



The influence of species abundance, diet and phylogenetic affinity on the co-occurrence of butterflyfishes

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Abstract

Understanding “why species are where they are” at different scales is one of the main focuses of ecological and biogeographical studies. Although ecological features, such as trophic group and species abundance, are thought to be more important for driving co-occurrence patterns at the habitat scale, it is not yet known if phylogenetic constraints can also exert some influence. Here, we studied global co-occurrence patterns of butterflyfishes in relation to species abundance, trophic characteristics, and evolutionary histories, specifically examining two questions—Question (1): does phylogenetic affinity and/or abundance explain co-occurrence at the habitat scale? To answer this, we used abundance data from 23 global localities to evaluate whether phylogenetic affinity alone as well as after accounting for differences in diet among sympatric species explains co-occurrences at the habitat scale. Question (2): are the diets of sister species from the Atlantic Ocean and the Eastern Pacific phylogenetically conserved? To examine this, we used a more detailed diet classification of species present within these realms. We found that phylogenetic distance per se fails to explain the co-occurrence of butterflyfish species pairs. Instead, species abundance exerted a major influence on interspecific co-occurrences. We also found no correlation between phylogenetic distance and diet similarities for Atlantic and East Pacific butterflyfishes; thus, in these regions, species’ diets do not seem to be phylogenetically conserved. This suggests that evolutionary processes are not the main drivers of butterflyfish co-occurrence highlighting species’ abundance and niche-related processes as the most important factors in determining whether species co-occur at the habitat scale.

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Introduction

Understanding species’ distributions across scales has always been one of the main focuses of ecological and biogeographical studies. The presence or absence of a species in a community can be influenced by several macroecological (McGill and Collins 2003), biogeographical (Ekman 1953), evolutionary (Whittaker 1972) and species-related processes (Whittaker 1972; Brown 1984; Burns and Strauss 2011). In most studies, however, these processes have been examined to disentangle species co-occurrences in a regional/geographical scale (e.g., Hodge et al. 2014; Hodge and Bellwood 2016; Gaboriau et al. 2018). So far, few studies have examined species co-occurrences at the smaller habitat scale (e.g., Early and Keith 2019; Eurich et al. 2019), particularly considering evolutionary and ecological processes simultaneously. According to Darwin’s naturalization conundrum, species have higher chances to occur in habitats where close relatives are present, due to facilitation by favourable niche conditions. However, this occurrence could be impaired by

competition with closely related species due to similarities in resource requirements (Diez et al. 2008; Thuiller et al. 2010).

Two species that share a direct common ancestor tend to have similar traits that could intensify competition for resources when in sympatry, leading to competitive exclusion (Harper et al. 1961; Abrams 1983; Germain et al. 2016). Based on this assumption, the “*Limiting similarity*” theory posits that there is a maximum level of similarity between species that would allow co-existence by minimizing competition (Abrams 1983). Relatedly, the “*Character displacement*” theory suggests that sympatric sister species will differ ecologically or morphologically to co-exist to minimize/avoid competitive pressures (Brown and Wilson 1956; Slatkin 1980; Abrams 1983). Besides these evolutionary theories, abundance is known to influence species co-occurrence by affecting the strength of interactions (Vazquez et al. 2009). Assuming interaction neutrality, resulting from the random encounter of individuals, abundant species will tend to co-occur more frequently than the rare ones, thus being central to co-occurrence networks (Vazquez et al. 2007, 2009). Thus, both ecological and evolutionary processes should contribute to co-occurrence patterns in high-diversity biological systems.

Among high-diversity systems, coral and rocky reefs stand out as the most productive ecosystems in marine shallow waters, supporting hundreds of thousands of species (Reaka-Kudla 1997; Roberts et al. 2002). Such biologically complex systems provide ideal models to test co-occurrence theories, being important for studies of pairwise species patterns (e.g. Auster et al. 2005) as well as species–habitat relationships (e.g. Reese 1981) at different temporal and spatial scales (e.g. Nickell and Sayer 1998; Mariani et al. 2001). Among the most conspicuous fishes on reefs, the Chaetodontidae (butterflyfishes) comprises around 134 species. It is one of the most studied reef fish families, known as a good model for ecological studies due to their close association with the benthic substrate, prevalence of diurnal foraging behaviour and the ability to explore different habitats (Blowes et al. 2013; Konow and Ferry 2013). In addition, the Chaetodontidae family has been relatively well studied in terms of phylogenetic relationships (Fessler and Westneat 2007; Bellwood et al. 2010; Floeter et al. 2018). Most of these studies, however, focused on butterflyfishes from the Indo-Pacific Ocean (e.g. Pratchett et al. 2014), where species diversity is higher (Findley and Findley 1989; Kulbicki et al. 2013), while species from the Atlantic Ocean and Eastern Pacific have received relatively less attention.

Butterflyfishes are usually divided into four major feeding guilds: hard-coral feeders, soft-coral feeders, non-coral feeders and generalists (Pratchett 2005). Species that feed almost exclusively on hard corals, such as *Chaetodon trifascialis* (Berumen and Pratchett 2008), tend to feed on a

single taxonomic group or species (Schoener 1971; Nagelkerken et al. 2009). Although specialists may assimilate energy from their prey more efficiently compared to generalists (Berumen and Pratchett 2008), this feeding strategy could make them vulnerable to stochastic fluctuations in food resources (Schoener 1971; Munday 2004; Berumen and Pratchett 2008). Contrastingly, generalist species consume a variety of prey and are distributed in a way that is not strictly related to a specific food resource (Schoener 1971). Thus, the generalist strategy may ensure population persistence, especially in unstable or hostile environments. Moreover, a generalist habit can allow the co-occurrence of sister species by minimizing competition pressure for feeding resources (Pratchett et al. 2004; Berumen and Pratchett 2008). For instance, the generalist invertivore *Chaetodon striatus* is widely distributed in the western Atlantic Ocean, from southern Brazil to Florida, USA, including oceanic islands. Throughout its distribution, *C. striatus* co-occurs with six other butterflyfishes, including its sister species *C. capistratus* in the Caribbean (Bellwood et al. 2010), which does not seem to affect population abundances (Liedke et al. 2016, 2018).

In this study, we aimed to understand the relationship between co-occurrence and evolutionary history of butterflyfishes, accounting for their abundance and trophic characteristics. We explored the global co-occurrence patterns of Chaetodontidae by asking—Question (1): does phylogenetic affinity and/or species abundance explain co-occurrence at the habitat scale? We hypothesize that co-occurrence will be positively related to both phylogenetic distance and abundance (Fig. 1a and b). Also, we expect that generalist species will co-occur more frequently than specialist ones (Fig. 1c). Question (2): are the diets of sister species from the Atlantic Ocean and the Eastern Pacific phylogenetically conserved? To answer that, we used a more detailed diet classification of species present within these less studied realms. We hypothesize that distantly related species will have different diets due to phylogenetic niche conservatism (Fig. 1d).

Materials and methods

Does phylogenetic affinity and/or species abundance explain co-occurrence at the habitat scale?

We used global visual censuses from 23 localities to obtain habitat scale abundance data of *Chaetodon* species (Fig. 2a; Table 1; derived from Morais et al. 2017; Barneche et al., 2019). The visual census method consists of belt transects in which a diver records and counts all the species inside an area on the reef. The transect area (m²) differed among the localities, but not within a locality (please refer to Table 1

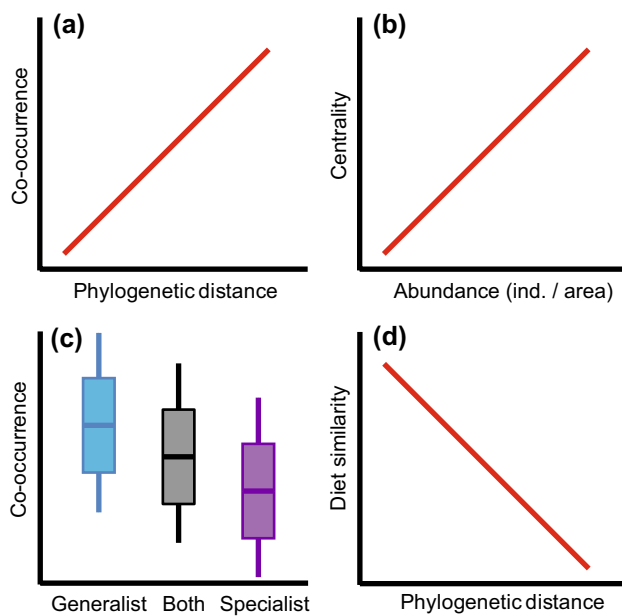


Fig. 1 Hypothetical relationships between: **a** co-occurrence and phylogenetic distance; **b** species centrality and abundance; **c** co-occurrence and diet of the *Chaetodon* species pair; **d** phylogenetic distance and diet similarity for *Chaetodontidae* species from the Atlantic and Eastern Pacific Oceans

for more information). We defined the “habitat scale” as the area of the transect, which ranged from 40 to 500 m² within a certain depth and reef type.

We used solely localities with two or more *Chaetodon* species inhabiting the same reef and only censuses in which at least one *Chaetodon* species was present. The *Prognathodes* genus was not included in this analysis since most species inhabit mesophotic reefs (Copus et al. 2019; Nunes et al. 2019). In total, 60 *Chaetodon* species were present in the censuses, which represent approximately 70% of the genus’ diversity. The possible combinations of co-occurring species (i.e. species pairs) at localities ranged from 3 (Ceará–Brazil) to 300 (central great barrier reef—Australia). To infer the proportion of censuses with species pairs, we used the Bray–Curtis index through the equation: $BC_{ij} = 1 - (1 - (2C_{ij}/(S_i + S_j)))$, where i and j are two *Chaetodon* species potentially co-occurring in a given habitat; C is the sum of only the lower abundance for each census found for both species; S_i is the sum of the abundance of species i ; and S_j is the sum of the abundance of species j . Abundance data was used in the model for co-occurrences due to its importance for species centrality in co-occurrence networks (see the statistical analysis below for details).

The phylogenetic distances between each species pair was extracted from the phylogeny of Cowman and Bellwood (2011), using the ‘ape’ R package (Paradis 2004). Distances represent the sum of branch lengths separating two species in the phylogeny. We imputed five species that were

not present in the phylogeny by utilizing morphologically similar and phylogenetically closely related species. These species were all considered part of the same clade (Kuitert 2002) and subgenus (Bellwood and Pratchett 2013) as the ones not included in the phylogeny.

Since diet can vary according to food item availability in each locality (Anderson et al. 1981) and is dependent on taxonomic resolution, we adopted a broader categorization for comparisons among localities. Species were classified as specialists or generalists according to their diet, which was obtained from literature (see Online Resource 1). Here, we define as “specialists” those species that feed preferentially (more than 75% of their diet) on a single taxon (e.g., Scleractinia). We considered a species as “generalist” when its diet was composed of a variety of sessile and mobile invertebrates, without clear preference for specific taxonomic groups (Schoener 1971; Nunes et al. 2019).

Are the diets of sister species from the Atlantic Ocean and the Eastern Pacific phylogenetically conserved?

We sampled eight species of *Chaetodon* and four species of *Prognathodes* that occur in the Atlantic and Eastern Pacific Oceans. Among the *Chaetodon* species, *C. capistratus* and *C. striatus* occur in the Western Atlantic, but are found in sympatry only in the Caribbean (Online Resource 2). *Chaetodon ocellatus* and *C. humeralis* occur in the Western Atlantic and Eastern Pacific, respectively (Online Resource 2). *Chaetodon robustus*, *C. hoeferi* and *C. marleyi* occur in West Africa, but only in *C. robustus* and *C. hoeferi* their ranges overlap (Online Resource 2). Finally, the closely related species *Chaetodon sanctaehelenae* and *C. sedentarius* occur separately in the Mid-Atlantic Ridge and Western Atlantic, respectively. In *Prognathodes*, *P. brasiliensis* and *P. aculeatus* are considered sister species that occur at the Brazilian and Caribbean provinces, respectively (Online Resource 3). *Prognathodes obliquus* is endemic to the St. Peter and St. Paul’s Archipelago, while its sister species, *P. dichrous*, occurs in the Mid-Atlantic Ridge (Online Resource 3).

To quantify the diet of each species, we combined literature and stomach content analyses. Literature data were obtained for *C. striatus*, *C. capistratus* and *P. aculeatus* in the Caribbean (Birkeland and Neudecker 1981; Liedke et al. 2018); *P. obliquus* in St. Peter and St. Paul’s Archipelago (Nunes et al. 2019) and *C. marleyi* in South Africa (Vine 1998). Additionally, we sampled the stomach contents of four *Chaetodon* and two *Prognathodes* species in six localities of the Atlantic as well as *Chaetodon humeralis* in the Eastern Pacific. The individuals were collected using hand spear and frozen to cease enzymatic action. Only adult individuals were sampled to avoid the effect of ontogenetic diet

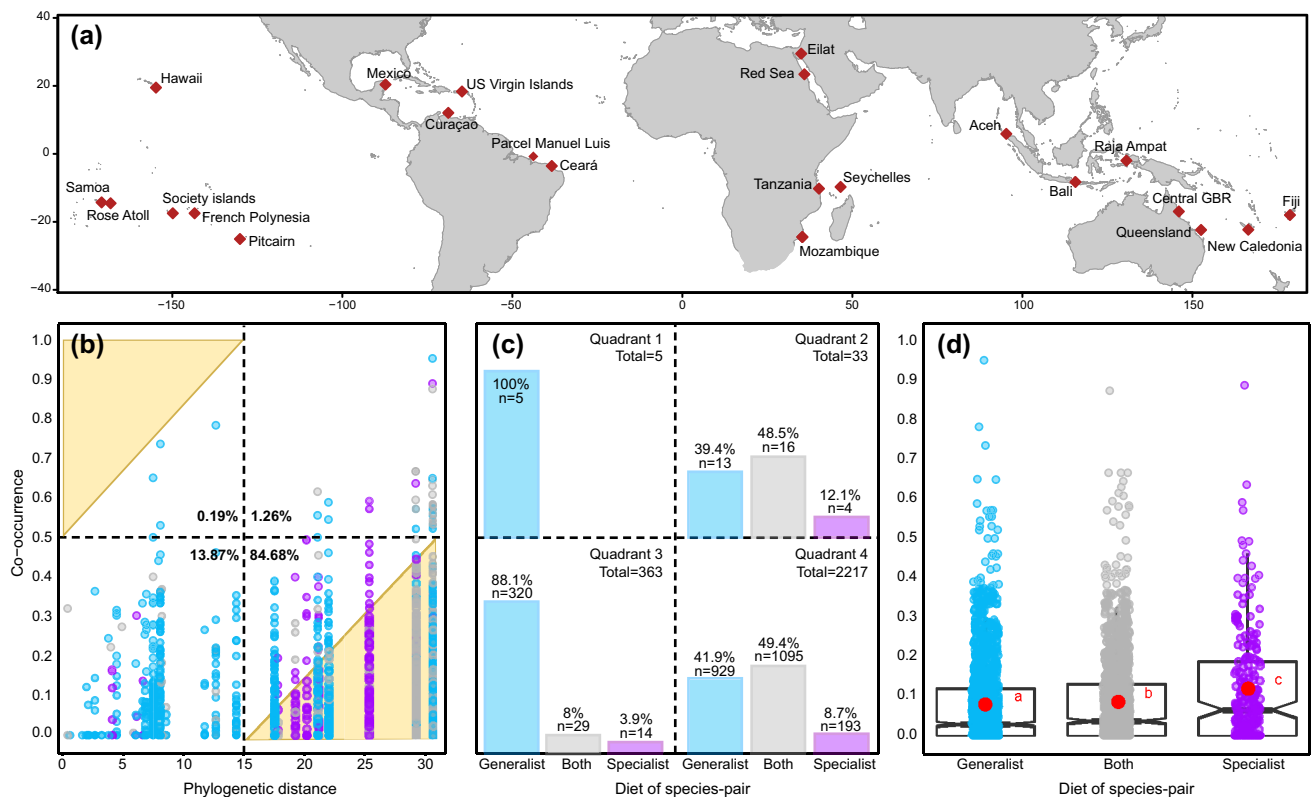


Fig. 2 **a** Global map showing the 23 sampled localities; **b** the correlation between co-occurrence and phylogenetic distance between species pairs (points) obtained through the Bray–Curtis index. Blue and purple points represent generalist and specialist species pairs, respectively. Grey points represent species pairs in which one is a generalist and the other is a specialist. The yellow triangle in the first quadrant represents a hypothetical area in which species pairs do not occur, while there is no impediment for a given species pair to occur

differences. All individuals were dissected in the laboratory where their stomachs were removed and fixed in 10% formaldehyde. The stomachs were subsequently sectioned in a Petri dish under a stereomicroscope, where its content was separated and identified to the lowest taxonomic category possible. Amorphous or partially digested food items were investigated under an optic microscope, in search of any cellular structures that could be used to better define a taxonomic group, such as spicules and nematocysts (Liedke et al. 2016; Nunes et al. 2019).

We quantified the diets according to the frequency of occurrence (%FO) that indicates how often a food item is present in the sampled stomachs and the volumetric index (%V), which relates the volume of each item to the total volume of the sampled stomach (Hynes 1950; Hyslop 1980). The volume of food items was measured through a millimetre Petri dish, where each item was placed between two 1 mm-thick coverslips and kneaded with a microscope slide, then the number of 1 mm³ grids were counted (Nunes et al. 2019). We assessed the importance of each food item

in the lower triangle; **c** proportion of diet types for each quadrant. *n* indicates the total number of pairs in the diet type. Percentages represent the proportional number of species pairs in each quadrant; **d** correlation between diet types and co-occurrences. Notched box plot represents median and confidence intervals. Red circles represent the mean co-occurrence of each diet type, Dunn test results represented by letters in red

through the Feeding Index equation: $\%IA_i = ((\%FO_i \cdot \%V_i) / \sum (\%FO_i \cdot \%V_i)) \cdot 100$, where $\%FO_i$ and $\%V_i$ represent the frequency of occurrence and volume of the food category *i*, respectively (Kawakami and Vazzoler 1980; Liedke et al. 2016; Nunes et al. 2019).

Statistical analyses

To test for an effect of abundances on co-occurrence strengths, we used network analyses and calculated the centrality of species in each locality. High centrality scores indicate species that are strongly connected to other species in the network, with these connected species also being strongly connected to other species (Delmas et al. 2019). Undirected, unipartite co-occurrence networks with weighted edges were created based on the Bray–Curtis co-occurrence matrices described above, with weights being the Bray–Curtis co-occurrence strength. Species' centrality was calculated through eigenvector centrality within each locality network. The centrality measure (dependent variable)

Table 1 Localities in which we obtained *Chaetodon* co-occurrence data. *Census* total number of censuses in which at least one *Chaetodon* species occur, *Area* census area in squared meters, *Total area* number of censuses multiplied by the area, which indicates the total reef area sampled in each locality. *Species* richness of *Chaetodon* species, *R* and *p* the correlation and significance, respectively. (1) Co-occurrence matrix; (2) phylogenetic matrix; (3) diet matrix. Values in bold indicate significant results ($p < 0.05$)

Province	Locality	Census	Area	Total area	Species	R_{12}	p_{12}	R_{13}	p_{13}	R_{32}	p_{32}	R_{123}	p_{123}
Brazil	Ceara	15	40	600	3	-0.846	0.340	na	na	na	na	na	na
Caribbean	Manuel Luis	15	40	600	3	0.500	0.002	na	na	na	na	na	na
	Curaçao	53	40	2120	3	-0.932	0.313	na	na	na	na	na	na
	Mexico	150	100	15,000	4	-0.938	0.044	na	na	na	na	na	na
	Virgin Islands	199	100	19,900	4	0.211	0.439	na	na	na	na	na	na
Central Pacific	Fiji	257	40	10,280	22	-0.108	0.058	-0.050	0.221	-0.505	0.001	-0.155	0.009
	Rose Atoll	16	500	8000	9	-0.289	0.077	0.667	0.002	-0.431	0.007	-0.003	0.500
	Samoa	307	150	46,050	20	0.049	0.253	-0.099	0.080	-0.380	0.001	0.013	0.434
Hawaiian	Hawaii	359	150	53,850	13	-0.033	0.396	-0.075	0.255	-0.279	0.008	-0.057	0.311
Indo-Pacific	Aceh	50	500	25,000	24	0.109	0.018	-0.112	0.061	-0.332	0.001	0.078	0.118
	Bali	18	500	9000	19	-0.088	0.113	0.073	0.176	-0.467	0.001	-0.062	0.185
	Raja Ampat	82	500	41,000	24	-0.021	0.364	0.007	0.422	-0.398	0.001	-0.019	0.375
	Eilat	5	500	2500	4	-0.713	0.099	0.283	0.261	-0.488	0.337	-0.687	0.132
North-western Indian	Red Sea	5	500	2500	8	0.126	0.263	0.050	0.389	-0.102	0.306	0.132	0.275
	French Polynesia	135	40	5400	14	-0.190	0.050	0.014	0.399	-0.472	0.001	-0.208	0.031
	Pitcairn	185	100	18,500	11	-0.261	0.041	-0.015	0.444	-0.403	0.001	-0.292	0.017
South-western Pacific	Society Islands	20	500	10,000	15	0.039	0.355	-0.107	0.131	-0.449	0.001	-0.010	0.471
	Central GBR	140	500	70,000	25	-0.063	0.135	-0.019	0.364	-0.322	0.001	-0.073	0.100
	New Caledonia	840	42	35,280	22	-0.198	0.008	0.049	0.232	-0.404	0.001	-0.195	0.003
	Queensland	66	500	33,000	23	0.040	0.264	0.036	0.284	-0.442	0.001	0.062	0.165
Western Indian	Mozambique	29	100	2900	16	-0.034	0.365	0.054	0.304	-0.384	0.001	-0.014	0.447
	Seychelles	76	100	7600	15	0.008	0.499	-0.147	0.059	-0.430	0.001	-0.062	0.269
	Tanzania	7	500	3500	10	0.149	0.187	-0.007	0.477	-0.434	0.001	0.162	0.137

was then regressed against species abundance (independent variable) to assess whether abundant species would co-occur more frequently when compared to the less abundant ones. In this study, connection strengths within networks are based on co-occurrences, therefore a relationship between centrality and abundance will suggest an influence of abundances on estimated co-occurrence strengths (i.e. more abundant species co-occur more often than less abundant species).

To correlate co-occurrence (dependent variable) with phylogenetic relationships (independent variables) after accounting for diet types at each locality, we performed a partial Mantel test with 999 permutations and the Pearson correlation method, using the ‘nfc’ R package (Bjornstad 2018). Additionally, we investigated possible differences among the proportion of species pairs (samples) in each diet type by performing Chi-squared with goodness-of-fit test. Due to discrepancies in the total number of samples among the graphical quadrants (see “Results”), we performed a bootstrap analysis with 1000 resamples (Online Resource 4). Finally, we verified differences between co-occurring diet types using Kruskal–Wallis and post hoc Dunn tests.

To verify similarities in species diets, we performed a cluster analysis with the IAI value grouped in nine major categories: Algae, Ectoprota, Hydrozoa, Octocorallia, Hexacorallia, Polychaeta, Crustacea, Eggs; and “Others” (i.e. items with low importance for the diet). We used a simprof (similarity profile analysis) test with Euclidian distance to unravel significant groups. To correlate the diet matrix (i.e. Euclidian distances among species) with the phylogenetic distance matrix, we performed a Mantel test. All analyses were performed using R software version 3.4.3, through the packages “ade4”, “boot”, “clustsig”, “dunn.test”, “ggdendro”, “ggplot2”, “gridExtra”, “igraph”, “map”, “maptools”, “plotrix”, “plyr”, “reshape” and “vegan” (R Core Team 2019).

Results

Among the 2618 species pairs analysed, we only found a correlation between co-occurrence and phylogenetic distance in a few localities (Table 1). Despite this, some patterns emerged when we analysed each quadrant of Fig. 2b separately. The top left quadrant represents closely related species (phy dist < 15 [representing an intermediate distance value]) that co-occur in more than 50% of the census. In this quadrant, only five species pairs were found, which represent less than 1% of the total species pairs analysed, showing that closely related species never co-occur in high frequency. The top right quadrant represents distantly related species (phy dist > 15) that co-occur in more than 50% of the census. In this quadrant, only 33 species pairs were found which represents 1.26% of the total

analysed (Fig. 2b). The bottom left quadrant represents closely related species (phy dist < 15) that co-occur in less than 50% of the census. In this quadrant, 363 species pairs were found, representing about 14% of the total (Fig. 2b). The bottom right quadrant represents phylogenetically distant species (phy dist > 15) that co-occur in less than 50% of the census. In this quadrant, 2217 species pairs were found which represents the majority of co-occurring species analysed (Fig. 2b).

When we looked at the proportion of species according to diet types, we found significant differences between quadrants (Quad. 2 $X^2 = 7.09$, $p = 0.03$; Quad. 3 $X^2 = 491.85$, $p < 0.01$; Quad. 4 $X^2 = 623.75$, $p < 0.01$), with predominance of generalist pairs in closely related co-occurring species (Quadrants 1 and 3; Fig. 2c). Specialist species pairs, on the other hand, were mainly found in the distantly related quadrants (Fig. 2c) and tended to co-occur more frequently than pairs involving generalist species (Fig. 2d). Finally, in most localities, we found that species abundance exerted a major influence in the co-occurrence patterns (Fig. 3).

We also found no correlation between phylogenetic distance and diet similarity among butterflyfishes from the Atlantic and the Eastern Pacific ($r = 0.04$, $p = 0.29$). Even though the diets of the 12 Chaetodontidae species consisted of several mobile and sessile invertebrates (from 4 to 30 feeding items depending on the species), Hexacorallia and Polychaeta were the preferred food resource for most species. Among Atlantic species, we found three *Chaetodon* and two *Prognathodes* that can be considered as specialists. The diet of *C. ocellatus* is the most specialized within the *Chaetodon* clade, being mainly composed of Zoanthids (IAi ~ 84%; Fig. 4). Its Eastern Pacific sister species, *C. humeralis*, is a generalist feeding predominantly on Hexacorallia, Polychaeta and Algae. Despite having different preferred items, the species *Chaetodon striatus* and *C. capistratus* also display a somewhat generalist diet, with no item showing an importance higher than 75%. *Chaetodon marleyi* is a specialist consuming Polychaeta (~ 73%), while its closely related *C. robustus* consumed mostly Hexacorallia (~ 90%; Fig. 4). The only individual of *Prognathodes dichrous* analysed in this study consumed mostly Hexacorallia (91%), while its sister species *P. obliquus* has a generalist diet composed of Polychaeta, Crustacea, Ectoprocta and Cnidaria. Algae was present in almost all species analysed, however, always with a low importance, which suggests accidental ingestion.

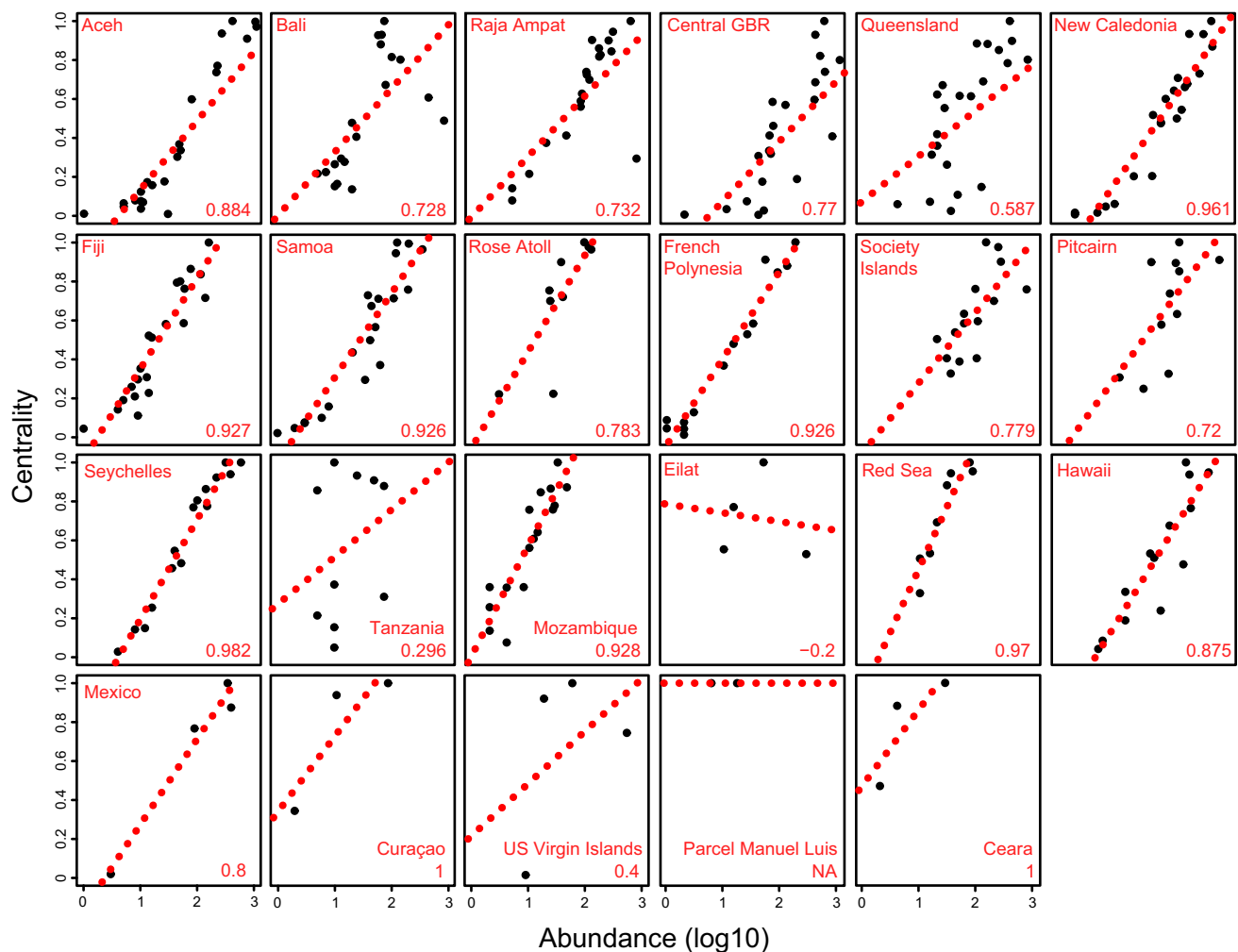


Fig. 3 Relationship between *Chaetodon* abundance and centrality, demonstrating that abundant species typically co-occur more frequently with other *Chaetodon* species. Black dots represent *Chaetodon* species in each locality. Values in red indicate the Pearson correlation

Discussion

Does phylogenetic affinity and/or species abundance explain co-occurrence at the habitat scale?

Phylogenetic distance between butterflyfishes fails to explain their co-occurrence at the habitat scale, although closely related species never co-occur at high frequency (i.e., Quadrant 1; Fig. 2b). The same lack of correlation was found in other studies for freshwater green algae (Narwani et al. 2013) and plant species (Germain et al. 2016), suggesting that evolutionary processes do not influence species co-occurrence at the habitat scale. Thus, we suggest that co-occurrences at this small scale might be modulated by: (1) “trait-matching” (Vazquez et al. 2009), where species co-occurrence will be linked to biological traits such as diet type or territorial behaviour (e.g., Keith et al. 2018; Fontoura

et al. 2020); or (2) neutral processes resulting from the random encounters among individuals, where locally abundant species co-occur more frequently just by chance (Vazquez et al. 2009). Based on our results (Fig. 3), the abundance of species is highly correlated with its centrality in the co-occurrence network, which provides support for the neutral hypothesis. This is supported by studies that demonstrated the central role of abundance in structuring biological interactions in several animal and plant groups (Vazquez et al. 2007; Floeter et al. 2007).

Although we did not find a correlation between co-occurrence and phylogenetic distance, we found that specialist pairs tend to co-occur more frequently than generalists or between generalist and specialist pairs. It is likely that the overlap in resource use may explain why generalist pairs co-occur less than specialist pairs, considering that specialists might show less overlap in food items consumed (Pratchett 2005). In that case, specialist species pairs would diverge in their preferred

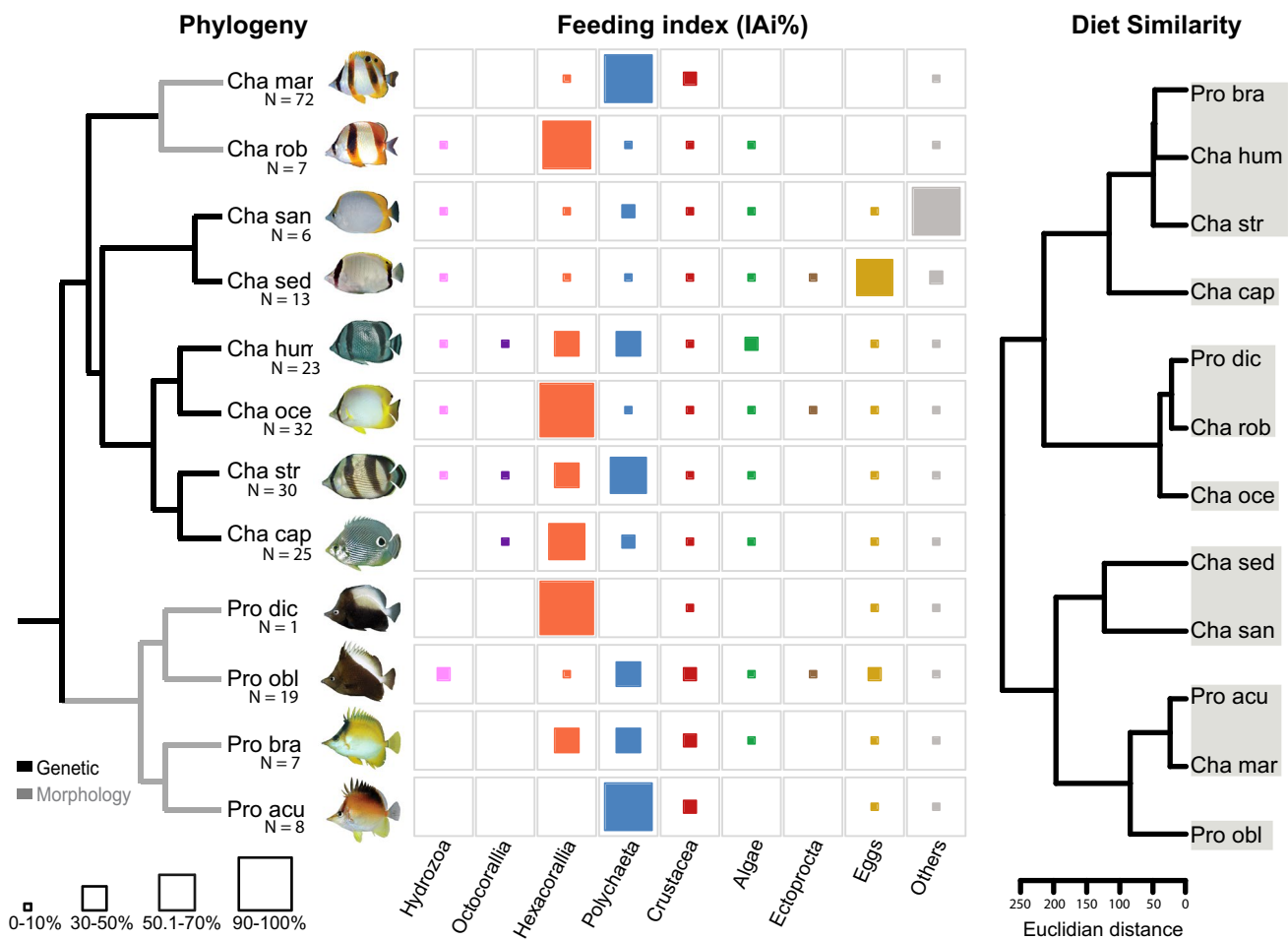


Fig. 4 Molecular phylogeny of *Chaetodon* species from the Atlantic and Eastern Pacific (pruned from Cowman and Bellwood 2011) with the respective number of individuals used for diet analyses (*N*). Coloured squares represent the feeding index (%IAi) of the eight most important diet items, plus “Others” (i.e. all other items found for species’ diet). Squares are proportional to the feeding index of each item. Empty squares represent absence of item in the diet. Cluster according to diet similarities, grey boxes represent simproportionally significant

cant groups. Cha mar: *Chaetodon marleyi* (data from Vine 1998), Cha rob: *Chaetodon robustus*, Cha san: *Chaetodon sanctaehelenae*, Cha sed: *Chaetodon sedentarius*, Cha hum: *Chaetodon humeralis*, Cha oce: *Chaetodon ocellatus*, Cha str: *Chaetodon striatus* and Cha cap: *Chaetodon capistratus* (Liedke et al. 2018), Pro dic: *Prognathodes dichrous*, Pro obl: *Prognathodes obliquus* (Nunes et al. 2019), Pro bra: *Prognathodes brasiliensis*, Pro acu: *Prognathodes aculeatus* (Birkeland and Neudecker 1981)

food items to avoid competition (Blowes et al. 2013), while generalists would only be able to co-occur with some degree of resource partitioning (Anderson et al. 1981; Bouchon-Navaro 1986). Thus, we suggest that species abundance and resource partitioning are more important in determining whether species can co-occur at the habitat scale (Anderson et al. 1981; Bouchon-Navaro 1986; Pratchett 2005; Early and Keith 2019) than phylogenetic relationships (Germain et al. 2016).

Are the diets of sister species from the Atlantic Ocean and the Eastern Pacific phylogenetically conserved?

For Atlantic and East Pacific butterflyfishes, species’ diet does not seem to be phylogenetically conserved (Fig. 4).

Our results diverge from a previous study where the authors found a significant correlation between phylogenetic distance and diet among *Chaetodon* species (Blowes et al. 2013). This difference, however, was likely related to the fact that Blowes et al. (2013) used the preferential substrate for foraging as a proxy for species diet, instead of stomach content analyses. Although quantifying diet through stomach content analysis might also have associated issues (e.g. difficulty to identify digested items; Liedke et al. 2018), it is still a very important approach for identifying the actual food intake when used in combination with substrate selection, even for specialist species. In addition to stomach content analysis, the use of other complementary methods, such as isotopic analyses and metabarcoding, is critical to access species trophic ecology. For

instance, the generalist *C. striatus* in South Brazil prefers to feed over Porifera and calcareous articulated algae substrates, but its diet is composed mainly of Cnidaria (Liedke et al. 2016). Through a broader feeding categorization (i.e. specialist and generalist) we were able to find an inverse correlation between phylogenetic distance and diet for *Chaetodon* species in most studied localities. This result corroborates our hypothesis that closely related species evolved to exploit similar substrates for foraging, such as the epilithic algal matrix or scleractinian corals (Floeter et al. 2018), but not necessarily the same food resource within this substrate (Nagelkerken et al. 2009).

Chaetodon sedentarius and *C. sanctaehelenae* were the only closely related species grouped based on diet. However, this clustering was not based on similarities between their diets, but rather on differences between their gut contents and the other butterflyfishes. These two species are thought to have separated from their shared ancestral lineage from the Indo-Pacific as a result from a recent invasion of the Atlantic (Floeter et al. 2008; Bellwood and Pratchett 2013). Despite not co-occurring throughout their distributions, both species share a more pelagic habit and are commonly found in schools in the water column (authors' personal observation). This differs from other analysed *Chaetodon* species that are benthic feeders and always forage solitarily or in pairs. The sister species *C. ocellatus* and *C. humeralis* are thought to have been separated by the rise of the Isthmus of Panama and, therefore, do not co-occur anywhere along their distributions (Bellwood et al. 2010). *Chaetodon ocellatus* is a specialist feeding on Zoanthids, while *C. humeralis* is a generalist. In the Caribbean, the sister species *Chaetodon striatus* and *C. capistratus* both possess a generalist diet. Both are syntopic species feeding over a variety of invertebrates (Liedke et al. 2018). *Chaetodon capistratus* is commonly recorded on the reef flat eating preferentially Hexacorallia, while *C. striatus* is mostly found on the reef interface eating mostly Polychaeta (Findley and Findley 1989; Liedke et al. 2018). The African clade of *Chaetodon* species is represented in this study by two species with a relatively more specialized diet: *Chaetodon marleyi*, which feeds mostly on Polychaeta, and its close relative *C. robustus*, a specialist in Hexacorallia. Both species occur along the African coast, but there is no overlap in their distribution (Online Resource 2). Species within the *Prognathodes* genus are distributed in different biogeographical provinces in the Atlantic Ocean (Online Resource 3). They also inhabit reefs with very distinct characteristics, which may have influenced the divergent diets found between sister species. Although we provide a better resolution about the diet of these poorly known species, we emphasize the need for a better phylogenetic resolution within the genus *Prognathodes* for a better investigation of the evolutionary patterns related to the ecology of this genus.

Both ecological and evolutionary processes could promote divergence in the diet of Atlantic and East Pacific butterflyfish sister species. This differentiation could be mediated by the opportunity to fill available niches following speciation and the emergence of coral reefs, with species being able to explore other food items in addition to scleractinian corals (Lobato et al. 2014; Floeter et al. 2018; Siqueira et al. 2020). Moreover, the availability and fluctuations in the abundance of food resources can alter predator's food plasticity (Pfennig et al. 2006).

Conclusions

Our study provides insights about the ecology and evolution of butterflyfishes, one of the most widely distributed and iconic reef fish families. Particularly, we bring new information about the less studied Atlantic and Eastern Pacific species. Co-occurrence patterns of butterflyfishes cannot be explained by the phylogenetic affinity, suggesting that resource availability and niche partitioning, plus species abundance, provide a better explanation for *Chaetodon* species pair co-occurrence. Additionally, we found that diets of Atlantic and Eastern Pacific butterflyfishes are not phylogenetically conserved, indicating that ecological processes are more important to dictate feeding preferences. These species are mostly generalists feeding on invertebrates, except for a few specialized species that consume different species of Hexacorallia.

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Author contributions LTN and SRF conceived the ideas and designed the study; LTN, ACS and BMF collected the data and/or performed statistical analyses; LTN and IC performed the stomach content analyses. LTN, IC, AMRL and CELF contributed to sampling effort; LTN led the writing; all the authors contributed to the writing and discussions. All authors gave final approval for publication.

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Data accessibility All the data and scripts will be available at the Zenodo platform (<https://zenodo.org/record/3895195#.XufO-NrQjIV>).

Compliance with ethical standards

Conflict of interest We declare that there is no conflict of interest.

Ethical approval We also declare that all individuals were sampled according to the international and national guidelines for sampling. Permission for sampling in Brazil was given by the ICMBio Institute (SISBio #55911-3 and #29953-10 to CEFL; and SISBio #41327-9 to SRF); In Ascension island permission was given by the Conservation Centre of the Ascension Government (ERP-2015-09 to Dr. Renato Morais). *Chaetodon robustus* individuals were obtained from the University of Cabo Verde (reference collection voucher: UCV 2020/00018-00024).

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