



What makes a species central in a cleaning mutualism network?

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Mutualisms often form networks of interacting species, characterized by the existence of a central core of species that potentially drive the ecology and the evolution of the whole community. Centrality measures allow quantification of how central or peripheral a species is within a network, thus informing about the role of each species in network organization, dynamics, and stability. In the present study we addressed the question whether the structural position of species in the network (i.e. their topological importance) relates to their ecological traits. We studied interactions between cleaner and client reef fishes to identify central and peripheral species within a mutualistic network, and investigated five ecological correlates. We used three measures to estimate the level of centrality of a species for distinct structural patterns, such as the number of interactions and the structural proximity to other species. Through the use of a principal component analysis (PCA) we observed that the centrality measures were highly correlated (92.5%) in the studied network, which indicates that the same species plays a similar role for the different structural patterns. Three cleaner and ten client species had positive values of centrality, which suggests that these species are modulating ecological and evolutionary dynamics within the network. Higher centralities were related to higher abundances and feeding habits for client fishes, but not for cleaners. The high correlation between centrality measures in the present study is likely related to the nested structure of the cleaning network. The cleaner species' set, by having central species that are not necessarily the most abundant ones, bears potentially more vulnerable points for network cohesiveness. Additionally, the present study generalizes previous findings for plant–animal mutualisms, as it shows that the structure of marine mutualisms is also related to a complex interplay between abundance and niche-related features.

Interspecific interactions such as mutualisms are main processes that shape biodiversity by influencing the ecology and the evolution of populations and communities (Thompson 2005, Bascompte and Jordano 2006, Bascompte 2009). At the community level, mutualisms are often organized as interaction networks (Jordano et al. 2006). Exploring the underlying ecological traits that create and shape the network structure is fundamental to understand the organization of ecological communities. Studies that focus on how ecological traits shape network structure of mutualisms are still in early stages (Jordano et al. 2003, Stang et al. 2006, 2007, Krishna et al. 2008), but it is widely accepted that differences in abundances of interacting species play a fundamental role and should be regarded as a null expectation from which to examine structure patterns found for most ecological networks (Vázquez et al. 2005, 2007, Lewinsohn et al. 2006, Floeter et al. 2007, Blüthgen et al. 2008). However, it was recently demonstrated that species-specific features might modulate abundance effects, bringing out the role of niche-related features in the assembly of mutualistic networks (Stang et al. 2006, 2007, Krishna et al. 2008). Current evidence is limited to plant–animal interactions, which raises the question about how general is the relevance

of ecological traits in shaping mutualistic networks (but see Floeter et al. 2007).

Several networks of mutualistic interactions in terrestrial and marine ecosystems are nested (Bascompte et al. 2003, Guimarães et al. 2006, 2007a, 2007b, Ollerton et al. 2007). The causes for the occurrence of the nested pattern are still under debate but available hypotheses indicate that this pattern may be expected due to differences in abundance among species (Vázquez et al. 2005, Lewinsohn et al. 2006, Krishna et al. 2008), coevolutionary convergence and complementarity (Guimarães et al. 2006, Stang et al. 2006, Santamaría and Rodríguez-Gironés 2007), or frequent extinctions of specialist–specialist interactions (Ollerton et al. 2003, 2007). Its origins notwithstanding, a nested network has a central core of species that holds the bulk of interactions (Bascompte et al. 2003). As it has been suggested that these central species may drive the ecology and the evolution of the whole community (Jordano et al. 2006, Bascompte and Jordano 2007, Guimarães et al. 2007a, Bascompte 2009), identifying core species and exploring ecological traits that influence structural position of species relates to fundamental questions on community organization (Martín González et al. 2009). Additionally, since species are not equivalent

in their patterns of interaction, removal of different species may have varied effects, based on each species' relevance to the network structure. Thus, the determination of structural centrality of species and their ecological correlates also relates to network resilience and stability (Jeong et al. 2001, Barthélemy 2004).

The characterization of a network and its composing species may be assessed through widely used metrics or concepts such as degree, connectance, and nestedness to mention a few (Bascompte and Jordano 2007, Blüthgen et al. 2008). Nevertheless, such network statistics fail to provide information about the relative influence of each species (Jordán et al. 2006). On the other hand, centrality indices measure the topological importance of nodes (i.e. species) in a network and, thus, some of these indices have the potential to easily and effectively detect the influential nodes (Barthélemy 2004, Jordán et al. 2006, Koschützki 2008). Additionally, since species may contribute differently to distinct patterns of interaction, the use of diverse centrality indices allow to determine which are the influential nodes according to different patterns of interactions (Barthélemy 2004, Jordán et al. 2006). For example, a species could be central for the network's patterns of connectivity by having a large number of interactions (i.e. degree, Jordano et al. 2003). Alternatively, a species with few interactions might be central by creating links between groups of otherwise isolated species (Olesen et al. 2007).

In general, the notion of centrality is associated with social network analysis, in which centrality indices are routinely used to detect central nodes (Freeman 1979, Newman 2003, de Nooy et al. 2005). Nevertheless, centrality measures can also be used as a tool to identify central species within bipartite ecological networks such as those composed by plant–animal interactions (Jordano et al. 2006, Bascompte and Jordano 2007, Martín González et al. 2009). Distinct centrality indices measure the importance of nodes for different structural patterns within a network and, thus, the term centrality can be interpreted according to the context (de Nooy et al. 2005, Koschützki 2008). Throughout the present study centrality is defined as a function that assigns a numerical value to each species of the network so that a rank of species is established, which reflects the species' structural position in the network (Koschützki 2008).

Herein, we used cleaning mutualism between coral reef fishes to investigate ecological traits that influence structural centrality for interacting species. Cleaning interactions between reef fishes comprise so-called clients that get rid of external parasites and diseased or injured tissue, removed from their bodies by other species called cleaners, which forage on these items (Losey 1987, Grutter 2005). Networks of cleaning interactions show strong patterns of nestedness (Guimarães et al. 2007b), and thus have a central core of species.

Many cleaner species play a significant ecological role (Grutter et al. 2003), as they reduce the parasite loads of their client species, potentially act on clients' wound healing, and supposedly lessen the clients' stress through tactile stimulation (Losey 1987, Sazima et al. 1999, Grutter 2005, Bshary et al. 2007). Seeking these benefits, a large number of client species and individuals visit cleaner species daily (Grutter 1996, 2005, Grutter et al. 2003). However, in a

given community, the number of species that clean is much smaller than the number of species seeking their services (Losey 1987, Sazima et al. 1999, Grutter 2005, Francini-Filho and Sazima 2008), which results in great differences in the ratio of species' richness between cleaners and clients (Guimarães et al. 2007b). Thus, judging by their ecological role and species' richness, cleaners would presumably have more influence in the network structure than the clients. This scenario raises several questions, and four basic ones were addressed herein: 1) Which interacting species show highest centralities? 2) What is the centrality of cleaner species? 3) What is the centrality of client species, which greatly outnumber the cleaners? 4) Are there specific ecological traits of cleaner or client species that affect their level of centrality?

Central species presumably modulate ecological and evolutionary dynamics within the network (Bascompte et al. 2003, Guimarães et al. 2007a, Martín González et al. 2009). Thus, the identification of the topological importance of each species within the network is potentially of general interest for studies of ecological networks, and we expect that our findings can be useful for other types of interactions. By investigating whether specific traits of interacting species influence the network structure of cleaning mutualism, we also expect to gain some insight into the generality of niche-related features in the organization of mutualistic networks. Additionally, since topological position of species in the network can be used to identify keystone species that possibly have increased topological roles (Estrada 2007, Martín González et al. 2009), the answer to these questions could help to identify target species for conservation purposes.

Material and methods

Network structure and centrality

In a mutualistic network, species are depicted as nodes and species' interactions by links (Jordano et al. 2003). Our network of cleaning mutualism (hereafter cleaning network) is defined by a matrix R that describes interactions between CR cleaner species and CT client species, where $r_{ij} = 1$ if the client i is cleaned by the cleaner j and zero otherwise. Network structure was drawn and centrality measures (see below) were computed using the software Pajek (<<http://vlado.fmf.uni-lj.si/pub/networks/pajek/>>). As previously stated, species might be central for different patterns of interaction and the levels of centrality for each species can be quantified through distinct centrality measures. In the present study we used three centrality metrics: 'degree centrality', 'closeness centrality' and 'betweenness centrality' (Fig. 1). These three metrics were elected for our analysis mainly because (1) they represent distinct concepts of centrality and (2) they are associated with patterns of interaction and processes that are relevant to ecological systems. All centrality measures vary between zero and one.

The 'degree centrality' (DC) of a given species is a normalized measure of its number of interactions, in which the degree centrality of a species i is:

$$DC_i = k_i / (N - 1)$$

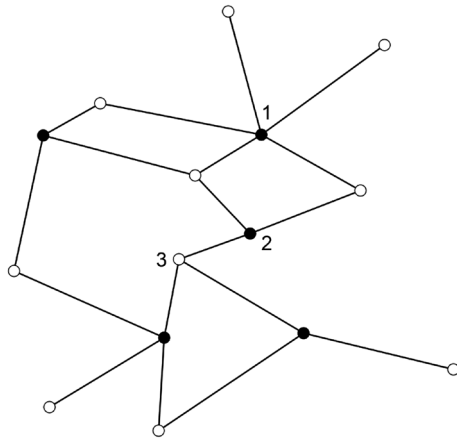


Figure 1. Hypothetical network representing any two sets of species (one set represented by black nodes and the other by white nodes), in which three species (1, 2 and 3) are central to different patterns of interaction and each one shows the highest value based on a distinct centrality measure. Species 1 has the highest value of degree centrality, species 2 has the highest value of closeness centrality, and species 3 has the highest value of betweenness centrality.

where N is species richness and k_i is i 's number of interactions. Species that are central due to a large number of interactions with other species in the network can be identified through this metric (Fig. 1). These species are generalists and have high DC values. In contrast, low DC values indicate species with few interactions, such as extreme specialists (Thompson 2005) or rare species (Vázquez et al. 2005, Krishna et al. 2008). Thus, DC can be related to degree of specialization and abundance-related effects within a community.

The 'closeness centrality' (CC) is based on the shortest number of direct or indirect interactions between one species and all other species in the network (hereafter shortest paths, p). Larger distances yield lower centrality scores (de Nooy et al. 2005, Martín González et al. 2009). For a given species i , CC is calculated as:

$$CC_i = (N - 1) / \sum_{j \neq i}^N p_{ij}$$

where N is species richness and p_{ij} is the length of the shortest path between species i and j , measured in number of links (Jordán et al. 2006). According to this metric a species is central because it is close, in terms of direct or indirect paths, to most other species within the network (Fig. 1), which means that a species with high CC interacts with others using none or just a few intermediaries (Freeman 1979, Martín González et al. 2009). Thus, closeness centrality may be useful to understand coextinction cascades in a mutualistic network (Rezende et al. 2007). Because high CC values indicate species that are close to many other species in the network (in terms of direct and indirect paths), the higher the CC score of a species that die out, the higher the probability of a coextinction cascade to occur.

The 'betweenness centrality' (BC) measures the extent to which a species lies on the shortest paths among other pairs of species (Newman 2003, Barthélemy 2004, Jordán et al. 2006). The BC of a given species i , BC_i , is defined as the

proportion of all shortest paths between all pairs of species in a network that pass through species i (Newman 2003, de Nooy et al. 2005). Species with BC values close to one are those that often are part of the shortest path between other species (de Nooy et al. 2005). Species with high BC scores (Fig. 1) might potentially modulate coextinction and coevolutionary cascades that propagate through the network (Barthélemy 2004, Martín González et al. 2009) by connecting subgroups of interacting species (e.g. modules or compartments, Olesen et al. 2007).

Different centrality criteria, hence different centrality measures, might be strongly correlated (Estrada 2007, Martín González et al. 2009). To investigate whether they were correlated in the cleaning network, principal component analysis (PCA) was performed with the three centrality measures. Centrality measures were arcsine transformed before conducting the analysis, to achieve a normal distribution and homogeneous variance. The high correlation observed among the centrality measures in the cleaning network (Results) allowed us to use the first principal component (principal component 1, hereafter PC1) resulting from the PCA, as a generalized centrality index that synthesize the information of the metrics analyzed herein. Since the PC1 retained most of the information of the centrality measures, in our subsequent analysis we used the PC1 scores as the single centrality measure that captured how central a species is in the cleaning network (see Estrada 2007 for similar procedure). This procedure assured that a unique and consistent measure of centrality would be available for each species, even if using different approaches of centrality (Estrada 2007).

Study site

Data on cleaning interactions and ecological correlates were collected on seagrass/sand flats and rocky reefs at the National Marine Park of Abrolhos, Abrolhos Archipelago (ca 17°58'S, 38°42'W), off eastern Brazil over 30 days in March and December 1999, totaling 70 h of observations distributed among five cleaner species and their clients. The bottom of the study site is sandy with scattered calcareous patch reefs and seagrass flats. Rocky ledges are sparsely to thickly covered with green, brown, and red algae, besides stony corals (see Leão 1994 for description of the Abrolhos reef complex). Cleaning activity was observed directly with use of scuba gear and 'focal animal' samplings during daylight hours, as cleaning symbiosis between reef fishes is a strictly diurnal behavior (Grutter 2005). Throughout the present study we use the word cleaner(s) as a synonym for cleaner species, and client(s) for clients species. One of the cleaners (*Gramma brasiliensis*) is cryptic and cleans very sporadically (Sazima et al. 1998), and another (*Chaetodon striatus*) cleans in very specific situations (Sazima and Sazima 2001). Nevertheless, sampling effort was similarly distributed among the five species. Thus, the number of client species and/or cleaning events recorded for each cleaner species is likely related to a set of characteristics of the cleaners and not to sampling effort.

Ecological correlates

To investigate whether the level of centrality was influenced by a specific ecological trait we performed simple linear

regressions and one-way ANOVA. Data on ecological traits were $\log(\log_{10} + 1)$ transformed before conducting the regressions. Species abundance may markedly affect the centrality of species in a given network (Vázquez et al. 2005, Floeter et al. 2007, Blüthgen et al. 2008). Thus, to control for the effects of relative abundance on centrality we used abundance as a covariate in an ANCOVA. Simple linear regression, ANOVA and ANCOVA analysis were performed using the JMP software (SAS).

We analyzed five ecological traits of the interacting species: body size, trophic category, mobility, activity cycle and abundance. During observational sessions, the estimated size to the nearest cm was recorded for each individual. Size estimates (total length, TL) were calibrated against actual specimens or objects of known size prior to sampling (Sazima et al. 1999). Based on our field observations and literature (Randall 1967), four trophic categories were assigned to the client species: omnivore, herbivore, zoobenthivore and zoobenthivore/piscivore (Francini-Filho and Sazima 2008). The same procedure was adopted to assign three mobility categories (low, medium, high) and three activity categories (diurnal, nocturnal and diurnal/nocturnal) to clients. For instance, low-mobility species generally are territorial, whereas high-mobility ones are rovers. For mobility categories we considered diurnal activity only, as cleaning between fishes is a diurnal interaction (Grutter 2005). For activity cycle we considered each species' main feeding period. Relative abundance was estimated using stationary sampling (Bohnsack and Bannerot 1986) with a total of 62 samples, in which individuals smaller than 10 cm were counted within a radius of 2 m, and individuals with 10 cm or more were counted within a radius of 4 m. Statistical analyses of ecological correlates and level of centrality for client species included all five characteristics, whereas for cleaner species, analyses were limited to two features (body size and relative abundance) due to their low species richness. Additionally, there was no or slight variation in the remaining ecological traits of the cleaner species (e.g. they only clean on established cleaning stations, be it on the substratum or in the water column, and thus have a very restricted mobility). Therefore, we performed the analyses of ecological correlates for the group of clients and cleaners separately.

Results

All three metrics of centrality (DC, CC and BC) were highly correlated (Pearson's $r \geq 0.821$, $p < 0.0001$ in all cases). Additionally, the PC1 retained more than 92.5% of the information and, thus, in the subsequent description of our results, we used the PC1 scores as the single value of centrality for each fish species. Centrality varied (PC1 values ranged from 6.083 to -1.385) among fish species within the network, which is composed of five cleaner species and 30 client species (Fig. 2, 3a). Thirteen species (three cleaners and 10 clients) had positive centrality measures, whereas 22 species (two cleaners and 20 clients) had negative values of centrality (Fig. 3a). Negative values indicate peripheral species, whereas positive values indicate that species are more central and probably affect the network dynamics. Three 'layers' of clients in terms of centrality can be noticed (Fig. 2) – a group of central

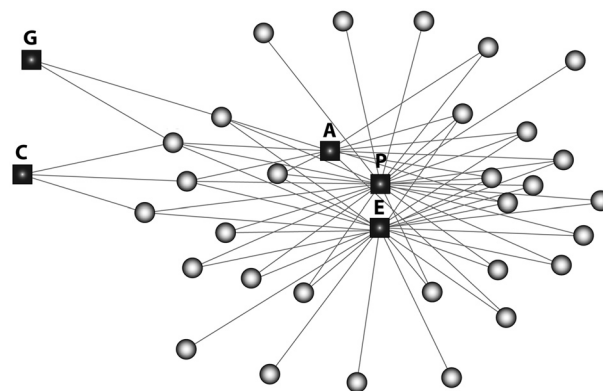


Figure 2. Network of interactions between cleaners (black squares) and their clients (gray circles) at Abrolhos, Brazil (E=*Elacatinus figaro*; P=*Pomacanthus paru*; A=*Anisotremus virginicus*; C=*Chaetodon striatus*; G=*Gramma brasiliensis*).

clients with three or more interactions and two groups of more peripheral species, with either one or two interactions.

Two cleaners, the goby *Elacatinus figaro* (Fig. 4a) and the angelfish *Pomacanthus paru* (Fig. 4b), had the highest centrality values for the whole network (Fig. 3a). Some client species, however, also played important roles in the network structure. For instance, the grunt *Haemulon plumieri* was the most central species among the clients and, more importantly, had the third highest centrality value for the whole network, being more central than the remaining three cleaners (Fig. 3a). The grunt *Anisotremus virginicus*, a cleaner, had the fourth highest centrality (Fig. 3a). However, the two remaining cleaners, the butterflyfish *Chaetodon striatus* and the basslet *Gramma brasiliensis*, were among the most peripheral species (the latter with the lowest centrality value for the whole network), and, thus, the bulk of client species showed higher centrality than either of these two cleaners (Fig. 3a).

Centrality (PC1) of cleaners was not related to either body size ($F=2.115$, $p=0.242$, $n=5$, $DF=1$) or abundance ($F=0.991$, $p=0.393$, $n=5$, $DF=1$). However, clients with higher abundances ($F=9.732$, $p=0.004$, $n=30$, $DF=1$) and particular trophic categories ($F=4.083$, $p=0.017$, $n=30$, $DF=3$) had more central positions than other types of clients. After controlling for differences in abundance, trophic categories still positively correlated with centrality ($F_{3,25}=3.494$, $p=0.03$). We performed a posteriori t-test to check which trophic category influences the significantly positive correlation and found that herbivorous and zoobenthivorous client species had more central positions than omnivorous and zoobenthivorous/piscivorous clients ($t=2.059$, $p=0.03$, Fig. 3b). Body size ($F=2.183$, $p=0.15$, $n=30$, $DF=1$), mobility ($F=0.149$, $p=0.702$, $n=30$, $DF=1$), and activity cycle ($F=0.179$, $p=0.836$, $n=30$, $DF=2$) were not correlated with centrality for clients.

Discussion

Centrality is a concept associated with different structural patterns in complex networks (de Nooy et al. 2005, Koschützki

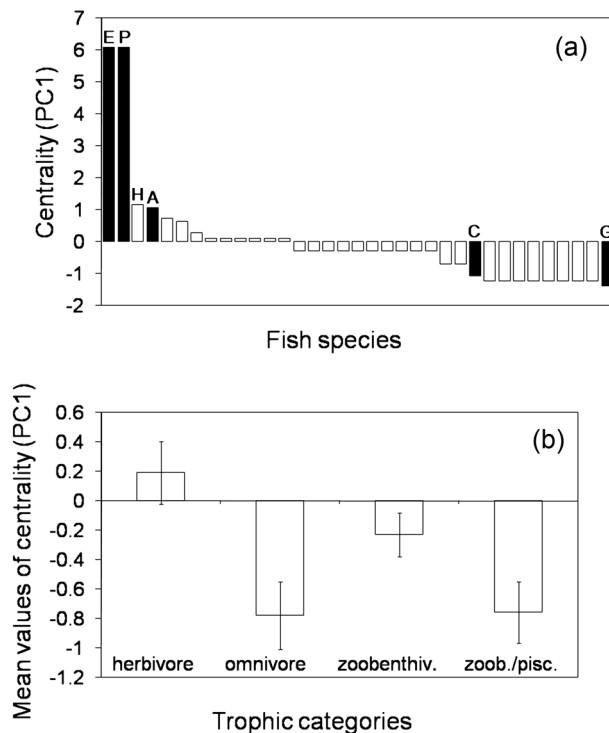


Figure 3. (a) Centrality of fish species in the cleaning mutualism network at Abrolhos, Brazil. Black columns are cleaner species and white columns are client species (E=*Elacatinus figaro*; P=*Pomacanthus paru*; H=*Haemulon plumieri*; A=*Anisotremus virginicus*; C=*Chaetodon striatus*; G=*Grama brasiliensis*). (b) Abundant client species with herbivorous or zoobenthivorous feeding habits have higher centralities than those with zoobenthivorous/piscivorous or omnivorous habits.

2008) and, thus, different types of measure may be correlated or not (Estrada 2007, Martín González et al. 2009). However, all centrality measures are strongly correlated in the cleaning network studied here. Thus, in our mutualistic network, if one species is central because it has a high number of interactions it is also central because it is close to many other species and stays in-between many pairs of species. The nested structure of cleaning interactions (Guimarães et al. 2007b) is probably related to this strong correlation among the centrality values. In nested networks, a few species (from the central core) often show a large number of interactions and all species are close to each other (Bascompte et al. 2003). A recent study has independently found similar correlation between degree and two centrality measures (BC and CC) in pollination networks, a mutualistic nested system (Martín González et al. 2009). Thus, we predict that other nested ecological networks would show strongly correlated centrality measures. If this prediction is confirmed, then ecological and evolutionary dynamics of mutualisms would be more influenced by some individual species in nested networks than in other networks, such as compartmented ones (Olesen et al. 2007), in which different centrality measures might not be correlated. In compartmented networks one species may be central by connecting different compartments, whereas another species may be central by having many connections within the compartment, which would dilute the influence of individual species to the overall dynamics of the

network. On the other hand, in nested networks the same species might be central in different situations.

Due to a considerably higher number of species in the ecological group of clients than in the group of cleaners, it may be expected that centrality of clients would be lowered by their dilution in their group's higher species richness (see Guimarães et al. 2007b for a similar view). Additionally, since cleaning interactions have a major impact on populations of clients (Grutter et al. 2003, Grutter 2005, Bshary et al. 2007), a large number of client species and individuals seek cleaning daily (Grutter 1996). Thus, the cleaners' low species richness and their significant ecological function would have the potential to raise the overall topological importance of this set of species. However, we found here that this does not apply to all cleaner species. We believe that the peripheral position of two cleaners in the studied network is related to a combination of these species' cleaning service, conspicuousness, and/or attractiveness, which might render them less appealing to the client fishes. Additionally, as proposed for plant–animal mutualisms, the number of partners that interact with a species can be limited by phenotypic traits of the latter (sensu Jordano et al. 2003). However, the occurrence of 'forbidden links' in cleaning networks and their influence in the level of centralization of species remain to be tested.

A noteworthy result we found is that cleaners' centrality was not related to their abundance. It is possible that the service type (e.g. parasite removal, necrotic tissue removal, tactile stimulation, or all three) and the service quality (e.g. cleaning duration) provided by each cleaner species (Losey 1987, Bshary and Schaffer 2002, Grutter and Bshary 2003, Grutter 2005, Bshary et al. 2007) is the main cause behind the lack of relation between their centrality and abundance. If this is true, clients in our network are seeking cleaner species that provide the more rewarding 'services' and not necessarily seeking the most abundant cleaners. This type of choice would raise the centralities of specific cleaners, and thus raise their influence on the network structure as well. Additionally, conspicuousness or attractiveness (e.g. color pattern, signaling behavior, keeping a cleaning station) vary between the studied cleaner species and could reduce the influence of abundance in the interaction patterns. It is important to note that the two most central cleaner species (*Pomacanthus paru* and *Elacatinus figaro*) are also the most conspicuous and/or attractive cleaners at the studied site (Sazima et al. 1999). However, future studies may investigate the role of conspicuousness (or attractiveness) on network patterns of interaction.

Centrality probably has a different ecological meaning for cleaners and clients. Central cleaners are the most generalist in their interactions, and thus clean a large number of client species. Central cleaners may be regarded as supergeneralists (sensu Thompson 2005), which are species that interact with a high number of species within the network and rely on a large diversity of partners (Thompson 2005). In the cleaning network herein studied, two cleaner species (*E. figaro* and *P. paru*) may be regarded as supergeneralists. Central nodes (in our case species) such as supergeneralist cleaners play a relevant role in network cohesiveness (Jeong et al. 2001, Olesen et al. 2007, Martín González et al. 2009). In some ecological networks, these generalist species are often the most abundant ones (Vázquez 2005, Krishna et al. 2008).



Figure 4. The two most central cleaner species and two of their clients at the study site: (a) The goby *Elacatinus figaro* cleans the flank of its client, the goatfish *Pseudupeneus maculatus*. Photograph by P. Meirelles. (b) The angelfish *Pomacanthus paru* inspects the base of the caudal peduncle of its posing client, the doctorfish *Acanthurus chirurgus*. Photograph by C. Sazima.

However, in the case of cleaning mutualism, central cleaners are not necessarily the most abundant species, which, in turn, has relevant implications for conservation. Not being highly abundant species, these supergeneralist cleaners are more prone to be wiped out than abundant supergeneralist species in other types of network.

Centrality among client fishes was arranged in 'layers' of structural position, the more central ones interacting mainly with the central cleaners, but as a rule having interactions with at least three cleaner species. Thus, central clients are also generalists in their interactions, seeking different cleaners. As a consequence, if a central client species dies out, this will imply in a reduction of food sources for several cleaner species. However, central clients are often abundant species, which would make the risk of primary extinction of these species lower than that for rare species. The positive relationship between abundance and centrality is related to the fact that a client with higher abundance has potentially a higher probability to meet (thus, to interact with) a cleaner than a client with lower abundance (Vázquez et al. 2005, Floeter et al. 2007, Krishna et al. 2008). This result generalizes previous findings from plant-animal mutualisms (Vázquez et al. 2005, Krishna et al. 2008) to marine cleaning mutualism, and emphasizes the potential role of neutral processes (Hubbell 2001, Krishna et al. 2008) to generate the structure of mutualistic networks. However, after controlling for the effects of clients' abundances we found that client species still differed in their influences in the network structure, these differences being related to their trophic category. We hypothesize that the relationship between trophic category and centrality may partly be related to preferences of cleaners towards some clients. For instance, some cleaners may choose not to clean, or rarely clean,

piscivorous species (peripheral species in our study), since predation of cleaners by this client type occurs under certain circumstances (Francini-Filho and Sazima 2008). A cleaner's choice would restrict access to cleaning interactions for some piscivorous species and, thus, would ultimately affect the level of centrality for this client type. As our study is observational rather than experimental, manipulating the presence and/or abundance of a particular cleaner or client species would shed additional light on the correlation between centrality and these particular traits. On the other hand, trophic category is not amenable to manipulation.

Our results stress the relevance of feeding habits and other niche-related, species-specific traits in the organization of mutualistic networks. Feeding habits may prove important to determine centrality of interacting species in other types of network as well, since nestedness is partially explained by species-specific traits (Stang et al. 2006, 2007, Krishna et al. 2008). For instance, the relative importance of fruits in the diet of a given frugivorous species may affect the nested organization in plant–frugivore networks (Krishna et al. 2008). Similar patterns would be expected in other mutualistic interactions, such as those between protective ants and honeydew-producing insects, in which ants vary widely in their diets, leading to testable hypotheses for other communities and ecosystems.

In conclusion, the present study generalizes previous findings for plant–animal mutualisms, by showing that the structure of marine mutualisms is also related to a complex interplay between abundance and niche-related features. More importantly, besides the nested structure, already demonstrated for cleaning mutualism in reef fishes and many other types of mutualism (Bascompte and Jordano 2007, Guimarães et al. 2007b), we found herein an additional resemblance between this marine mutualism and at least one terrestrial mutualism type: as demonstrated for interactions between plants and their pollinators (Martín González et al. 2009), the central species within the cleaning network are the most generalized ones in their interactions. However, a relevant difference between cleaning and plant–animal interactions was also found herein: contrary to the tendency found in other mutualisms (Vázquez 2005, Krishna et al. 2008), in one set of species (cleaners) of the cleaning network, the most generalized ones are not necessarily the most abundant in the network, but likely the most conspicuous and/or providing the more rewarding services. This finding has direct implications for conservation, since extinction of these potentially more vulnerable species could affect a large number of interacting species and eventually threaten the network cohesiveness.

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