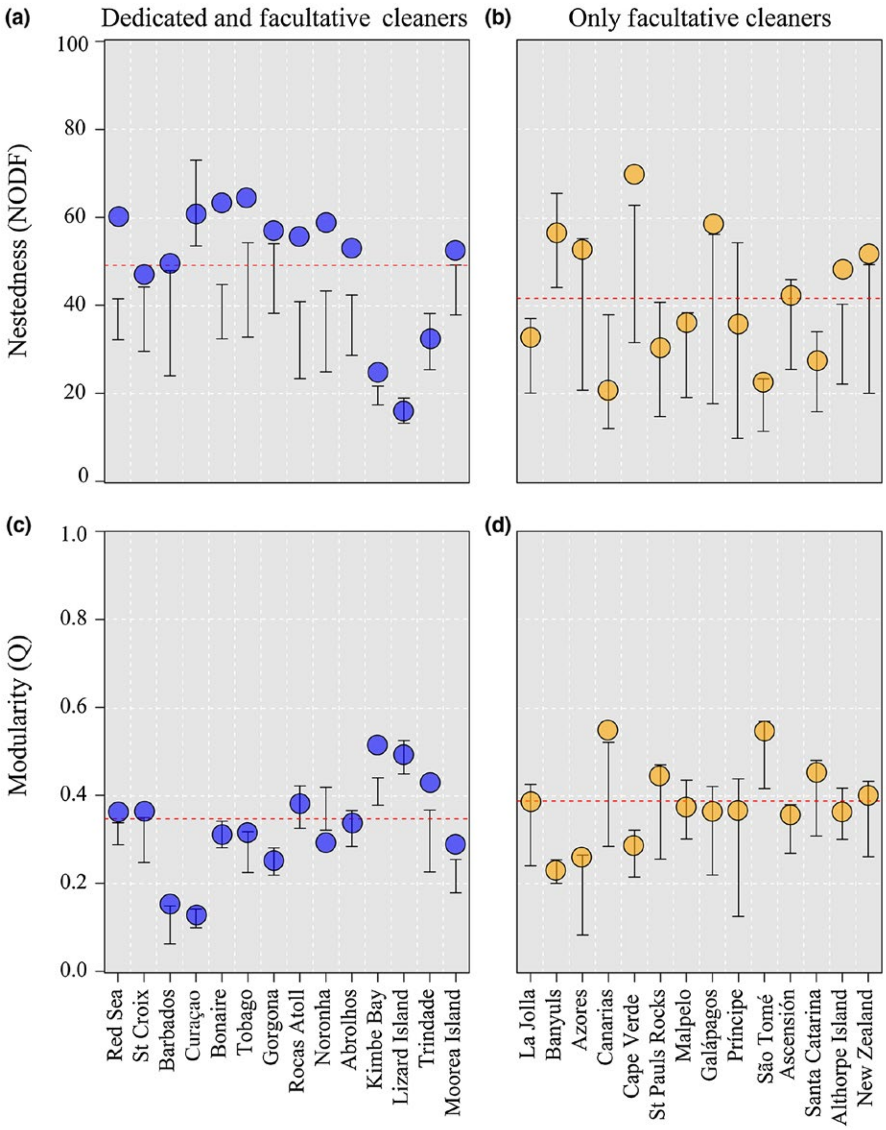

FIGURE 4 Network topological metrics of marine cleaning networks. Nestedness (*NODF*) and Modularity (*Q*) of cleaning networks in localities with both dedicated and facultative cleaner species (a, c) and in localities with only facultative cleaners (b, d). Red dotted lines represent mean *NODF* and *Q*-values. Significantly nested or modular networks display empirical values (circles) outside the 95% confidence intervals generated by null models (whiskers). Localities are ordered by decreasing latitude [Colour figure can be viewed at wileyonlinelibrary.com]

efficient where dedicated species are present; Quimbayo et al., 2012; Sazima et al., 2010). Moreover, where dedicated species are missing, more species engage in cleaning (Quimbayo, Schlickmann, Floeter, & Sazima, 2018); for example, in Cape Verde and São Tomé Island, where multiple cleaner species stations are the norm and parasite-loaded clients seem vehemently to "request" cleaning from facultative cleaners (Quimbayo et al., 2012). However, where dedicated *Labroides* cleaners occur, few opportunities are left for the less-effective facultatives (Barbu et al., 2011). Morphological and behavioural adaptations of dedicated cleaners seem fundamental for their overall effectiveness.

Dedicated cleaners often have coloured bodies (Cheney et al., 2009), with dark lateral stripes associated with yellow or blue, strongly contrasting with background (Arnal, Verneau, & Desdevises, 2006; Cheney et al., 2009). They also show more cleaning-specific cognitive skills (Gingins & Bshary, 2016) and higher escape performance than facultatives (Gingins, Roche, & Bshary, 2017). Finally, their usual small bodies may facilitate interaction with a large range of clients (Vaughan et al., 2017). Although these traits may make dedicated cleaners more attractive to clients, our results showed that colour, body size and behaviour do not explain the distribution of cleaning interactions at the community level. This corroborates the apparent lack of relationship between cleaning and body morphology (Arnal et al., 2006; Côté, 2000) and suggests that life-history traits other than specificity in cleaning play a minor role, if any, in structuring cleaning networks. Nevertheless, we acknowledge that our coarse, first-order measures of behaviour and morphology might have failed to capture subtle differences that could influence cleaning behaviour; we assessed coloration patterns as the number of human-visible colours, and the variation in body size turned out to be too low. Quantifying more accurate proxies of cleaner performance will help to illuminate the influence of the traits of cleaners on mutualistic networks.

4.3 | Cleaning at large spatial scales

Cleaning mutualism occurs in all ocean basins, forming networks that, although structured in different ways, are similar in containing a relatively low richness of cleaners. Although one caveat here is the inherent incompleteness of our database, the number of cleaners around the globe, especially the dedicated ones, is strikingly small: only 16 fish species and eight shrimp species from two families each (Vaughan et al., 2017; Supporting Information Table S4). After controlling for the total local cleaner richness, we found no geographical or environmental influence on the structure of the resulting cleaning networks. This contrasts with terrestrial mutualisms, in which climatic seasonality and past climate stability can lead to modular or nested networks (e.g., Schleuning et al., 2014; Sebástián-González et al., 2015).

Marine cleaning interactions and dedicated cleaners are apparently more common towards tropical latitudes. In animal–plant mutualisms, tropical ecosystems have lower network specialization (i.e., low modularity and high nestedness) than temperate counterparts. Avian seed dispersal in temperate regions tends towards modules of frugivorous species specialized on particular fruiting plants, suggesting niche partition (Dalsgaard et al., 2017). In contrast, as obligate frugivory is more common among tropical birds, the consumption of fruiting plants in these regions overlaps more, leading to nested, non-modular networks (e.g., Bascompte et al., 2003; Schleuning et al., 2014). Likewise, our nestedness results support low network specialization in marine cleaning mutualism in tropical and subtropical areas (Quimbayo et al., 2018). If evolutionary processes can influence the specificity of ecological interactions (Thompson et al., 2013), low resource-use specialization in tropical areas could have followed the evolution of obligate mutualists (Dalsgaard et al., 2017; Schleuning et al., 2014), here the dedicated cleaners.

The number of dedicated cleaner species is not directly proportional to the regional species pool or to their clade diversity (Baliga & Law, 2016), probably owing to the rarity of trait combinations that favour cleaning behaviour over evolutionary time: small body size (Baliga & Law, 2016), aposematic colours (Cheney et al., 2009) and signalling behaviour to the clients (Côté, 2000). Dedicated cleaners are restricted to only two fish genera (*Labroides* and *Elacatinus*) and four shrimps genera (*Lysmata*, *Ancylomenes*, *Periclimenes* and *Urocaridella*), which share these cleaning-facilitating traits (Sims et al., 2014; Taylor & Hellberg, 2005). If such traits are conserved along phylogenies and influence the set of clients for the bearer, they could ultimately shape mutualistic networks (e.g., Martín-González et al., 2015; Schleuning et al., 2014). The evaluation of phylogenetic signals in mutualistic networks remains challenging because it requires phylogenies on both sides of the interaction (e.g., Martín-González et al., 2015; Rezende et al., 2007), but it is a promising avenue for resolving whether evolutionary pathways of teleost fish and shrimps modulate cleaning mutualisms.

5 | CONCLUSIONS

Dedicated, more efficient cleaner species shape the global structure of marine cleaning mutualism. The presence of such obligate mutualists modulates trophic niche variation amongst species in marine communities, driving the asymmetry in marine cleaning at local and large spatial scales. The rarity of modular networks suggests that cleaning specialization is not as marked at the community level as it is at the species level. Instead, the recurrence of nested networks in communities with dedicated cleaners suggests that the partitioning of clients as resources happens hierarchically, in which dedicated cleaners tend to interact with many clients and facultatives tend to interact with the most common clients. Phenotypic specialization, and the resultant trophic niche variation, are key underlying mechanisms that shape the structure of mutualistic networks in the ocean.

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DATA ACCESSIBILITY

Data can be found at the Zenodo data repository: https://doi.org/10.5281/zenodo.1253028.

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BIOSKETCHES

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J.P.Q., M.C., M.S.D., and S.R.F. conceived the idea. J.P.Q. and M.C. analysed the data, and M.S.D. contributed to coding and to interpretation of results. J.P.Q., S.G., A.S.G., J.A.H.B. and S.R.F. collected data, and J.P.Q. compiled data from the literature. J.P.Q. and M.C. wrote the paper and led the revisions, and M.S.D., S.R.F., S.G. and A.S.G. critically reviewed several versions of the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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