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Did biogeographical processes shape the monogenean community of butterflyfishes in the tropical Indo-west Pacific region?

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18 **Abstract**

19       Geographical distribution of parasite species can provide insights into the evolution and  
20 diversity of parasitic communities. Biogeography of marine parasites is poorly known, especially  
21 because it requires an understanding of host-parasite interactions, information that is rare, especially  
22 over large spatial scales. Here, we have studied the biogeographical patterns of dactylogyrid  
23 parasites of chaetodontids, one of the most well-studied fish families, in the tropical Indo-west  
24 Pacific region. Dactylogyrid parasites were collected from gills of 34 butterflyfish species ( $n = 560$ )  
25 at nine localities within an approximate area of 62 million km<sup>2</sup>. Thirteen dactylogyrid species were  
26 identified, with richness ranging from 6–12 species at individual localities. Most dactylogyrid  
27 communities were dominated by *Haliotrema angelopterum* or *Haliotrema aurigae*, for which  
28 relative abundance was negatively correlated ( $\rho = -0.59$ ). Parasite richness and diversity were  
29 highest in French Polynesia and the Great Barrier Reef (Australia) and lowest in Palau. Three  
30 biogeographic regions were identified based on dactylogyrid dissimilarities: French Polynesia,  
31 characterized by the dominance of *H. angelopterum*, the western Pacific region dominated by *H.*  
32 *aurigae*, and Ningaloo Reef (Australia), dominated by *Euryhaliotrema berenguelae*. Structure of  
33 host assemblages was the main factor explaining the dissimilarity (turnover and nestedness  
34 components of the Bray-Curtis dissimilarity and overall Bray-Curtis dissimilarity) of parasite  
35 communities between localities, while environment was only significant in the turnover of parasite  
36 communities and overall dissimilarity. Spatial structure of localities explained only 10% of the  
37 turnover of parasite communities. The interaction of the three factors (host assemblages,  
38 environment and spatial structure), however, explained the highest amounts of variance of the  
39 dactylogyrid communities, indicating a strong colinearity between the factors. Our findings show  
40 that spatial arrangement of chaetodontid dactylogyrids in the tropical Indo-west Pacific is primarily  
41 characterised by the turnover of the main *Haliotrema* spp., which is mainly explained by the  
42 structure of host assemblages.

43 *Keywords:* Butterflyfish, Community nestedness, Community turnover, Dactylogyrids,  
44 Ectoparasites, Host specificity, Indo-Pacific, Parasite biogeography

ACCEPTED MANUSCRIPT

## 1. Introduction

The biogeography of free-living marine taxa (e.g. corals, fish, bacteria) has been the focus of much research in recent decades (Tittensor et al., 2010; Briggs and Bowen, 2012; Ghiglione et al., 2012). The mechanisms that underpin their biogeographical patterns are relatively well understood (Leprieur, 2011; Rombouts et al., 2011; Chust et al., 2012). In contrast, the biogeography of marine parasites is virtually unknown, especially because evaluating their large-scale distribution implies an understanding of their host-parasite interactions, information that is very rare, especially over large spatial scales (Rohde, 2002; Poulin et al., 2011b; Cribb et al., 2016).

Parasites are strictly dependent on their hosts for essential resources (nutrients and physical attachment); thus, their geographical distribution, biodiversity and evolutionary history must, in some part, be influenced by that of their hosts (Poulin et al., 2011b). Host-parasite interactions may lead to the development of strict host specificity and subsequently to tight host-parasite co-evolution (Klein et al., 2004). Therefore, the study of the biogeography of parasite communities, coupled with the study of their hosts and parasite specificities, can provide insights into the evolution of parasitic communities and diversity over large spatial scales.

The analysis of beta-diversity, the extent of change in community structure among sites (Whittaker, 1960), has recently been shown to be a powerful tool in the analysis of biogeographical patterns (Leprieur, 2011; Baselga, 2012). One of the most widely used relationships in biogeography to evaluate beta-diversity is distance decay of similarity, which describes how similarity in community structure varies with increasing distance between localities (McNight et al., 2007; Soininen et al., 2007; Morlon et al., 2008). Numerous studies have shown that the similarity of parasite communities decreases with increasing distance (e.g. Oliva and Gonzalez, 2005; Pérez del Olmo et al., 2009; Timi et al., 2010). However, some studies have shown that other parameters such as host phylogenetic distance or environmental conditions may play a more important role in driving similarity of parasite communities than geographical distance (Vinarski et al., 2007; Thieltges et al., 2010; Warburton et al., 2016).

In a recent study, Locke et al., (2012) showed that distance decay depends upon the geographic scale of the study and latitude, being more significant further from the Equator. However, Vignon and Sasal (2009) found that fish parasite abundances at a global scale were determined by the site sampled, host species and host size. To date, most studies of parasite communities have used either presence/absence or abundance data to analyse variation in the overall similarity in structures of communities (e.g. Jaccard, Sørensen, Bray-Curtis algorithms). However, recent studies have shown that incidence-based measures of dissimilarities reflect two different components of dissimilarity, namely turnover and nestedness, turnover being the replacement of some species, while nestedness reflects the dissimilarity due to variation in the absence of turnover (Baselga, 2010, 2012). Disentangling the relative contribution of spatial turnover and nestedness components to the overall dissimilarity among communities is crucial to understand biogeographic patterns, since they can be generated from different underlying processes (Williams et al., 1999). For example, spatial turnover patterns may suggest the existence of spatial and historical constraints, whereas nestedness mainly reflects processes related to variation in species richness (Baselga, 2010).

In terms of biogeographical delineation, one of the best known and most well-studied fish families is the Chaetodontidae (butterflyfishes) (Blum, 1989; Fessler and Westneat, 2007; Kulbicki et al., 2013). Butterflyfishes are a diverse and emblematic family of coral reef fishes, and some butterflyfish species are among the most broadly distributed reef fishes (diBattista et al., 2015). Their ecology has been studied extensively (Pratchett et al., 2013) and they are known to harbour a diverse array of parasites (Morand et al., 2000; McNamara et al., 2012, 2014; Yong et al., 2013). Thus, the Chaetodontidae represent an ideal host group to study spatial distribution and biogeography of parasite species. Butterflyfishes are regularly and reliably parasitized by gill monogeneans belonging to the family Dactylogyridae. Dactylogyrids are the primary monogenean group found on this fish family; a few capsalids are the only other monogeneans known to infect chaetodontids (Bullard et al., 2000). Fifteen dactylogyrid species have been reported from

chaetodontids to date (Plaisance and Kritsky, 2004; Plaisance et al., 2004). In a recent study, we found that prevalence, intensity and taxonomic composition of butterflyfish dactylogyrid communities differed significantly between butterflyfish species (Reverter et al., 2016). However, in contrast to most monogeneans, which are typically reported as having strict (species-specific or oioxenous) specificity, dactylogyrids of chaetodontids display an unusually low specificity, allowing the exploration of their biogeography as a special case. The wide distribution of the hosts and the broad overlap in host specificity of the parasite species means that suitable hosts are available for each dactylogyrid species across much of the tropical Indo-west Pacific region.

This study aims to investigate biogeographical patterns of dactylogyrid parasites of butterflyfishes in the tropical Indo-west Pacific region. We studied the area of distribution, prevalence and intensity of 13 dactylogyrids species from butterflyfishes at nine localities and identified distinct bioregions in the tropical Indo-west Pacific on the basis of dactylogyrid communities. Most parasite community studies consider one host species. Here, we studied 34 host species belonging to the same family, Chaetodontidae, which allows a deeper understanding of the spatial arrangement of dactylogyrids and which factors shape parasite communities. We have evaluated the relative contribution of geographic distance, similarity in host communities and environmental similarities on both components of parasite community dissimilarity, turnover and nestedness, on what it is possibly the largest marine spatial scale to date. The purity of our dataset, which was comprised of only one group of parasites (dactylogyrids), limited other types of variability (e.g. parasite dispersal, longevity, life cycle complexity) that can introduce extra noise into distance decay studies.

## 2. Materials and methods

### 2.1. Sampling

Thirty-four species of butterflyfish ( $n = 560$ ) were examined from eight localities in the Pacific region: Palau, Wallis and Futuna, Lizard Island (Great Barrier Reef (GBR), Australia), and



the five archipelagos in French Polynesia (Society Archipelago, Tuamotu Archipelago, Austral Archipelago, Gambier Archipelago and Marquesas Archipelago). Butterflyfish were also sampled from a single locality in the Indian Ocean, Ningaloo Reef on the western Australian coast (Supplementary Table S1).

Adult butterflyfish were spear-fished and killed immediately by cranial pithing, put in individual plastic bags with seawater and transported to a laboratory, where the gills were dissected and fixed in 70% ethanol. Dactylogyrids were removed from the gills using a stereo microscope and mounted on glass slides in Malmberg's ammonium picrate-glycerine.

All dactylogyrid specimens from each individual fish were observed under a compound microscope, and parasite species and numbers were recorded. Dactylogyrid species were identified using the published taxonomic literature (Plaisance et al., 2004; Plaisance and Kritsky, 2004; Kritsky, 2012), which is based on the morphological characters of the sclerotised structures of the haptor and reproductive organs. As reported by Reverter et al., (2016), two of the dactylogyrid species encountered are undescribed. These species are identified here as *Haliotrema* sp. A and *Haliotrema* sp. B and will be formally characterised elsewhere.

Sampling of hosts was performed in order to be as representative as possible of the butterflyfish community for each of the localities, thus differential sampling of butterflyfish species reflects differences in butterflyfish presence among localities (Supplementary Table S1).

## 2.2. Data analysis

Dactylogyrid prevalence (percentage of parasitized fish) and mean intensity (the number of parasites on parasitized fish) were determined for each dactylogyrid species at each geographic site surveyed during this study. The effect of host size on dactylogyrid prevalence, intensity and taxonomic composition was evaluated in a previous work and it was found non-significant (Reverter et al., 2016). Areas of dactylogyrid distribution were determined using presence-absence of the dactylogyrid species at the nine studied geographic locations. Previous records found in the

literature (Yamaguti, 1968; Dyer et al., 1989; Zhang et al., 2001; Plaisance et al., 2004; Plaisance and Kritsky, 2004) were also taken into account only for the distribution, in order not to limit the area of distribution to our sampling sites. Pearson correlation was used to test correlations between dactylogyrid species prevalences.

The relative abundance of dactylogyrid species (contribution of a dactylogyrid species to the overall dactylogyrid community expressed as a percentage) and the weighted parasite intensity were calculated for each site. The weighted parasite intensity at each geographic site ( $Iw_{site}$ ) was computed in order to correct for the effect of differential parasite intensities from different butterflyfish species sampled at different geographic locations (Reverter et al., 2016). Weighted parasite ( $Iw$ ) intensity was calculated according to the following equation:

$$Iw_{site} = \frac{\sum_{sp1}^{spx} (Isp_{site}/Isp)}{n^{\circ} sp_{site}}$$

where  $Isp_{site}$  is the mean parasite intensity of a fish species ( $sp_{1,2,x}$ ) at one geographic site,  $Isp$  is the global mean parasite intensity of that fish species and  $n^{\circ} sp_{site}$  is the number of fish species sampled at that geographic site.

Parasite diversity at each geographic site was computed using the Shannon diversity index ( $H$ ) and parasite richness was also determined. A hierarchical cluster analysis («hclust» package for R) using the Bray-Curtis distance was used to identify geographic regions with similar monogenean assemblages. The Unweighted Pair Group Method with Arithmetic Mean (UPMGA) agglomerative algorithm was chosen after analysis of the cophenetic correlation coefficients (Pearson correlation between the cophenetic distances calculated on cluster branches and the parasite dissimilarity matrix). The Kelley-Gardner-Sutcliffe (KGS) penalty function was used to define the optimal number of clusters (Bottegoni et al., 2006).

The function "bray.part" from the package betapart (R Software, [www.r-project.org](http://www.r-project.org)) was used to obtain three distance matrices of the parasite communities at different locations, accounting for the balanced variation (dBC-bal), the abundance gradient (dBC-gra) components of Bray-Curtis dissimilarity, and the sum of both values (Bray-Curtis dissimilarity, dBC) (Baselga, 2013). These

are an extension of the turnover and nestedness concepts to the case of an abundance matrix instead of a presence/absence matrix.

We used redundancy analysis (RDA) with variation partitioning (Borcard et al., 1992) in order to assess the relative contribution of environmental conditions, spatial structure and the structure of hosts assemblages in explaining the dissimilarity in parasite communities among locations (dBC-gra and dBC-bal). Environmental conditions of our locations were characterised according to chlorophyll concentration, cloud cover, photosynthetically available radiation, dissolved oxygen, nitrate concentration, phosphate concentration, silicate concentration, salinity and sea surface temperature, extracted from the Bio-Oracle database (Tyberghein et al., 2012), a global database successfully employed in various biogeographical applications (Parravicini et al., 2013, 2015). Linear geographic distances between pairs of geographic locations were obtained from the Latitude/Longitude Distance Calculator of the National Hurricane Center from the National Oceanic and Atmospheric Administration (<http://www.nhc.noaa.gov/gccalc.shtml>). In order to characterise the spatial structure of the locations, we generated a set of multiscale principal coordinates of neighbour matrices (PCNM) from the geographic distance matrix (Dray et al., 2006). PCNM eigenfunctions consist of the spectral decomposition of the spatial relationships among locations. The structures of the host assemblages at our locations were assessed according to a Bray-Curtis dissimilarity matrix on species abundance at each location. The procedure involved the partitioning of the global variation into distinct components: a pure environmental component, a pure spatial component, a pure host assemblage component, their interaction and the residual component. First, forward selection was used for each set of variables separately in order to select only those variables that explained a significant proportion of the variation ( $P < 0.05$ , after 999 random permutations). The retained variables were then used in the variation partitioning using adjusted- $R^2$  values that correct for the variation jointly explained by multiple variables (Peres-Neto et al., 2006). Prior to the analysis, dissimilarity matrices were transformed into data frames by conducting a principal coordinate analysis according to Legendre and Anderson (1999).

201

### 202 3. Results

#### 203 3.1. Dactylogyrid area of distribution

204 Thirteen dactylogyrid species were detected infecting the 34 species of chaetodontids  
205 examined (Supplementary Table S2). Overwhelmingly the dactylogyrid species were found to be  
206 widely distributed throughout the tropical Indo-west Pacific region, from Ningaloo Reef in the  
207 Indian Ocean to the most easterly Polynesian archipelago, the Gambiers (Fig. 1). Six species were  
208 found at all nine locations explored by us, and a further four were found at six or more sites (Fig. 1,  
209 Supplementary Fig. S1). Three species were each found at only two localities. *Haliotrema* sp. A and  
210 *Haliotrema* sp. B were both found at Lizard Island and French Polynesia (Australis and Tuamotus,  
211 respectively). *Haliotrema scyphovagina* (Yamaguti, 1968) was found only at the Tuamotus, having  
212 been originally described from Hawaii (Yamaguti, 1968) (Supplementary Table S2).

213 Although the dactylogyrid species were generally widespread, their prevalences and  
214 intensities varied strikingly between host species and locations. Between them, *Haliotrema*  
215 *angelopterum* Plaisance, Bouamer and Morand 2004 and *Haliotrema aurigae* Plaisance, Bouamer  
216 and Morand 2004 comprised 55.2% of all individual dactylogyrids counted. In contrast, the  
217 combination of the seven least abundant species comprised just 4.2% of all individuals  
218 (Supplementary Table S2). *Euryhaliotrema pirulum* (Plaisance & Kritsky, 2004) was especially  
219 striking in terms of low abundance, being represented by single specimens at four localities, and  
220 just two, five and 15 at the other three localities for which counts were available (Supplementary  
221 Table S2). In terms of contrasts for individual species (Fig. 1), *H. angelopterum* had its highest  
222 prevalences and abundances in French Polynesia (all five sites), whereas the highest prevalences of  
223 *H. aurigae* were found at Ningaloo Reef (80%) and Lizard Island (57%). *Euryhaliotrema*  
224 *berenguelae* (Plaisance & Kritsky, 2004) was a relatively rare species at most sites (total prevalence  
225 < 15%), however, 73% of fish from Ningaloo Reef were parasitized by this species, often in high  
226 numbers (Fig. 1). *Euryhaliotrema grandis* (Mizelle & Kritsky 1969) was most prevalent in the

227 Tuamotus (48%), but the highest intensities were observed on fish from Ningaloo Reef.  
 228 *Euryhaliootrema microphallus* (Yamaguti, 1968) was most prevalent on fish from Lizard Island  
 229 (44%), but its greatest mean abundance per fish was observed in the Marquesas (Fig. 1). For  
 230 *Euryhaliootrema triangulovagina* (Yamaguti, 1968) the highest prevalence was observed in the  
 231 Marquesas (40%).

232 Pearson correlation was used to study the interspecific interactions between the parasite  
 233 species. Results showed that *H. angelopterum* is negatively correlated with *H. aurigae* (-0.59, *P*  
 234 value < 0.05) and *Euryhaliootrema cribbi* (Plaisance & Kritsky, 2004) (-0.69, *P* value < 0.05), and  
 235 *H. aurigae* is positively correlated with *E. berenguelae* (0.79, *P* value < 0.05) and *E. grandis* (0.63,  
 236 *P* value < 0.05). *Euryhaliootrema microphallus* is also strongly positively correlated with  
 237 *Euryhaliootrema annulocirrus* (0.73) (Fig. 2).

238

### 239 3.2. Biogeographic structure of dactylogyrid communities

240 Weighted intensity, that is, dactylogyrid intensity corrected for the effect of differential host  
 241 species intensities, showed striking differences among geographic locations. Fish from the  
 242 Marquesas Archipelago presented the lowest intensity of parasites ( $I_{W\text{Marquesas}} = 0.57$ ), followed by  
 243 Palau ( $I_{W\text{Palau}} = 0.65$ ) and the Gambier Archipelago ( $I_{W\text{Gambiers}} = 0.67$ ). Fish from the Tuamotu  
 244 Archipelago had the highest intensity of dactylogyrid parasites ( $I_{W\text{Tuumotu}} = 1.49$ ) followed by the  
 245 Society Archipelago ( $I_{W\text{Society}} = 1.12$ ) and Ningaloo Reef ( $I_{W\text{NR}} = 1.09$ ) (Fig. 3, Table 1).

246 Twelve out of the 13 identified dactylogyrid species were found at the Tuamotu Archipelago  
 247 and Lizard Island, while the Marquesas had the lowest number of dactylogyrid species ( $n=6$ ) (Table  
 248 1). Dactylogyrid diversity (Shannon diversity index (*H*)) varied between geographic locations  
 249 (Table 1). The highest diversity was found at Lizard Island (1.96) on the Great Barrier Reef,  
 250 followed by the Gambier Archipelago (1.74) and the Tuamotus (1.64). The lowest dactylogyrid  
 251 diversity was observed in the Society Archipelago (1.12), where the community was strongly  
 252 dominated by *H. angelopterum* (65%). Palau and the Marquesas also presented notably low

dactylogyrid diversity (1.22). Palau dactylogyrid assemblages were dominated mostly by *H. aurigae* (66%), while *H. angelopterum* (46%) and *E. triangulovagina* (36%) were the most abundant parasites in the Marquesas (Table 1, Fig. 3).

A hierarchical cluster analysis identified three distinct biogeographic regions based on dissimilarities among their dactylogyrid communities: the eastern Pacific region containing five sites from French Polynesia; the western Pacific containing Lizard Island, Palau, and Wallis and Futuna; and Ningaloo Reef in the Indian Ocean (Fig. 4). Localities in French Polynesia were united especially by a high abundance of *H. angelopterum*, whereas those in the western Pacific region exhibited higher abundances of *H. aurigae*. Ningaloo Reef was distinguished by the high abundance of *E. berenguelae* (Figs. 3, 4).

### 3.3. Factors shaping biogeographic differences in dactylogyrid communities

The structure of host assemblages was identified as the factor that explained the highest variance in dactylogyrid communities among geographic sites (Fig. 5). The pure host assemblage component explained 20% of the balanced variation (dBC-bal, turnover) of the dactylogyrid communities, 21% of the abundance gradient (dBC-gra, nestedness) and 15% of the overall Bray-Curtis dissimilarity of the dactylogyrid communities. The pure environmental component explained 18% of the balanced variation and 4% of the overall Bray-Curtis dissimilarity of the dactylogyrid communities (Fig. 5A, C). The pure spatial component only accounted for 10% of the balanced variation of the dactylogyrid communities (Fig. 5A). However, most of the variation was explained by the interaction between the three components (spatial structure, environment and host assemblages), which explained 42% of the balanced variation, 38% of the abundance gradient and 16% of the overall Bray-Curtis dissimilarity of the dactylogyrid communities; indicating an interaction between environment and host assemblage structure (Fig. 5). Finally, a considerable amount of variance remained unexplained by the components that were studied (residual variance) (Fig. 5).

279

#### 280 4. Discussion

281 Most dactylogyrid species from butterflyfishes were broadly distributed throughout the  
282 study locations in the tropical Indo-west Pacific region. There were three exceptions, *Haliotrema*  
283 sp. A and sp. B. and *H. scyphovagina*. *Haliotrema* sp. A and sp. B were both found at Lizard Island  
284 on the GBR and at single, separate sites within French Polynesia. Given that both species were  
285 relatively rare (just 0.8% and 0.4% of all dactylogyrids collected, respectively), it seems likely, or at  
286 least plausible, that these species were simply missed at other sites between the GBR and French  
287 Polynesia. In contrast, *H. scyphovagina* was found only at the Tuamotus in French Polynesia,  
288 having been described originally from Hawaii by Yamaguti (1968). In Hawaii the species has been  
289 reported from *Chaetodon miliaris* Quoy and Gaimard, 1825 and *Chaetodon multicinctus* Garrett,  
290 1863, whereas in the Tuamotus it was only found on *Chaetodon unimaculatus* Bloch, 1787, and  
291 *Chaetodon vagabundus* Linnaeus, 1758, two species sampled at the other locations in this study.  
292 Thus, it seems at least possible that this species is restricted to Hawaii and parts of French  
293 Polynesia. Overall, however, the broad distributions reported here suggest that, despite the possible  
294 distinct origins and evolutionary ages of the dactylogyrid species as proposed by Plaisance et al.,  
295 (2007), these species share similar dispersal strategies that enable similar geographic ranges.

296 The Coral Triangle, which encompasses the Philippines, Indonesia and New Guinea, is the  
297 area of highest marine biodiversity in the world, with marine richness decreasing radially from it  
298 (Bellwood and Hughes, 2001; Carpenter and Springer, 2005). For example, richness of shore fishes  
299 declines from 1693 at the centre of the Coral Triangle in the Philippines to 1579 in the main island  
300 of New Caledonia, to 702 fish species in the Society Archipelago and just 245 fish species in the  
301 Gambier Archipelago (Kulbicki, 2007). Changes in biodiversity of parasitic organisms, with  
302 increasing distance from the Coral Triangle, have been much less studied. A few studies have  
303 shown that some heteroxenous helminths follow the same trend as free-living species, showing a  
304 west-to-east reduction in diversity in the Pacific region (e.g. Rigby et al., 1997; McNamara et al.,



2012; Cribb et al., 2014). In contrast, previous studies on butterflyfish dactylogyrids suggested that their greatest richness is actually in French Polynesia and that there is an east-to-west reduction towards the GBR (Plaisance et al., 2004, Plaisance and Kritsky, 2004). However, our study does not support that finding; we discovered equal parasite richness and diversity in French Polynesia and the GBR. The lowest parasite richness, in the Marquesas Archipelago, is potentially explained by the isolation of this archipelago coupled with the absence of lagoons and the very low coral cover there. As a result, there are relatively fewer susceptible host species and individuals in the Marquesas than in other nearby archipelagos (Kulbicki, 2007). In contrast, the relatively close Tuamotu Archipelago is characterised by enormous lagoons and rich coral growth and is exceedingly rich in dactylogyrids.

Although we have demonstrated that most dactylogyrid species occur in all or nearly all localities, there are clear differences in the structure of the dactylogyrid communities at different localities. The cluster analysis, based on differences in the dactylogyrid communities of butterflyfishes, showed that three distinct biogeographic regions can be recognised: French Polynesia, the western Pacific (Palau, Lizard Island, and Wallis and Futuna) and Ningaloo Reef. Thus, our results show that the two bioregions in the western Pacific region (the southwestern Pacific and French Polynesia), support quantitatively different monogenean assemblages.

The key basis of this difference is that Pacific communities tend to be dominated by two *Haliotrema* spp. (*H. angelopterum* and *H. aurigae*) throughout the whole studied geographical range, but that they are negatively correlated; *H. angelopterum* was more abundant than *H. aurigae* in French Polynesia by a factor of three, whereas *H. aurigae* was nearly five times more abundant than *H. angelopterum* in the western Pacific region. These data indicate a significant but incomplete species turnover in the dactylogyrid community between French Polynesia and the western Pacific region. The phylogeography of two dactylogyrid parasites from butterflyfishes was studied by Plaisance et al. (2008), who found clear genetic differentiation of *E. grandis* between the population in Moorea (French Polynesia) and all the other populations (western Pacific), but, perhaps



surprisingly, no such biogeographical structuring in *H. aurigae*. They suggested that differentiation of *E. grandis* could have been driven by isolation of French Polynesia during Pleistocene sea-level fluctuation. It seems plausible that such fluctuation might have driven the overall differences in the dactylogyrid communities between the eastern and western Pacific regions. Macpherson et al. (2010) also found different communities of galatheid squat lobsters between French Polynesia and the rest of the western Pacific region with a high proportion of endemism, suggesting French Polynesia as a centre of diversity.

Our results show, contrary to expectations, that geographic distance between host populations is not the most significant factor in either the turnover or nestedness of the parasite community. Instead, structure of host populations between sites was identified as the main driver responsible for the dissimilarity in parasite communities (turnover, nestedness and overall dissimilarity). Similarly, Locke et al. (2013) found that parasite community similarity was mostly associated with host phylogeny while distance decay was mainly a within-host species phenomenon. In a previous study, sympatric butterflyfish species were shown to harbour well-delineated communities of dactylogyrids, and six clusters consisting of chaetodontid species infected by similar dactylogyrid assemblages were identified (Reverter et al., 2016). The two main clusters of butterflyfish species based on similarity of their dactylogyrid parasites were characterized by the dominance of *H. aurigae* (cluster 1) and *H. angelopteron* (cluster 2). Most of the species from cluster 1 were found most frequently in the western Pacific region (e.g. *Chaetodon baronessa* Cuvier, 1829, *Chaetodon speculum* Cuvier, 1831, *Chaetodon semeion* Bleeker, 1855, *Chaetodon lineolatus* Cuvier, 1831) and species from cluster 2 were found most frequently in French Polynesia (e.g. *Chaetodon reticulatus* Cuvier 1831, *Chaetodon trichrous* Günther, 1874, *Chaetodon ornatissimus* Cuvier 1831) (Reverter et al., 2016). Plaisance et al. (2007) found that *H. aurigae* showed little biogeographical genetic structure in the tropical Indo-west Pacific region, suggesting its recent evolutionary age compared with other dactylogyrid species. *Haliotrema aurigae* and *H. angelopteron* are phylogenetically close (Plaisance et al., 2005), and we

hypothesise that *H. aurigae* and *H. angelopterum* diverged from a common ancestor during the French Polynesia Pleistocene isolation from the western Pacific region, and that these past biogeographical processes might have shaped the observed parasite specificity among the different butterflyfish species. It is noteworthy that *H. aurigae* and *H. angelopterum* are also among the biggest species of dactylogyrid parasites found on butterflyfishes (Plaisance et al., 2004); their size may thus be important as a basis of their numerical dominance on individual fishes.

Recent studies have shown that environmental factors such as salinity and temperature are important in driving the compositions of parasite communities (Thieltges et al., 2010; Poulin et al., 2011a; Blasco-Costa et al., 2015). For example, Campiao et al. (2012) found that change in parasite composition of the frog *Leptodactylus podicipinus* Cope, 1862, was mainly related to variation in environmental conditions rather than to species distribution. Warburton et al. (2016) also observed that environmental variables, rather than spatial variables, explained variation in helminth community similarities of big brown bats (*Eptesicus fuscus*, Palisot de Beauvois 1796). In our study, the environment was a significant factor in the turnover and overall dissimilarity of dactylogyrid communities. Since chaetodontid larvae, the only planktonic phase of butterflyfishes, are not parasitized by monogenean parasites (Peyrusse et al., 2012) and dactylogyrid oncomiracidia live only a few hours without a host (Whittington, 1997), it has been proposed that dactylogyrid dispersal takes place through the passive dispersion of their eggs by oceanic currents (Ganicott and Tinsley, 1998; Plaisance et al., 2008). Previous studies have shown that monogenean egg hatching and larval infection processes are highly dependent on environmental parameters such as water temperature (Cecchini et al., 1998; Pietrock and Marcogliese, 2003; Tubbs et al., 2005). Our results are thus consistent with the idea that environmental parameters can affect the turnover of parasite species, suggesting the importance of suitable environmental conditions for larval development, egg hatching, and successful infection of fishes.

Interestingly, the interaction of the three factors studied (host assemblage, environment and spatial structure) explained an important part of the parasite dissimilarity, indicating a strong

colinearity between them. This finding may indicate that both host assemblage and environment dissimilarity are important factors underlying the commonly observed distance decay. Finally, a significant amount of variance remained unexplained by the study of these three factors, suggesting that other factors (e.g. host phylogeny) might affect parasite dissimilarity.

We have observed two main biogeographic regions in the Pacific Ocean that can be differentiated mainly by a partial turnover in two species of *Haliotrema*. To the best of our knowledge, this is the first study on the biogeography of parasite communities that distinguishes between the balanced variation (turnover) and abundance gradient (nestedness) components of dissimilarity. Differences between chaetodontid assemblages are the main factor influencing parasite community turnover. Coupled with the results from previous work (Reverter et al. 2016), this finding suggests that biogeographical processes shaped parasite specificity through a tight but not species-specific host-parasite coevolutionary process. Environmental dissimilarity is also identified as an important factor explaining the turnover of dactylogyrid communities, indicating the importance of favourable environmental conditions for dactylogyrid egg hatching and successful host infection.

This study dramatically increases knowledge of communities of dactylogyrid monogeneans of butterflyfishes and their distribution in the tropical Indo-west Pacific region. However, more study is needed to determine the complete distribution of these parasite species, which might include other oceans (e.g. *E. annulocirrus* has been recorded in the Red Sea) (Paperna, 1972). The Indian Ocean in general remains poorly studied for ectoparasites and much could be learned from focused surveys in this region. Butterflyfishes are well known for their propensity to hybridize (Montanari et al., 2014). The study of dactylogyrid communities of hybrids and closely related sister species from the Indian Ocean might also provide further insight into the biogeography and evolutionary history of dactylogyrids. Similarly, the integrated study of the biogeography of direct cycle parasites (monogeneans) and complex cycle parasites (digeneans) might provide new insight into the biogeography of coral reef parasites.

409

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## References

- Baselga, A., 2013. Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. *Methods Ecol. Evol.* 4, 552–557.
- Baselga, A., 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecol. Biogeogr.* 21, 1223–1232.
- Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecol. Biogeogr.* 19, 134–143.
- Bellwood, D.R., Hughes, T.P., 2001. Regional-scale assembly rules and biodiversity of coral reefs. *Science* 292, 1532–1535.
- Blasco-Costa, I., Rouco, C., Poulin, R., 2015. Biogeography of parasitism in freshwater fish: spatial patterns in hot spots of infection. *Ecography* 38, 301–310.
- Blum, S.D., 1989. Biogeography of the Chaetodontidae: an analysis of allopatry among closely related species. *Env. Biol. Fish.* 25, 9–31.
- Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. *Ecology* 73, 1045–1055.
- Bottegoni, G., Rocchia, W., Recanatini, M., Cavalli, A., 2006. AClAP, Autonomous hierarchical agglomerative Cluster Analysis based protocol to partition conformational datasets. *Bioinformatics* 22, e58–65.
- Briggs, J.C., Bowen, B.W., 2012. A realignment of marine biogeographic provinces with particular reference to fish distributions. *J. Biogeogr.* 39, 12–30.
- Bullard, S.A., Benz, G.W., Overstreet, R.M., Williams, E.H., Hemdal, J., 2000. Six new host records and an updated list of wild hosts for *Neobenedenia melleni* (MacCallum) (Monogenea: Capsalidae). *Comp. Parasitol.* 67, 190–196.
- Campiao, K.M., Delatorre, M., Rodrigues, R.B., da Silva, R.J. Ferreira, V.L., 2012. The effect of local environmental variables on the helminth parasite communities of the pointedbelly frog *Leptodactylus podicipinus* from ponds in the Pantanal wetlands. *J. Parasitol.* 98, 229–235.

- 446 Carpenter, K.E., Springer, V.G., 2005. The center of the center of marine shore fish biodiversity:  
447 the Philippine Islands. *Env. Biol. Fish.* 72, 467–480.
- 448 Cecchini, S., Saroglia, M., Berni, P., Cognetti-Varriale, A.M., 1998. Influence of temperature on the  
449 life cycle of *Diplectanum aequans* (Monogenea, Diplectanidae), parasitic on sea bass,  
450 *Dicentrarchus labrax* (L.). *J. Fish Dis.* 21, 73–75.
- 451 Chust, G., Irigoien, X., Chave, J., Harris, R.P., 2012. Latitudinal phytoplankton distribution and the  
452 neutral theory of biodiversity. *Global Ecol. Biogeogr.* 22, 531–543.
- 453 Cribb, T.H., Adlard, R.D., Bray, R.A., Sasal, P., Cutmore, S.C., 2014. Biogeography of tropical  
454 Indo-West Pacific parasites: a cryptic species of *Transversotrema* and evidence for rarity of  
455 Transversotrematidae (Trematoda) in French Polynesia. *Parasitol. Int.* 63, 285–294.
- 456 Cribb, T.H., Bray, R., Diaz, P.E., Huston, D.C., Kudhlay, O., Martin, S.B., Yong, R. Q-Y., Cutmore,  
457 S.C., 2016. Trematodes of fishes of the Indo-west Pacific: told and untold richness. *Syst.*  
458 *Parasitol.* 93, 237–247.
- 459 DiBattista, J.D., Waldrop, E., Rocha, L.A., Craig, M.T., Berumen, M.L., Bowen, B.W., 2015.  
460 Blinded by the bright: a lack of congruence between colour morphs, phylogeography and  
461 taxonomy for a cosmopolitan Indo-Pacific butterflyfish, *Chaetodon auriga*. *J. Biogeogr.* 42,  
462 1919–1929.
- 463 Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modelling: a comprehensive framework for  
464 principal coordinate analysis of neighbour matrices (PCNM). *Ecol. Model.* 196, 483–493.
- 465 Dyer, W.G., Williams, E.H.J., Williams, L.B., 1989. Monogeneans from marine fishes of Okinawa,  
466 Japan. *Proc. Helm. Soc. Wash.* 56, 64–68.
- 467 Fessler, J.L., Westneat, M.W., 2007. Molecular phylogenetics of the butterflyfishes  
468 (Chaetodontidae): taxonomy and biogeography of a global coral reef fish family. *Mol. Phyl.*  
469 *Evol.* 45, 50–68
- 470 Gannicott, A.M., Tinsley, R.C., 1998. Larval survival characteristics and behaviour of the gill  
471 monogenean *Discocotyle sagittata*. *Parasitology* 117, 491–498.

- 472 Gaston, K.J., 2000. Global patterns in biodiversity. *Nature* 405, 220–227.
- 473 Ghiglione, J-F., Galand, P.E., Pommier, T., Pedrós-Alió, C., Maas, E.W., Bakker, K., Bertilsson, S.,  
474 Kirchman, D.L., Lovejoy, C., Yager, P.L., Murray, A.E., 2012. Pole-to-pole biogeography  
475 of surface and deep marine bacterial communities. *Proc. Nat. Acad. Sci. USA* 109, 17633–  
476 17638.
- 477 Klein, S.L., Zink, M.C., Glass, G.E., 2004. Seoul virus infection increases aggressive behaviour in  
478 male Norway rats. *Anim. Behav.* 67, 421–429.
- 479 Kritsky, D.C., 2012. Dactylogyrids (Monogeneoidea: Polyonchoinea) parasitizing the gills of  
480 snappers (Perciformes: Lutjanidae): Revision of *Euryhaliotrema* with new and previously  
481 described species from the Red Sea, Persian Gulf, the eastern and Indo-west Pacific Ocean,  
482 and the Gulf of Mexico. *Zoologia* 29, 227–276.
- 483 Kulbicki, M., 2007. Biogeography of reef fishes of the French Territories in the South Pacific.  
484 *Cybium* 31, 275–288.
- 485 Kulbicki, M., Parravicini, V., Bellwood, D.R., Arias-González, E., Chabanet, P., Floeter, S.R.,  
486 Friedlander, A., McPherson, J., Myers, R.E., Vigliola, L., Mouillot, D., 2013. Global  
487 biogeography of reef fishes: A hierarchical quantitative delineation of regions. *PLoS One* 8,  
488 e81847. doi:10.1371/journal.pone.0081847
- 489 Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies  
490 responses in multifactorial ecological experiments. *Ecol. Monogr.* 69, 1–24.
- 491 Leprieur, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Dürr, H.H., Brosse, S. and Oberdorff, T.,  
492 2011. Partitioning global patterns of freshwater fish beta diversity reveals contrasting  
493 signatures of past climate changes. *Ecol. Lett.* 14, 325–334.
- 494 Locke, S.A., Levy, M.S., Marcogliese, D.J., Ackerman, S., McLaughlin, J.D., 2012. The decay of  
495 parasite community similarity in ring-billed gulls *Larus delawarensis* and other hosts.  
496 *Ecography* 35, 530-538.

- 497 Locke, S.A., McLaughlin, J.D., Marcogliese, D.J., 2013. Predicting the similarity of parasite  
498 communities in freshwater fishes using the phylogeny, ecology and proximity of hosts.  
499 *Oikos* 122, 73–83.
- 500 Macpherson, E., Richer de Forges, B., Schnabel, K., Samadi, S., Boisselier, M.-C., Garcia-Rubies,  
501 A., 2010. Biogeography of the deep-sea galatheid squat lobsters of the Pacific Ocean. *Deep*  
502 *Sea Res. PtI: Oceanogr. Res. Pap.* 57, 228–238.
- 503 McNamara, M.K.A., Adlard, R.D., Bray, R.A., Sasal, P., Cribb, T.H., 2012. Monorchiids  
504 (Platyhelminthes: Digenea) of chaetodontid fishes (Perciformes): Biogeographical patterns  
505 in the tropical Indo-West Pacific. *Parasitol. Int.* 61, 288–306.
- 506 McNamara, M.K.A., Miller, T.L., Cribb, T.H., 2014. Evidence for extensive cryptic speciation in  
507 trematodes of butterflyfishes (Chaetodontidae) of the tropical Indo-West Pacific. *Int. J.*  
508 *Parasitol.* 44, 37–48.
- 509 McKnight, M.W., White, P.S., McDonald, R.I., Lamoreux, J.F., Sechrest, W., Ridgely, R.S., Stuart,  
510 S.N., 2007. Putting beta-diversity on the map: broad-scale congruence and coincidence in  
511 the extremes. *Plos Biol.* 5, e272.
- 512 Montanari, S.R., Hobbs, J.-P.A., Pratchett, M.S., Bay, L.K., Van Herwerden, L., 2014. Does genetic  
513 distance between parental species influence outcomes of hybridization among coral reef  
514 butterflyfishes? *Mol. Ecol.* 23, 2757–2770.
- 515 Morand, S., Cribb, T. H., Kulbicki, M., Rigby, M. C., Chauvet, C., Dufour, V., Faliex, E., Galzin,  
516 R., Lo, C. M., Lo-Yat, A., Pichelin, S. and Sasal, P., 2000. Endoparasite species richness of  
517 New Caledonian butterfly fishes: host density and diet matter. *Parasitology* 121, 65–73.
- 518 Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R., Green,  
519 J.L., 2008. A general framework for the distance-decay of similarity in ecological  
520 communities. *Ecol. Lett.* 11, 904–917.
- 521 Oliva, M.E., Teresa González, M., 2005. The decay of similarity over geographical distance in  
522 parasite communities of marine fishes. *J. Biogeogr.* 32, 1327–1332.



- 523 Paperna, I., 1972. Monogenea of Red Sea fishes: III. Dactylogyridae from littoral and reef fishes. J.  
524 Helminthol. 46, 47–62.
- 525 Parravicini, V., Azzurro, E., Kulbicki, M., Belmaker, J., 2015. Niche shift can impair the ability to  
526 predict invasion risk in the marine realm: an illustration using Mediterranean fish invaders.  
527 Ecol. Lett. 18, 246–253.
- 528 Parravicini, V., Kulbicki, M., Bellwood, D.R., Friedlander, A.M., Arias-Gonzalez, J.E., Chabanet,  
529 P., Floeter, S.R., Myers, R., Vigliola, L., D'Agata, S., Mouillot, D., 2013. Global patterns  
530 and predictors of tropical reef fish species richness. Ecography 36, 1254–1262.
- 531 Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data  
532 matrices: estimation and comparison of fractions. Ecology 87, 2614–2625.
- 533 Pérez-del-Olmo, A., Fernández, M., Raga, J.A., Kostadinova, A., Morand, S., 2009. Not everything  
534 is everywhere: the distance decay of similarity in a marine host–parasite system. J.  
535 Biogeogr. 36, 200–209.
- 536 Peyrusse, K., Sasal, P., Lecchini, D., 2012. Parasite acquisition by larval coral-reef fishes. J. Fish  
537 Biol. 81, 2040–2043.
- 538 Pietrock, M., Marcogliese, D.J., 2003. Free-living endohelminth stages: at the mercy of  
539 environmental conditions. Trends Parasitol. 19, 293–299.
- 540 Plaisance, L., Bouamer, S., Morand, S., 2004. Description and redescription of *Haliotrema* species  
541 (Monogenoidea: Poloyonchoinea: Dactylogyridae) parasitizing butterfly fishes (Teleostei:  
542 Chaetodontidae) in the Indo-West Pacific Ocean. Parasitol. Res. 93, 72–78.
- 543 Plaisance, L., Kritsky, D.C., 2004. Dactylogyrids (Platyhelminthes: Monogenoidea) parasitizing  
544 butterfly fishes (Teleostei: Chaetodontidae) from the coral reefs of Palau, Moorea, Wallis,  
545 New Caledonia, and Australia: species of *Euryhaliotrematoides* n. gen. and *Aliatrema* n.  
546 gen. J. Parasitol. 90, 328–341.
- 547 Plaisance, L., Littlewood, D.T.J., Olson, P.D., Morand, S., 2005. Molecular phylogeny of gill  
548 monogeneans (Platyhelminthes, Monogenea, Dactylogyridae) and colonization of Indo-

- 549 West Pacific butterflyfish hosts (Perciformes, Chaetodontidae). Zool. Scripta 34, 425–436.
- 550 Plaisance, L., Rousset, V., Morand, S., Littlewood, D.T.J., 2008. Colonization of Pacific islands by  
551 parasites of low dispersal ability: phylogeography of two monogenean species parasitizing  
552 butterflyfishes in the South Pacific Ocean. J. Biogeogr. 35, 76–87.
- 553 Poulin, R., Krasnov, B.R., Mouillot, D., 2011a. Host specificity in phylogenetic and geographic  
554 space. Trends Parasitol. 27, 355–361.
- 555 Poulin, R., Krasnov, B.R., Mouillot, D., Thieltges, D.W., 2011b. The comparative ecology and  
556 biogeography of parasites. Phil. Trans. Roy. Soc. Lond. B: Biol. Sci. 366, 2379–2390.
- 557 Pratchett, M.S., Berumen, M.L., Kapoor, B.G., 2013. Biology of Butterflyfishes. CRC Press,  
558 U.S.A.
- 559 Reverter, M., Cutmore, S.C., Bray, R., Cribb, T.H., Sasal, P., 2016. Gill monogenean communities  
560 (Platyhelminthes, Monogenea, Dactylogyridae) of butterflyfishes from tropical Indo-West  
561 Pacific Islands. Parasitology 143, 1580–1591.
- 562 Rigby, M.C., Holmes, J.C., Cribb, T.H., Morand, S., 1997. Patterns of species diversity in the  
563 gastrointestinal helminths of a coral reef fish, *Epinephelus merra* (Serranidae), from French  
564 Polynesia and the South Pacific Ocean. Can. J. Zool. 75, 1818–1827.
- 565 Rohde, K., 2002. Ecology and biogeography of marine parasites. Adv. Mar. Biol. 43, 1–86.
- 566 Rombouts, I., Beaugrand, G., Ibañez, F., Chiba, S., Legendre, L., 2011. Marine copepod diversity  
567 patterns and the metabolic theory of ecology. Oecologia 166, 349–355.
- 568 Soininen, J., McDonald, R., Hillebrand, H., 2007. The Distance decay of similarity in ecological  
569 communities. Ecography 30, 3–12.
- 570 Thieltges, D.W., Dolch, T., Krakau, M., Poulin, R., 2010. Salinity gradient shapes distance decay of  
571 similarity among parasite communities in three marine fishes. J. Fish Biol. 76, 1806–1814.
- 572 Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., de Clerck, O., 2012. Bio-  
573 ORACLE: a global environmental dataset for marine species distribution modelling. Glob.  
574 Ecol. Biogeogr. 21, 272–281

- 575 Timi, J.T., Luque, J.L., Poulin, R., 2010. Host ontogeny and the temporal decay of similarity in  
576 parasite communities of marine fish. *Int. J. Parasitol.* 40, 963–968.
- 577 Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Bergue, E.V., Worm, B., 2010. Global  
578 patterns and predictors of marine biodiversity across taxa. *Nature* 466, 1098–101.
- 579 Tubbs, L.A., Poortenaar, C.W., Sewell, M.A., Diggles, B.K., 2005. Effects of temperature on  
580 fecundity in vitro, egg hatching and reproductive development of *Benedenia seriolae* and  
581 *Zeuxapta seriolae* (Monogenea) parasitic on yellowtail kingfish *Seriola lalandi*. *Int. J.*  
582 *Parasitol.* 35, 315–327.
- 583 Vignon, M., Sasal, P., 2009. Multiscale determinants of parasite abundance: A quantitative  
584 hierarchical approach for coral reef fishes. *Int. J. Parasitol.* 40, 443–451.
- 585 Vinarski, M.V., Korallo, N.P., Krasnov, B.R., Shenbrot, G.I., Poulin, R., 2007. Decay of similarity  
586 of gamasid mite assemblages parasitic on Palaearctic small mammals: geographic distance,  
587 host-species composition or environment. *J. Biogeogr.* 34, 1691–1700.
- 588 Warburton, E.M., Kohler, S.L., Vonhof, M.J., 2016. Patterns of parasite community dissimilarity:  
589 the significant role of land use and lack of distance-decay in a bat–helminth system. *Oikos*  
590 125, 374–385.
- 591 Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol.*  
592 *Monogr.* 30, 280–338.
- 593 Whittington, I.D., 1997. Reproduction and host-location among the parasitic Platyhelminthes. *Int. J.*  
594 *Parasitol.* 27, 705–714.
- 595 Williams, P.H., de Klerk, H.M., Crowe, T.M., 1999. Interpreting biogeographical boundaries  
596 among Afrotropical birds: spatial patterns in richness gradients and species replacement. *J.*  
597 *Biogeogr.* 26, 459–474.
- 598 Yamaguti, S., 1968. Monogenetic Trematodes of Hawaiian Fishes. University of Hawaii Press,  
599 Honolulu, USA.
- 600 Yong, R. Q.-Y., Cutmore, S. C., Miller, T. L., Adlard, R. D. and Cribb, T. H., 2013. The ghost of

601 parasites past: eggs of the blood fluke *Cardicola chaetodontis* (Aporocotylidae) trapped in  
602 the heart and gills of butterflyfishes (Perciformes: Chaetodontidae) of the Great Barrier  
603 Reef. Parasitology 140, 1186–1194.

604 Zhang, J., Yang, T., Liu, L., 2001. Monogeneans of Chinese Marine Fishes. Agriculture Press,  
605 Beijing, People's Republic of China.

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## Figure legends

**Fig. 1.** Areas of distribution (blue shadow), prevalence (circle colour) and abundance (mean abundance per fish) (circle size) of dactylogyrid parasites from butterflyfishes in the tropical Indo-west Pacific region. Only parasites (*Haliotrema angelopterum*, *Haliotrema aurigae*, *Euryhaliotrema triangulovagina*, *Euryhaliotrema grandis*, *Euryhaliotrema berenguelae*, *Euryhaliotrema microphallus*) with prevalences > 20% for at least one locality were plotted (areas of distribution for other dactylogyrid species are shown in Supplementary Fig S1).

**Fig. 2.** Correlation matrix between dactylogyrid species (Pearson correlation) of the tropical Indo-west Pacific region. Only dactylogyrid species (*Haliotrema angelopterum*, *Haliotrema aurigae*, *Euryhaliotrema triangulovagina*, *Euryhaliotrema berenguelae*, *Euryhaliotrema microphallus*, *Euryhaliotrema grandis*, *Euryhaliotrema pirulum*, *E. annulocirrus*, *Euryhaliotrema cribbi*) found at five or more locations were plotted.  $*P < 0.05$ . Blue colors indicate positive correlations, while red colors indicate negative correlations. The color intensity and circle size indicate the strength of the correlation.

**Fig. 3.** Structure of dactylogyrid communities at nine locations in the tropical Indo-west Pacific region. The size of each circle is relative to the weighted intensity (Iw) for each location. Parasite species belonged to the genera *Haliotrema* and *Euryhaliotrema*.

**Fig. 4.** Cluster analysis of the dissimilarities in parasite communities (Bray-Curtis distance, « average » algorithm) of the tropical Indo-west Pacific region (French Polynesia: Marquesas, Australs, Society, Gambiers and Tuamotu; Ningaloo Reef, western Australia; Palau; Lizard Island, eastern Australia; Wallis and Futuna). Y-axis represents the heights at which the clusters diverge. Different colors indicate different clusters corresponding to assigned biogeographic regions.

633

634 **Fig. 5.** Visual representation of the variance partitioning redundancy analysis (RDA) on (A)  
635 balanced variation (dBC-bal, turnover) of parasite communities, (B) gradient (dBC-gra, nestedness)  
636 of parasite communities and (C) overall Bray-Curtis (BC) parasite dissimilarity showing the relative  
637 contribution of different classes of explanatory variables alone and in combination. Partial R<sup>2</sup>  
638 values are provided for each fraction (negative numbers omitted). Red circle (X1) represents spatial  
639 structure, green circle (X2) represents environment and blue circle (X3) represents host assemblage  
640 structure.

641

642 **Supplementary Fig. S1.** Areas of distribution (blue shadow), prevalence (circle colour) and  
643 abundance (mean abundance per fish) (circle size) of dactylogyrid parasites from butterflyfishes in  
644 the tropical Indo-west Pacific region with prevalences < 20%.

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646

**Table 1.** Dactylogyrid diversity index (Shannon index (H)), richness, intensity and weighted intensity at nine geographic locations in the tropical Indo-west Pacific region.

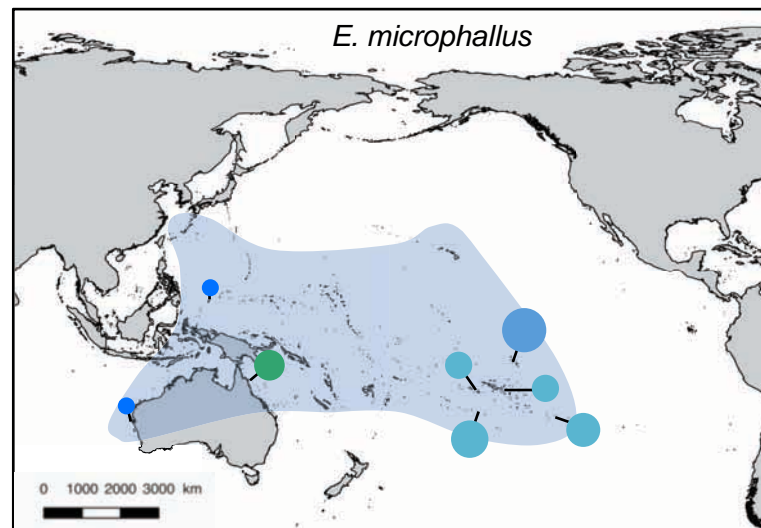
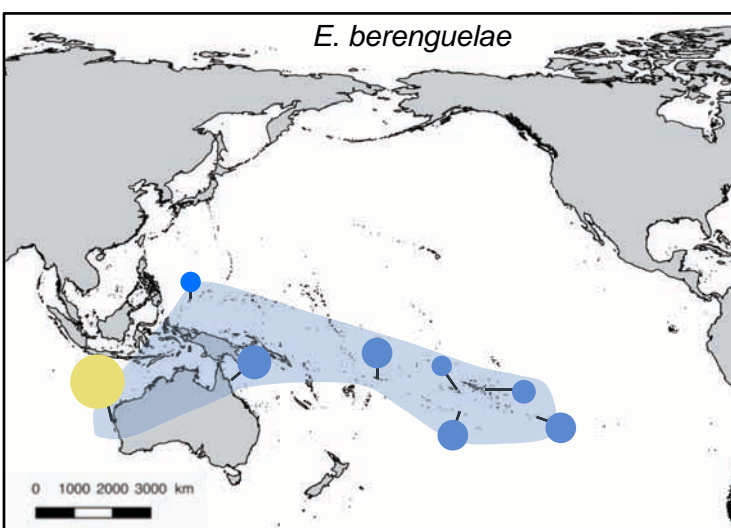
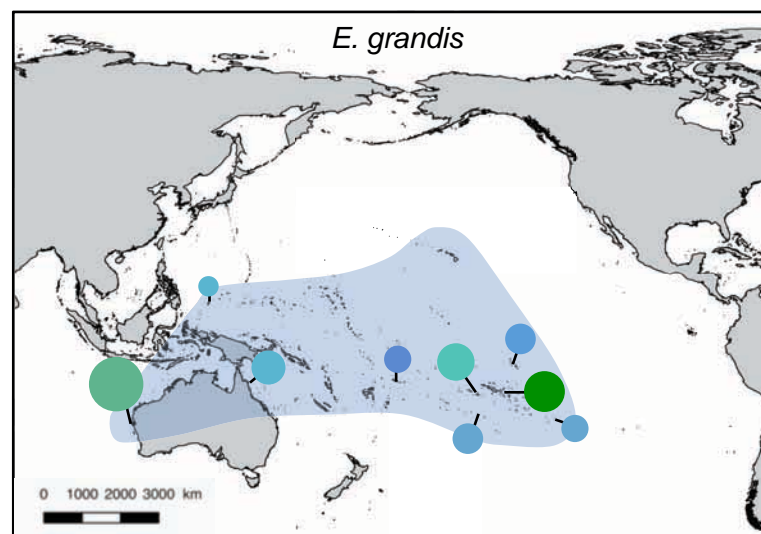
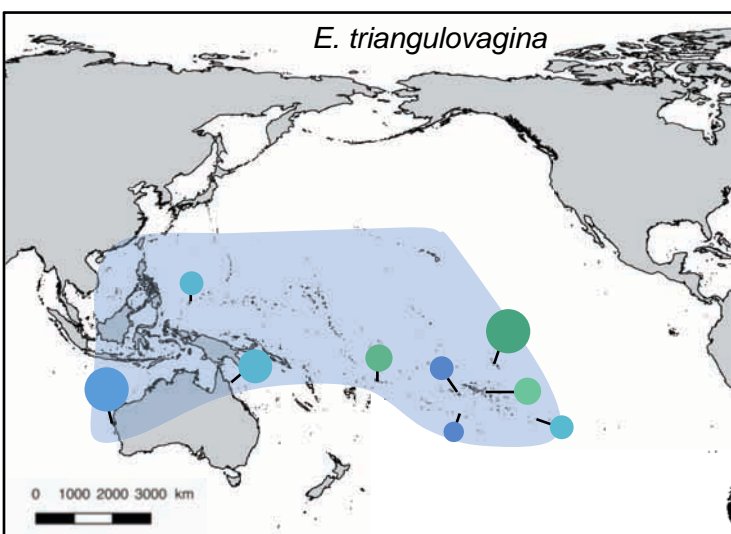
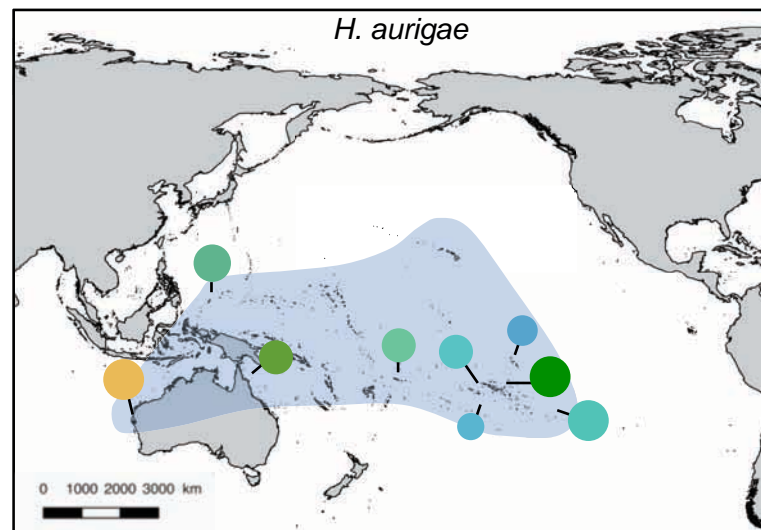
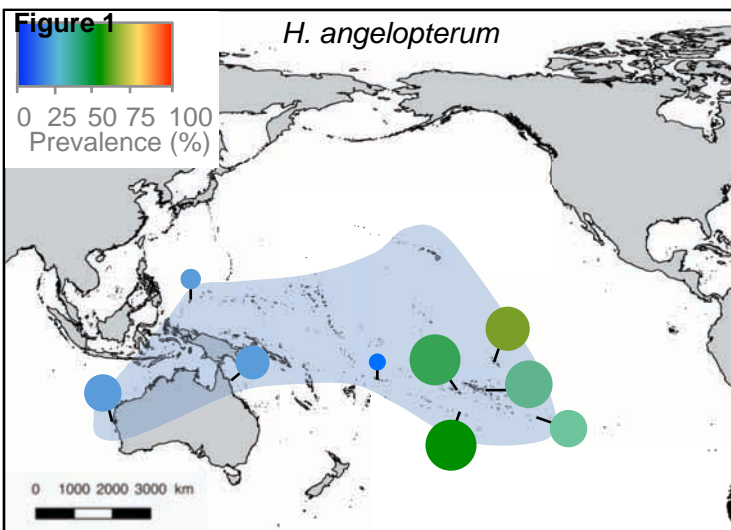
Site	Richness	Shannon index (H)	Intensity	Weighted intensity
Society <sup>a,b</sup>	9	1.12	111.3	1.12
Palau <sup>a</sup>	8	1.22	24.4	0.65
Marquesas <sup>a,b</sup>	6	1.22	60.7	0.57
Australs <sup>a,b</sup>	11	1.24	79.8	0.99
Ningaloo Reef <sup>c</sup>	7	1.25	132.4	1.09
Wallis and Futuna <sup>a</sup>	6	1.45	19.7	0.90
Tuamotus <sup>a,b</sup>	12	1.65	126.5	1.49
Gambiers <sup>a,b</sup>	9	1.74	26.5	0.67
Lizard Island <sup>a</sup>	12	1.96	56.5	0.86

<sup>a</sup> Pacific location.

<sup>b</sup> Archipelago in French Polynesia.

<sup>c</sup> Indian Ocean, off the western Australian coast.







## Figure 2

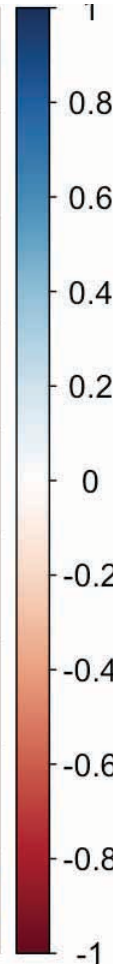
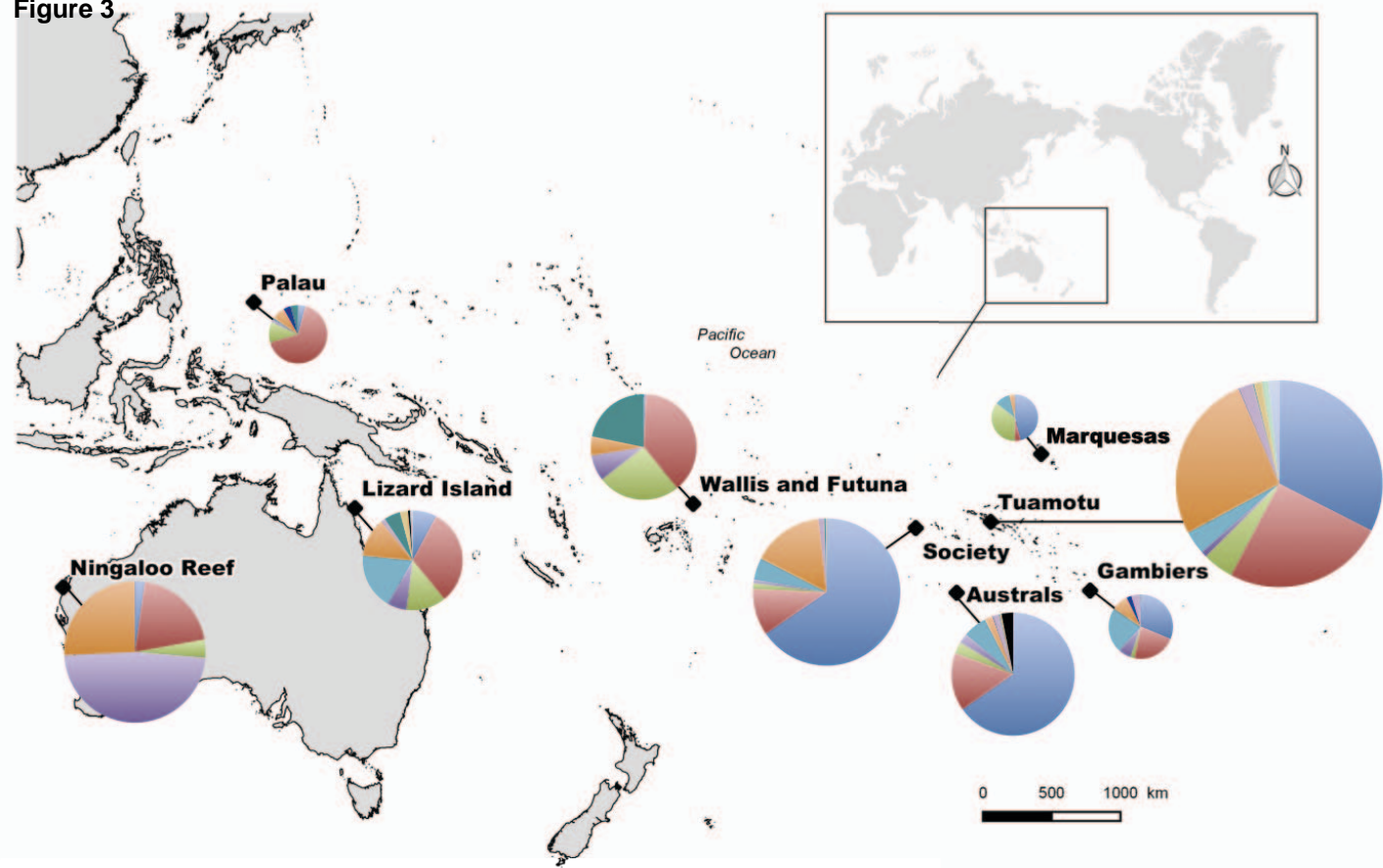


Figure 3



■ *H. angelopterus*

■ *H. aurigae*

■ *E. microphallus*

■ *E. grandis*

■ *E. aspistis*

■ *E. cribbi*

■ *E. triangulovagina*

■ *E. berenguelae*

■ *E. pirulum*

■ *E. annulocirrus*

■ *Haliotrema*  
sp. A

■ *H. scyphovagina*

■ *Haliotrema*  
sp. B

Figure 4

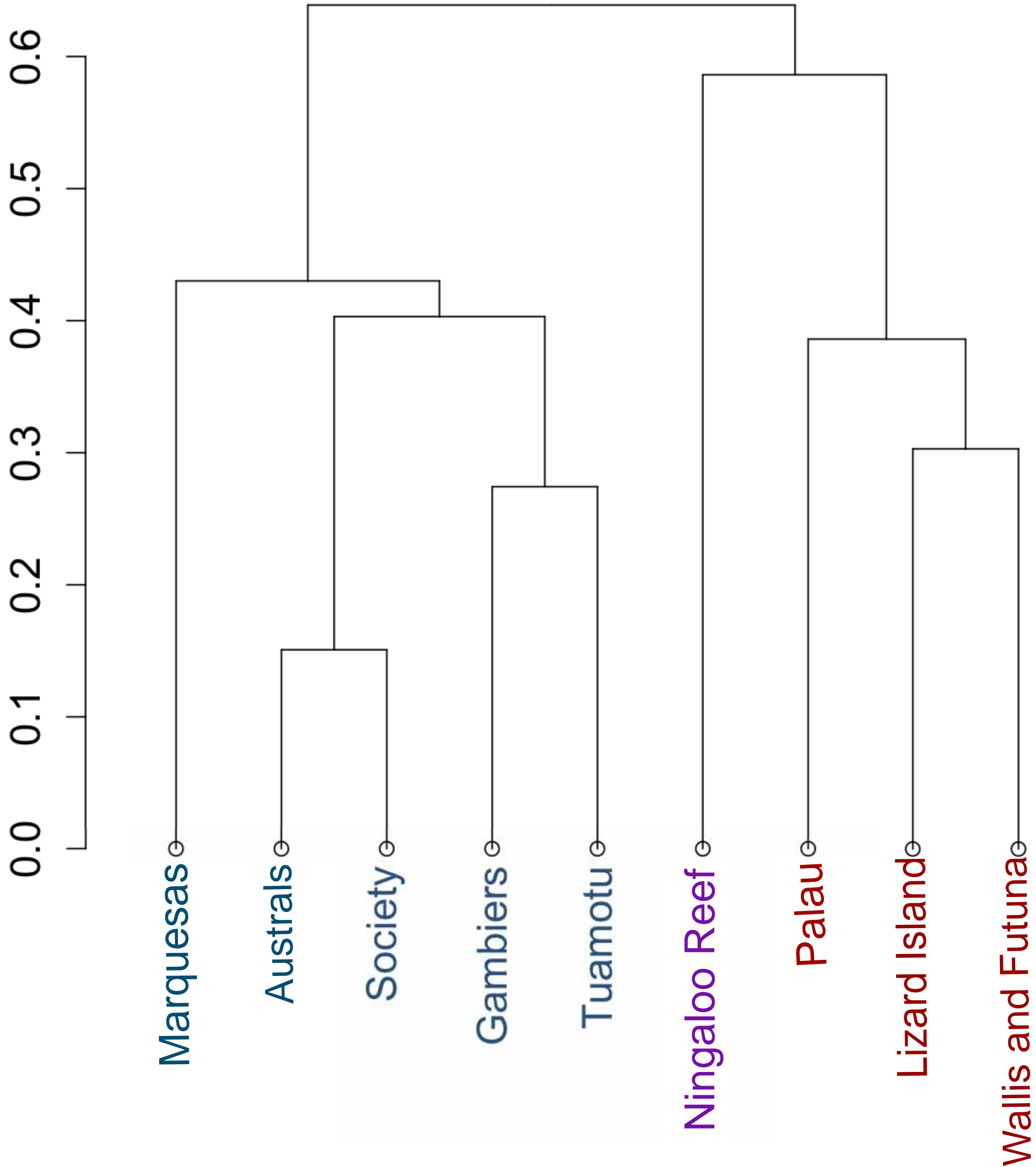
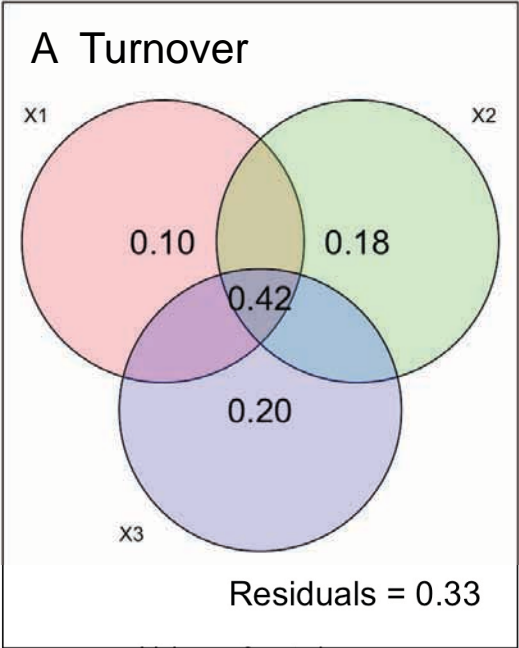
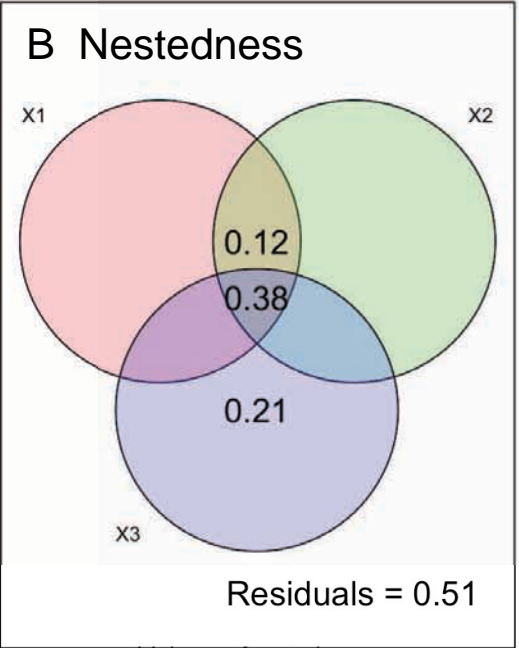


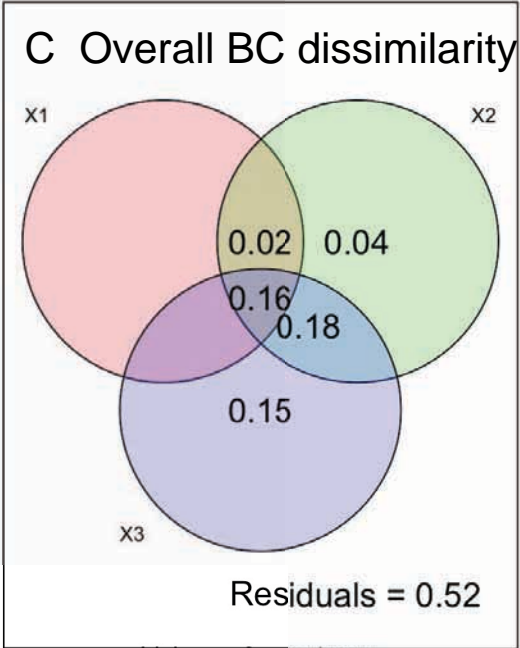
Figure 5 revised



Values <0 not shown

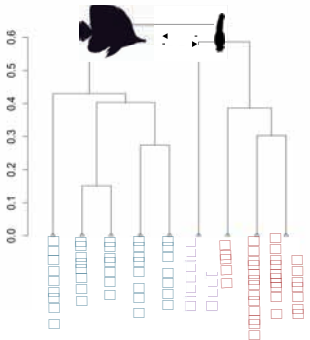


Values <0 not shown



Values <0 not shown

# Biogeography of butterflyfish dactylogyrds



## Highlights

- Biogeography of butterflyfish dactylogyrids from the Indo–west Pacific was studied.
- Three biogeographic regions were identified based on dactylogyrid dissimilarities.
- The two main *Haliotrema* species were negatively correlated.
- Structure of hosts' assemblage was the main factor explaining parasite dissimilarity.