The macroecology of marine cleaning mutualisms

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Summary

1. Marine cleaning mutualisms generally involve small fish or shrimps removing ectoparasites and other material from cooperating 'client' fish. We evaluate the role of fish abundance, body size and behaviour as determinants of interactions with cleaning mutualists.

2. Data come from eight reef locations in Brazil, the Caribbean, the Mediterranean and Australia.

3. We conducted a meta-analysis of client–cleaner interactions involving 11 cleaner and 221 client species.

4. There was a strong, positive effect of client abundance on cleaning frequency, but only a weak, negative effect of client body size. These effects were modulated by client trophic group and social behaviour.

5. This study adds to a growing body of evidence suggesting a central role of species abundance in structuring species interactions.

Key-words: abundance, body size, cleaning interactions, ectoparasites, reef fish, symbiosis.

Introduction

Cleaning mutualisms occur frequently among terrestrial vertebrates (Dickman 1992) and are widespread among marine animals (Côté 2000; Grutter 2002). During cleaning interactions in the sea, the 'cleaner' removes parasites, skin, scales and mucus from the body surface of their 'clients', which include fishes, turtles, marine iguanas, whales and octopuses (Feder 1966; Grutter 2002). Despite the extensive literature on marine cleaning mutualisms (reviewed in Côté 2000 and Grutter 2002), the question of what ecological factors determine the interactions between cleaners and their clients remains largely open. Here we report results of a quantitative review of the literature on marine cleaning interactions that provides some answers to this question.

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Recent studies have linked broad-scale macroecological variables with community-wide patterns of species interactions (Cohen, Jonsson & Carpenter 2003; Vázquez *et al.* 2005b; Woodward *et al.* 2005; Stang, Klinkhamer & van der Meijden 2006; Vázquez & Aizen 2006). Because a positive relationship between species abundance or body size and interaction frequency can result from random encounters among interacting species, a link between these macroecological variables and species interactions would suggest an important role of neutrality in determining species interactions and community structure, an issue of much current controversy in ecology (Chave 2004; Gaston & Chown 2005; Vázquez 2005).

Client body size and abundance could influence the frequency of cleaning interactions through multiple mechanisms. First, larger hosts may provide a greater opportunity for cleaning than smaller-bodied species, because of both greater parasite loads (Grutter & Poulin 1998a,b; Combes 2001) and greater quantity and/or quality of mucus (Grutter 1995; Arnal & Morand 2001), all of which would result in a positive relationship between client body size and cleaning frequency (Grutter 1995). Second, cleaners could interact more frequently with abundant clients than with rare ones, both due to

a higher probability of encounter and to greater parasite loads, resulting in a positive relationship between client abundance and cleaning frequency (Hobson 1971; Arnal *et al*. 2000; Sasal 2003). However, because species abundance and body size are usually negatively correlated (Blackburn & Gaston 1997; Ackerman & Bellwood 2003), their net effect on cleaning frequency will depend on the strength of this correlation and the relative magnitude of their variances.

The influence of abundance and body size of clients on cleaning frequency could be modulated by biological characteristics of clients. First, schooling or gregarious clients could interact with cleaners more often than solitary clients, both because they are more likely to find patchily distributed cleaning stations (Pitcher & Parrish 1993; SRF and ASG pers. obs.) and because they are likely to have greater parasite loads (Hobson 1971; Côté & Poulin 1995; Sasal 2003). Second, for sedentary species the cost of seeking cleaners (e.g. increased predation risk when moving between reefs, loss of territory, and energy output) may outweigh the cost of not being cleaned; thus, sedentary species could be less likely to encounter cleaning stations than mobile species (Grutter 1995). Third, carnivores (both specialized piscivores and generalist carnivores whose diet include fish) could interact less frequently with cleaners than noncarnivores (e.g. planktivores, herbivores, spongivores), because they are seen as a risk by cleaner fish. These arguments lead to the prediction that the relationship between abundance or body size and cleaning frequency should be more strongly positive for gregarious, mobile, noncarnivorous species than for solitary, sedentary, carnivorous species.

The relationship between client abundance, body size and cleaning frequency could also be modulated by cleaner feeding behaviour. Because obligate cleaners (e.g. *Elacatinus*, *Labroides*) rely on cleaning interactions as sources of food throughout their entire life (Côté 2000; Grutter 2000), the relationships between abundance or body size and cleaning interactions would be stronger for this type of cleaner than for facultative cleaners (e.g. *Thalassoma*, *Bodianus*), which rely on other food sources at least during part of their life cycle (Côté 2000; Francini-Filho, Moura & Sazima 2000). Furthermore, this relationship could be stronger for obligate than for facultative cleaners, because the latter are expected to experience a relatively higher predation risk when cleaning potentially 'dangerous' clients (Darcy, Maisel & Ogden 1974; Côté 2000; Francini-Filho *et al*. 2000). Based on these arguments we predicted that the relationship between client abundance or body size and cleaning frequency should be stronger for obligate than for facultative cleaners, and that among facultative cleaners it should be stronger for noncarnivorous than for carnivorous clients.

We conducted a meta-analysis to evaluate the above predictions about the role of abundance, body size and behavioural characteristics of fish as determinants of cleaning interactions in the sea, using a large database on client–cleaner interactions in Brazil, the Caribbean, the Mediterranean and Australia.

Methods

DATA SETS

To evaluate the above predictions we compiled data from the literature on cleaning interaction frequency (number of cleaning events per cleaner and client species). Data included 10 cleaner fish species (six genera), one cleaner shrimp (*Periclimenes pedersoni*) and 221 client fish species at three locations in Brazil, three in the Caribbean, one in the Mediterranean and one in Australia (Table 1); thus, data included in our study

Table 1. Cleaner species, their facultativeness and sites with codes used in the figures and appendices

Cleaner species	Species code	Facultativeness*	Site	Site code	Region
Bodianus rufus	bod_ruf	Facultative	bona	Bonaire	Caribbean
			stcr	St Croix	Caribbean
Pomacanthus paru	pom_par	Facultative	abro	Abrolhos	Brazil
Symphodus melanocerus	sym_mel	Facultative	medi	France	Mediterranean
Thalassoma bifasciatum	tha_bif	Facultative	bona	Bonaire	Caribbean
			stcr	St Croix	Caribbean
Thalassoma noronhanum	tha_nor	Facultative	fern	Fernando de Noronha	Brazil
Elacatinus evelynae	ela_eve	Obligate	barb	Barbados	Caribbean
			stcr	St Croix	Caribbean
Elacatinus figaro	ela_fig	Obligate	saop	São Paulo	Brazil
Elacatinus prochilus	ela_pro	Obligate	barb	Barbados	Caribbean
Elacatinus spp.	ela_spp	Obligate	bona	Bonaire	Caribbean
Elacatinus randalli	ela_ran	Obligate	fern	Fernando de Noronha	Brazil
Labroides dimidiatus	lab_dim	Obligate	liza	Lizard Island	Great Barrier Reef
Periclimenes pedersoni	per_ped	Obligate†	bona	Bonaire	Caribbean
			stcr	St Croix	Caribbean

*Based on Côté (2000).
†Although considered an obligate cleaner it was not included in our obligate/facultative analysis because we wanted to restrict comparison to fish only.

represent a broad taxonomic, functional and geographical sample of marine cleaning mutualisms.

A cleaning event is defined as the period of association between a single cleaner and a single host, beginning when physical contact is initiated and ending when the cleaner leaves the host (or client); one cleaning event may include many individual nips from the cleaner and may last from one second to several minutes (Johnson & Ruben 1988). Because of limitations of data sets included in our analyses, we were not able to consider other components of cleaning interactions, particularly the duration of individual interactions. Such lack of consideration could be problematic for the interpretation of our analyses if the duration of cleaning events and cleaning frequency were negatively correlated. However, studies conducted in Brazil, Australia and in the Mediterranean indicate that total duration of cleaning events per client species is positively correlated with cleaning frequency (Grutter 1995; Arnal & Morand 2001; R.B. Francini-Filho and I. Sazima, unpubl. ms.). We also compiled data on client abundance, body size, trophic group (carnivorous or noncarnivorous), mobility (mobile or resident, the latter defined as having very limited home range, not roving among reefs), and social behaviour (gregarious or solitary, the latter including also species living in pairs; Appendix S2). We used the best body size data available for each site; if none were available we used total length for the region (see Appendix S3). We found that data obtained in the field were significantly correlated with data on total body length from the literature (Appendix S4); we thus used field data when available.

STATISTICAL ANALYSES

To assess the generality of the effect of the continuous independent variables on the frequency of cleaning interactions, we evaluated the strength of the relationship between each independent variable and frequency of cleaning separately for each group defined by each of the categorical variables describing client characteristics (i.e. trophic habits, social behaviour and mobility). We used the correlation coefficient as an estimate of the strength of the relationship. It is important to point out that Hillebrand (2004) differentiates between the 'strength' of a regression, which is given by the correlation coefficient, and its 'steepness', which is given by the slope of the relationship. However, for slopes to be comparable among different variables it is more appropriate to use the standardized slope (i.e. the standardized regression coefficient in multiple regression parlance), which in a simple regression is equal to the correlation coefficient. Thus, in a simple regression 'strength' and 'slope' are actually the same thing. Continuous variables were log-transformed for analyses.

We used the normalized (z-transformed) Pearson's correlation coefficient (r) as a measure of effect size, and calculated the 95% confidence intervals (bootstrap, 10 000 replicates) of the correlation coefficient to test the null hypothesis that $r = 0$. To this end, correlation coefficients were first normalized by applying Fisher's z transform, $z = 0{\cdot}5 \ln[(1 + r)/(1 - r)]$ (Zar 1999), and then weighted by multiplying them by the inverse of the sampling variance, $w = 1/\mathrm{var}(z) = N - 3$ (Rosenthal 1991; Gurevitch, Curtis & Jones 2001). The weighted mean of z is thus defined as $\bar{z} = \sum(w_i z_i)/\sum(w_i)$. We used the MetaWin (Rosenberg *et al.* 2000) software to calculate the bootstrapped $\bar{z}_i$ and its 95% percentile confidence limits.

PHYLOGENETIC CORRECTION

We evaluated whether frequency of interaction between a given cleaner species and its clients at a given site was a function of the phylogenetic nonindependence of client species. To this end, we used a nested ANOVA design with cleaning frequency as dependent variable and client family and genus as fixed factors, with genus nested within family. We used taxonomic rather than phylogenetic relationships among species because there is no well-resolved phylogeny for the majority of the studied client fishes. We defined family and genus as fixed rather than random factors because we were interested in the effect of these particular groups rather than in the universe of possible families and genera. Defining these factors as fixed rather than random has the additional advantage that it makes our test stronger, because it makes it more likely to detect significant phylogenetic effects. Because the distribution of frequencies of interaction deviated substantially from a normal distribution, we performed the analyses on the rank-transformed data. Analyses were performed in the Generalized Linear Model procedure of SAS (SAS Institute 2002).

Results and discussion

Over the wide range of cleaners, clients and locations covered, there was a generally positive relationship between client abundance and their frequency of interaction with cleaners (Fig. 1). However, as predicted, the strength of this relationship was contingent upon client characteristics. While effect size was strongly positive for noncarnivorous and gregarious clients, it was substantially weaker for carnivorous and solitary species (Fig. 2a,c; Appendices S1, S5 and S6). Albeit significantly positive, the relationship between abundance and cleaning frequency did not differ among mobility classes (Fig. 2e). This result could be linked to the fact that half of the studied sites were continuous rocky reef habitats, and the relationship with mobility classes would be more likely to occur in coral reef patches. In the majority of the case studies the most frequently cleaned client species was always a mid-water, gregarious, mainly planktivorous species in one of four genera (*Abudefduf*, *Acanthochromis*, *Chromis*, *Clepticus*). Thus, abundant clients tend to be cleaned more frequently than rare ones, but the strength of this relationship is
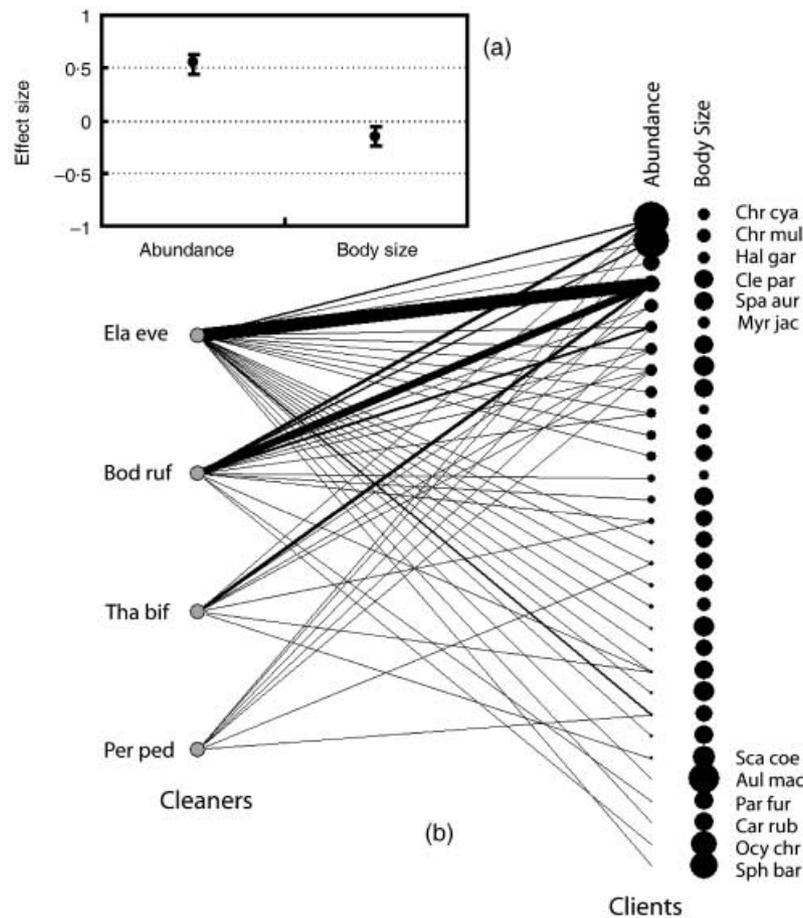
Fig. 1. Relationship between client abundance and body size and the frequency of cleaning interactions. (a) Overall mean effect sizes (± 95% confidence intervals, CI) of abundance and body size on cleaning frequency. Effect is an estimate of the correlation between abundance or body size and cleaning frequency. (b) Cleaner–client interaction network in St Croix (Caribbean) as an example of how cleaning frequency relates to abundance and body size of their clients. Circles represent cleaner (left) and client (right) species, with circle diameter proportional to relative abundance and body size of client species. Lines represent cleaner–client interactions, with line width proportional to the square root of interaction frequency. Data sources in Appendix S3. Cleaners: Ela eve = *Elacatinus evelynae*, Bod ruf = *Bodianus rufus*, Tha bif = *Thalassoma bifasciatum*, Per ped = *Periclimenes pedersoni*. Clients: Chr cya = *Chromis cyanea*, Chr mul = *Chromis multilineata*, Hal gar = *Halichoeres garnoti*, Cle par = *Clepticus parrae*, Spa aur = *Sparisoma aurofrenatum*, Myr jac = *Myripristis jacobus*, Sca coe = *Scarus coeruleus*, Aul mac = *Aulostomus maculatus*, Par fur = *Paranthias furcifer*, Car rub = *Carangoides ruber*, Ocy cry = *Ocyurus chrysurus*, Sph bar = *Sphyraena barracuda*.

modulated by the trophic habits and social behaviour of client species (Fig. 2a,c). An exception to this pattern is the cleaner *Pomacanthus paru* in the Abrolhos Archipelago (Brazil; Sazima, Moura & Sazima 1999), whose frequency of cleaning interactions was unrelated to client abundance. This lack of relationship could have resulted either from the unique fish community structure of the studied site (most notably the absence of common planktivore species that dominate cleaning interactions in other Atlantic localities; see Ferreira *et al.* 2004) or from the preferences of some clients for *P. paru* cleaning services being strong enough to counterbalance the influence of abundance (Sazima *et al.* 1999).

The overall effect of body size on cleaning frequency was weakly negative [back-transformed $\bar{z} = -0.15$; 95% CI = (−0·26, −0·06); Fig. 1]. Mean effect size did not differ significantly from zero for carnivorous, solitary and mobile clients, while it was weakly negative

for noncarnivorous, gregarious and sedentary clients (Fig. 2). Effect size did not differ significantly between carnivorous and noncarnivorous and between mobile and sedentary clients but did between solitary and gregarious clients. It is noteworthy that a negative relationship between body size and cleaning frequency is opposite to the prediction that large-bodied species are cleaned more frequently than smaller species because they represent a greater opportunity for cleaners. This result may be explained by an underlying negative relationship between client abundance and body size [back-transformed $\bar{z} = -0.42$; 95% CI = (−0·50, −0·27); Appendix S7]; thus, differences in body size among client species are overridden by differences in relative abundance.

Contrary to our expectation, the effect size of abundance and body size on cleaning frequency did not differ significantly between obligate and facultative
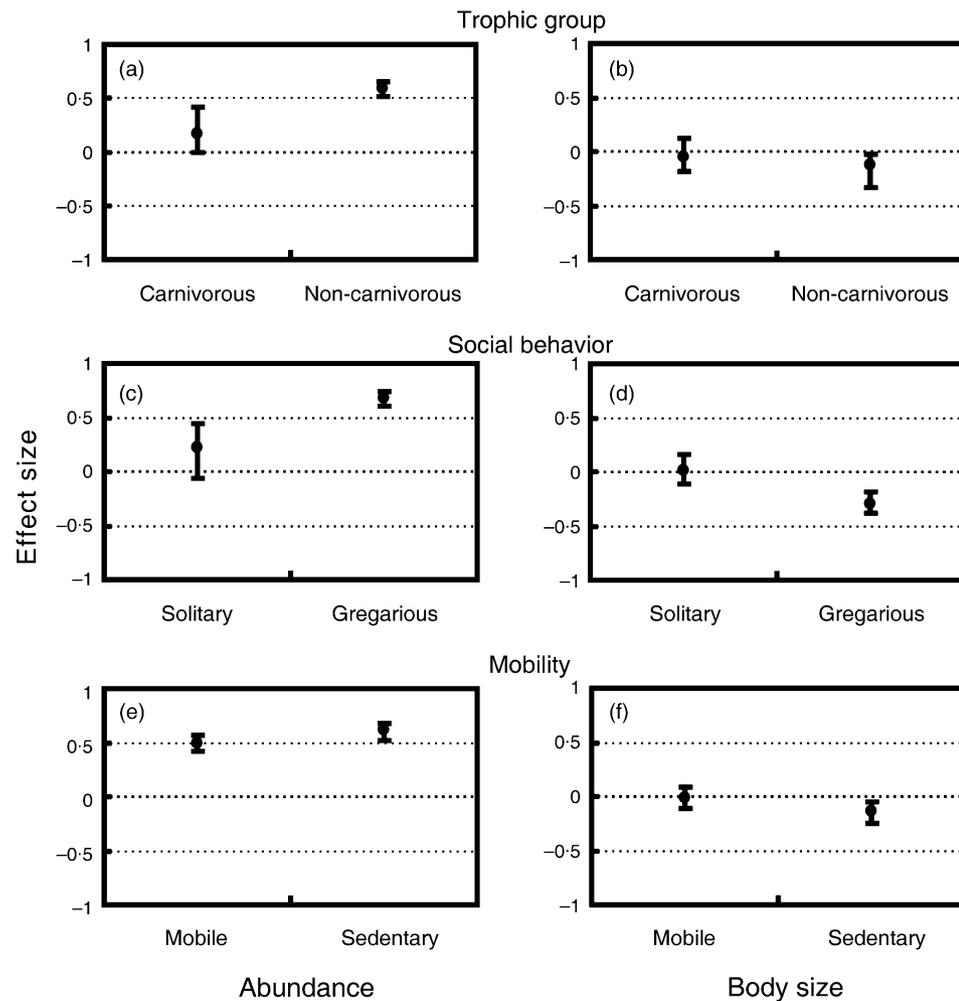
Fig. 2. Mean effect sizes of abundance and body size on the frequency of cleaning interactions. Effect size is Pearson's correlation coefficient between abundance or body size and cleaning frequency by trophic group (a,b), social behaviour (c,d), and mobility (e,f). Error bars are bootstrap 95% confidence intervals of mean effect size.
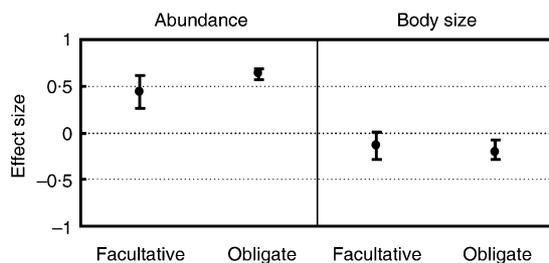

Fig. 3. Mean effect size of abundance and body size on cleaning frequency of facultative and obligate cleaner species. Other conventions as in Fig. 2.

cleaner species (Fig. 3). Likewise, effect size did not differ when carnivorous and noncarnivorous clients were considered separately (Fig. 4), which contradicts the widely accepted view (Darcy *et al.* 1974; Côté 2000; Francini-Filho *et al.* 2000) that obligate cleaner species clean carnivorous clients (i.e. capable of eating the cleaner) more often than facultative cleaners.

Because phylogenetic nonindependence among client species could affect patterns of interaction with cleaners, we evaluated whether the frequency of inter-

action between a given cleaner species and its clients at a given site was explained by the phylogenetic relationship among client species. For a majority of cleaner species there were no significant effects of taxonomic categories on their frequency of interaction with clients (Appendix S8). Only for *Bodianus rufus* was such an effect significant in the two sites for which we have data on this species (Appendix S7). We therefore conclude that the statistical effects reported above are not an artefact of the phylogenetic relatedness of client species.

Our results suggest that marine cleaning mutualisms exhibit similar macroecological patterns worldwide, despite the phylogenetic disparity of cleaners and clients and the diverse geographical contexts of the locations included. Our study adds to a growing body of evidence suggesting a central role of species abundance in structuring complex networks of interacting species (Cohen *et al.* 2003; Vázquez *et al.* 2005b; Vázquez & Aizen 2006). Taken together, this evidence suggests that the ubiquitous right-skewed distribution of abundance observed in most ecological communities (Preston 1962a,b; May 1975) leads to a similarly right-skewed distribution of interaction frequencies.
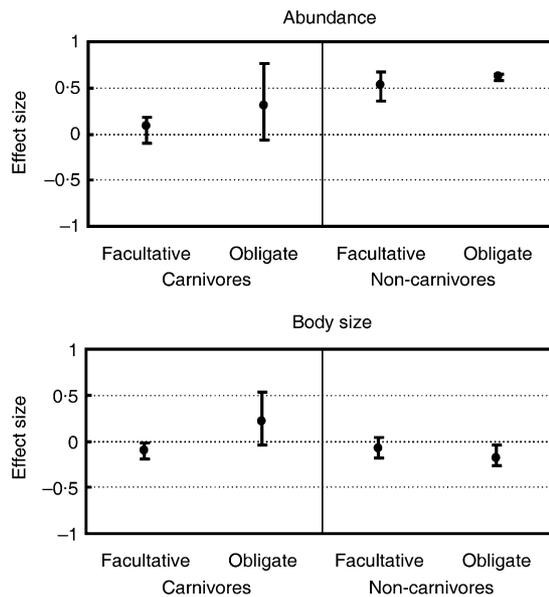
Fig. 4. Mean effect size of abundance and body size on cleaning frequency of facultative and obligate cleaner species regarding the trophic group of the clients. Other conventions as in Fig. 2.

Thus, cleaning interactions will often be dominated by a few abundant, frequently interacting clients with potentially strong effects on their cleaners, accompanied by many rare, seldom interacting clients whose overall influence on cleaners is low. Furthermore, because a positive relationship between species abundance and interaction frequency can result from random encounters among interacting species, our results suggest an important role of neutrality in determining cleaning interactions. However, our study also suggests that the influence of species abundance on cleaning interactions is modulated by the ecological characteristics of interacting species, particularly their trophic habits and social behaviour. Thus, neutrality alone is not a sufficient explanation of patterns of cleaning interactions, and the identity of interacting species must be taken into account.

The fact that cleaner species interact with many client species might suggest that clients do not represent a consistent selection pressure for cleaners. Lack of consistent selection would in turn suggest little opportunity for adaptation of cleaners to clients. However, if abundance patterns were consistent throughout time and space, selection exerted by the most abundant, frequently interacting species would also be spatio-temporally consistent. Thus, as it has been suggested for other types of mutualisms (Vázquez, Morris & Jordano 2005a), abundant, frequently interacting species could also be the ones with the strongest effects on their interaction partners. This conjecture suggests that extremely abundant clients (e.g. *Abudefduf*, *Acanthochromis*, *Chromis*, *Clepticus*) would dominate cleaning interactions not only numerically, but would also have the strongest influence on the evolutionary dynamics of their cleaners.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://www.blackwell-synergy.com

Appendix S1. Relationships between client abundance, social behaviour and cleaning frequency of 11 cleaner species at eight different locations.

Appendix S2. Client body size, geographical distribution, and classification in terms of taxonomy, trophic category, social behaviour, and mobility.

Appendix S3. Number of cleaner and client species and sources of data at each site.

Appendix S4. Relationship between body size measures obtained in the field and maximum body size from the literature.

Appendix S5. Pearson's correlation coefficients calculated for meta-analysis shown in Figs 2–4.

Appendix S6. Multiple linear regression analyses estimating regression parameters for each of two groups of each categorical variable.

Appendix S7. Analysis of relationship between body size and abundance for the eight sites.

Appendix S8. Results of fixed-effects nested ANOVA to evaluate of phylogenetic independence of frequency of cleaning interactions of a given cleaner species with its clients.