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1 Did biogeographical processes shape the monogenean community of butterflyfishes in the tropical
2 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 km². Thirteen dactylogyrid species were
26 identified, with richness ranging from 6–12 species at individual localities. Most dactylogyrid
27 communities were dominated by *Haliotrema angeloferum* 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. angeloferum*, 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

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1. Introduction

47 The biogeography of free-living marine taxa (e.g. corals, fish, bacteria) has been the focus of
48 much research in recent decades (Tittensor et al., 2010; Briggs and Bowen, 2012; Ghiglione et al.,
49 2012). The mechanisms that underpin their biogeographical patterns are relatively well understood
50 (Leprieur, 2011; Rombouts et al., 2011; Chust et al., 2012). In contrast, the biogeography of marine
51 parasites is virtually unknown, especially because evaluating their large-scale distribution implies
52 an understanding of their host-parasite interactions, information that is very rare, especially over
53 large spatial scales (Rohde, 2002; Poulin et al., 2011b; Cribb et al., 2016).

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

61 The analysis of beta-diversity, the extent of change in community structure among sites
62 (Whittaker, 1960), has recently been shown to be a powerful tool in the analysis of biogeographical
63 patterns (Leprieur, 2011; Baselga, 2012). One of the most widely used relationships in
64 biogeography to evaluate beta-diversity is distance decay of similarity, which describes how
65 similarity in community structure varies with increasing distance between localities (McNight et al.,
66 2007; Soininen et al., 2007; Morlon et al., 2008). Numerous studies have shown that the similarity
67 of parasite communities decreases with increasing distance (e.g. Oliva and Gonzalez, 2005; Pérez
68 del Olmo et al., 2009; Timi et al., 2010). However, some studies have shown that other parameters
69 such as host phylogenetic distance or environmental conditions may play a more important role in
70 driving similarity of parasite communities than geographical distance (Vinarski et al., 2007;
71 Thieltges et al., 2010; Warburton et al., 2016).

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

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

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

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

119

120 **2. Materials and methods**

121 *2.1. Sampling*

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

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

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

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

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

142

143 2.2. Data analysis

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

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

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

$$I_{w_{site}} = \frac{\sum_{sp1}^{spx} (I_{sp_{site}}/I_{sp})}{n^{\circ} sp_{site}}$$

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

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

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

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

177 We used redundancy analysis (RDA) with variation partitioning (Borcard et al., 1992) in
178 order to assess the relative contribution of environmental conditions, spatial structure and the
179 structure of hosts assemblages in explaining the dissimilarity in parasite communities among
180 locations (dBC-gra and dBC-bal). Environmental conditions of our locations were characterised
181 according to chlorophyll concentration, cloud cover, photosynthetically available radiation,
182 dissolved oxygen, nitrate concentration, phosphate concentration, silicate concentration, salinity and
183 sea surface temperature, extracted from the Bio-Oracle database (Tyberghein et al., 2012), a global
184 database successfully employed in various biogeographical applications (Parravicini et al., 2013,
185 2015). Linear geographic distances between pairs of geographic locations were obtained from the
186 Latitude/Longitude Distance Calculator of the National Hurricane Center from the National
187 Oceanic and Atmospheric Administration (<http://www.nhc.noaa.gov/gccalc.shtml>). In order to
188 characterise the spatial structure of the locations, we generated a set of multiscale principal
189 coordinates of neighbour matrices (PCNM) from the geographic distance matrix (Dray et al., 2006).
190 PCNM eigenfunctions consist of the spectral decomposition of the spatial relationships among
191 locations. The structures of the host assemblages at our locations were assessed according to a
192 Bray-Curtis dissimilarity matrix on species abundance at each location. The procedure involved the
193 partitioning of the global variation into distinct components: a pure environmental component, a
194 pure spatial component, a pure host assemblage component, their interaction and the residual
195 component. First, forward selection was used for each set of variables separately in order to select
196 only those variables that explained a significant proportion of the variation ($P < 0.05$, after 999
197 random permutations). The retained variables were then used in the variation partitioning using
198 adjusted- R^2 values that correct for the variation jointly explained by multiple variables (Peres-Neto
199 et al., 2006). Prior to the analysis, dissimilarity matrices were transformed into data frames by
200 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 *Euryhaliotrema 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 *Euryhaliotrema 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. angeloapterum* is negatively correlated with *H. aurigae* (-0.59, *P*
234 value < 0.05) and *Euryhaliotrema 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). *Euryhaliotrema microphallus* is also strongly positively correlated with
237 *Euryhaliotrema 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. angeloapterum* (65%). Palau and the Marquesas also presented notably low

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

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

263

264 3.3. Factors shaping biogeographic differences in dactylogyrid communities

265 The structure of host assemblages was identified as the factor that explained the highest
266 variance in dactylogyrid communities among geographic sites (Fig. 5). The pure host assemblage
267 component explained 20% of the balanced variation (dBC-bal, turnover) of the dactylogyrid
268 communities, 21% of the abundance gradient (dBC-gra, nestedness) and 15% of the overall Bray-
269 Curtis dissimilarity of the dactylogyrid communities. The pure environmental component explained
270 18% of the balanced variation and 4% of the overall Bray-Curtis dissimilarity of the dactylogyrid
271 communities (Fig. 5A, C). The pure spatial component only accounted for 10% of the balanced
272 variation of the dactylogyrid communities (Fig. 5A). However, most of the variation was explained
273 by the interaction between the three components (spatial structure, environment and host
274 assemblages), which explained 42% of the balanced variation, 38% of the abundance gradient and
275 16% of the overall Bray-Curtis dissimilarity of the dactylogyrid communities; indicating an
276 interaction between environment and host assemblage structure (Fig. 5). Finally, a considerable
277 amount of variance remained unexplained by the components that were studied (residual variance)
278 (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

331 surprisingly, no such biogeographical structuring in *H. aurigae*. They suggested that differentiation
332 of *E. grandis* could have been driven by isolation of French Polynesia during Pleistocene sea-level
333 fluctuation. It seems plausible that such fluctuation might have driven the overall differences in the
334 dactylogyrid communities between the eastern and western Pacific regions. Macpherson et al.
335 (2010) also found different communities of galatheid squat lobsters between French Polynesia and
336 the rest of the western Pacific region with a high proportion of endemism, suggesting French
337 Polynesia as a centre of diversity.

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

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

363 Recent studies have shown that environmental factors such as salinity and temperature are
364 important in driving the compositions of parasite communities (Thieltges et al., 2010; Poulin et al.,
365 2011a; Blasco-Costa et al., 2015). For example, Campiao et al. (2012) found that change in parasite
366 composition of the frog *Leptodactylus podicipinus* Cope, 1862, was mainly related to variation in
367 environmental conditions rather than to species distribution. Warburton et al. (2016) also observed
368 that environmental variables, rather than spatial variables, explained variation in helminth
369 community similarities of big brown bats (*Eptesicus fuscus*, Palisot de Beauvois 1796). In our
370 study, the environment was a significant factor in the turnover and overall dissimilarity of
371 dactylogyrid communities. Since chaetodontid larvae, the only planktonic phase of butterflyfishes,
372 are not parasitized by monogenean parasites (Peyrusse et al., 2012) and dactylogyrid oncomiracidia
373 live only a few hours without a host (Whittington, 1997), it has been proposed that dactylogyrid
374 dispersal takes place through the passive dispersion of their eggs by oceanic currents (Ganicott and
375 Tinsley, 1998; Plaisance et al., 2008). Previous studies have shown that monogenean egg hatching
376 and larval infection processes are highly dependent on environmental parameters such as water
377 temperature (Cecchini et al., 1998; Pietrock and Marcogliese, 2003; Tubbs et al., 2005). Our results
378 are thus consistent with the idea that environmental parameters can affect the turnover of parasite
379 species, suggesting the importance of suitable environmental conditions for larval development, egg
380 hatching, and successful infection of fishes.

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

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

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

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

409

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607 **Figure legends**

608

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

615

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

623

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

627

628 **Fig. 4.** Cluster analysis of the dissimilarities in parasite communities (Bray-Curtis distance,
629 « average » algorithm) of the tropical Indo-west Pacific region (French Polynesia: Marquesas,
630 Australs, Society, Gambiers and Tuamotu; Ningaloo Reef, western Australia; Palau; Lizard Island,
631 eastern Australia; Wallis and Futuna). Y-axis represents the heights at which the clusters diverge.
632 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 R²
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%.

645

646

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

649
650

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

656
657 ^a Pacific location.

658 ^b Archipelago in French Polynesia.

659 ^c Indian Ocean, off the western Australian coast.

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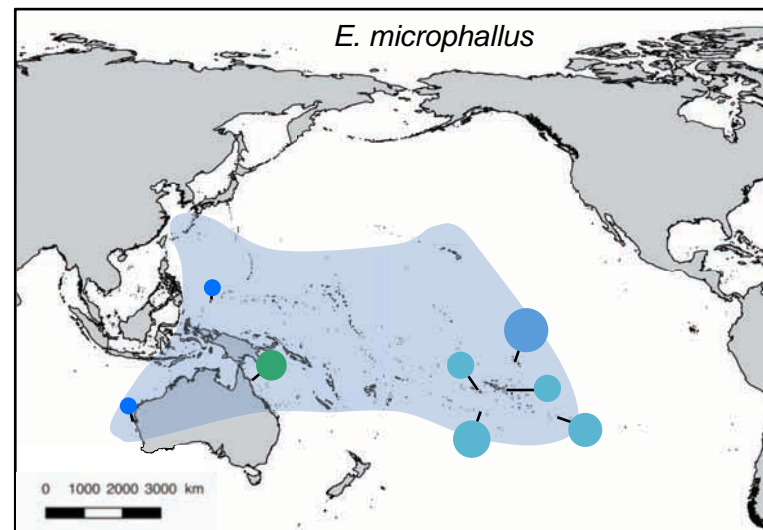
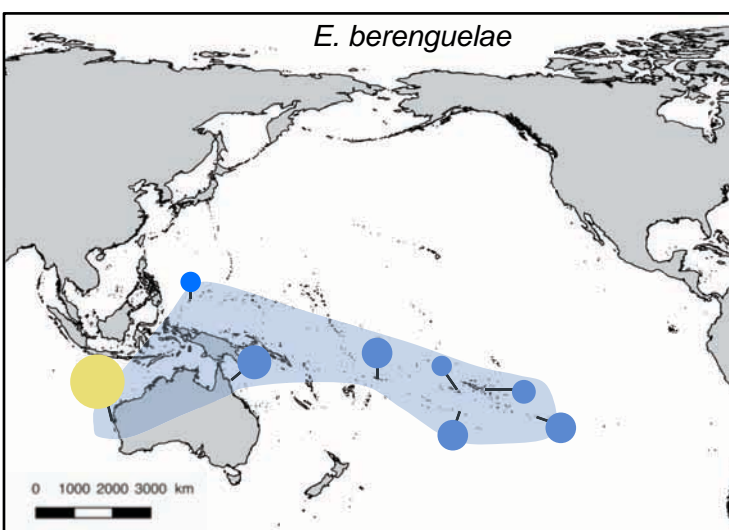
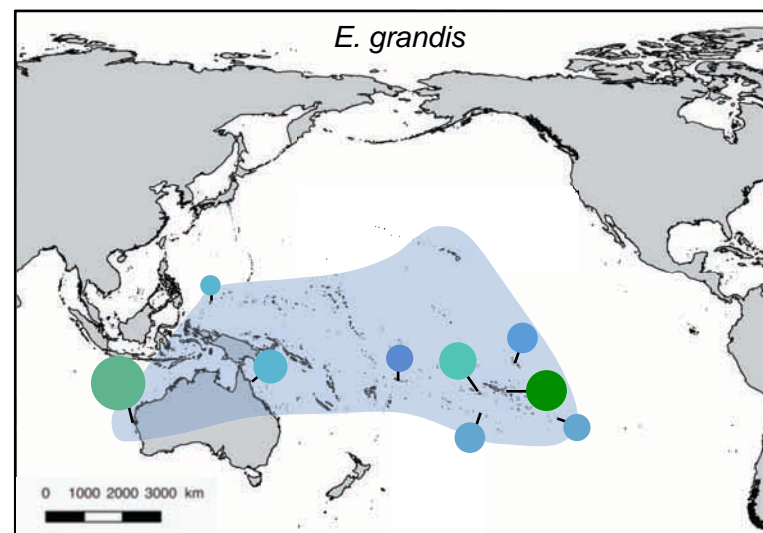
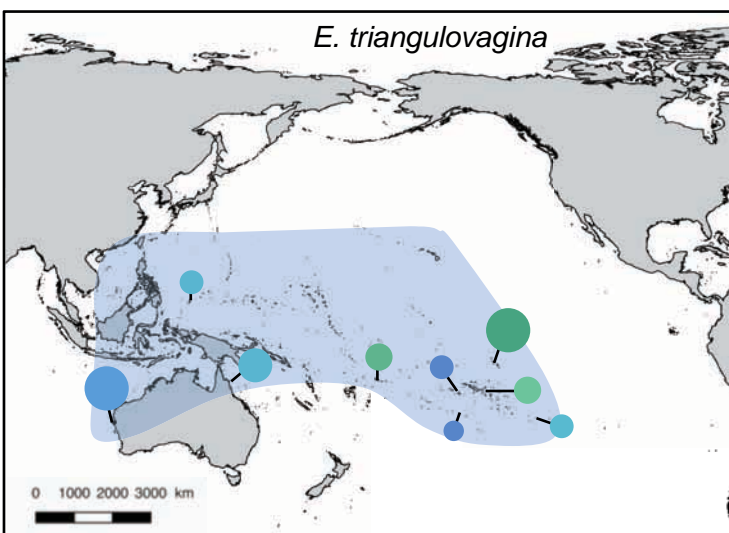
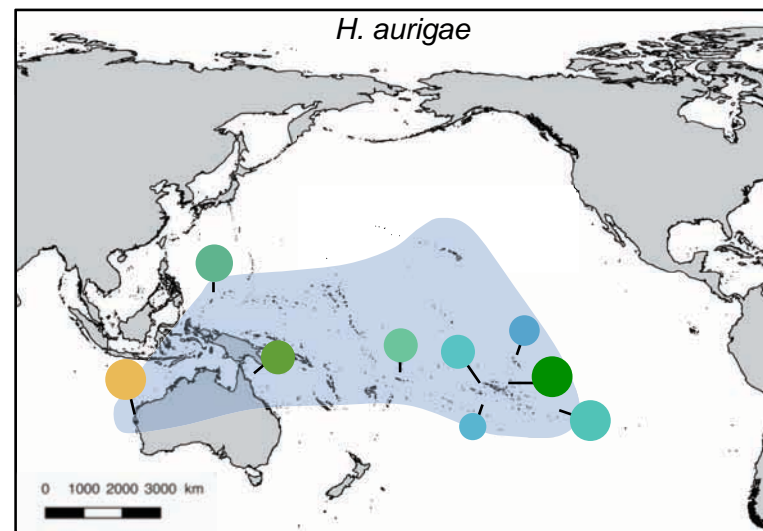
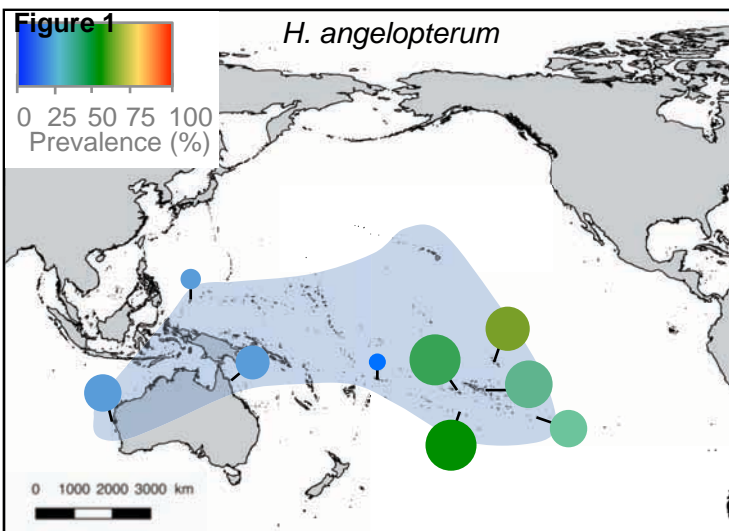
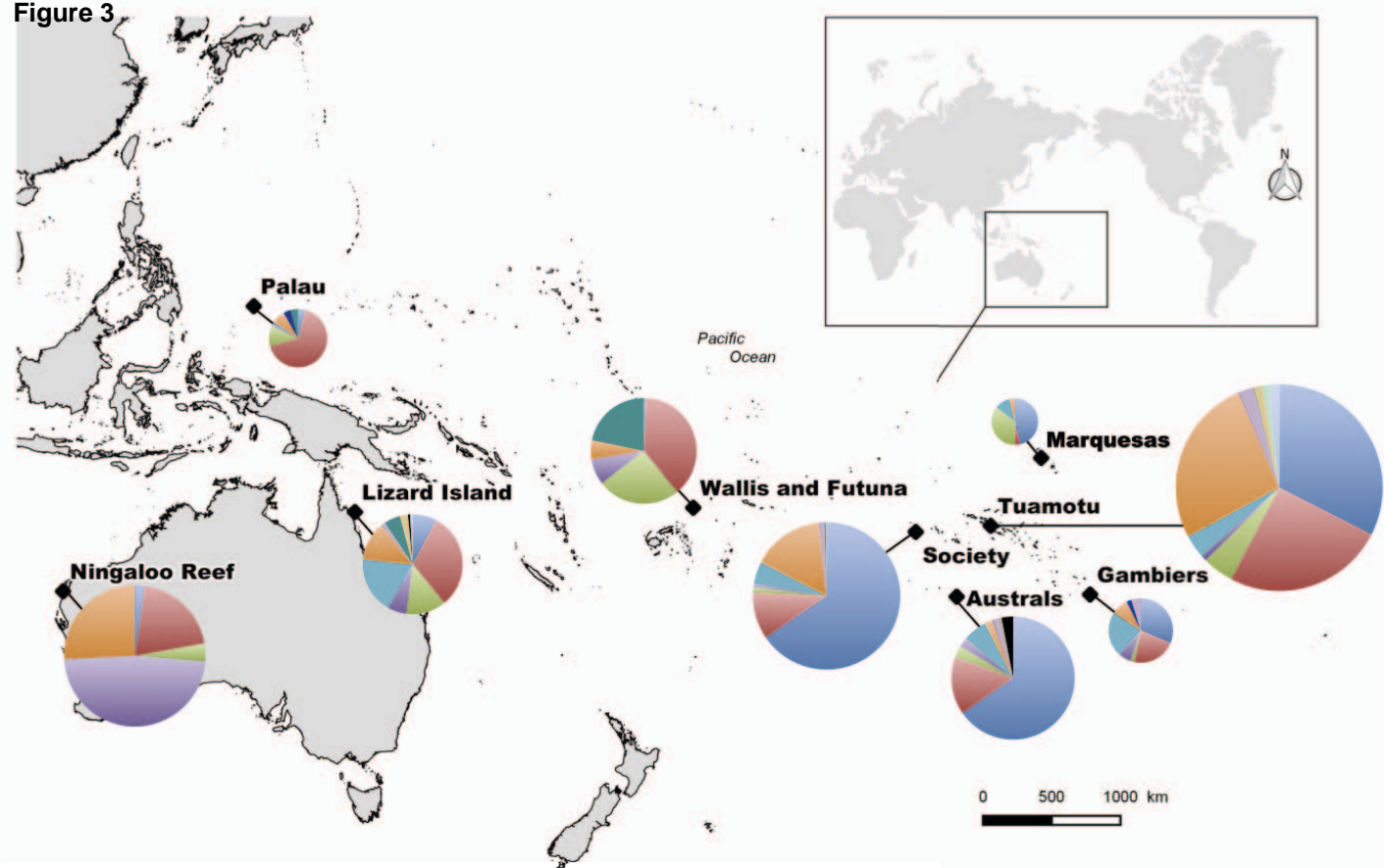


Figure 3



- | | | | | | |
|---------------------------|-----------------------|------------------------|------------------------|-------------------------|-------------------------|
| <i>H. angelopterum</i> | <i>H. aurigae</i> | <i>E. microphallus</i> | <i>E. grandis</i> | <i>E. asistis</i> | <i>E. cribbi</i> |
| <i>E. triangulovagina</i> | <i>E. berenguelae</i> | <i>E. pirulum</i> | <i>E. annulocirrus</i> | <i>Haliotrema</i> sp. A | <i>H. scyphovagina</i> |
| | | | | | <i>Haliotrema</i> sp. B |

Figure 4

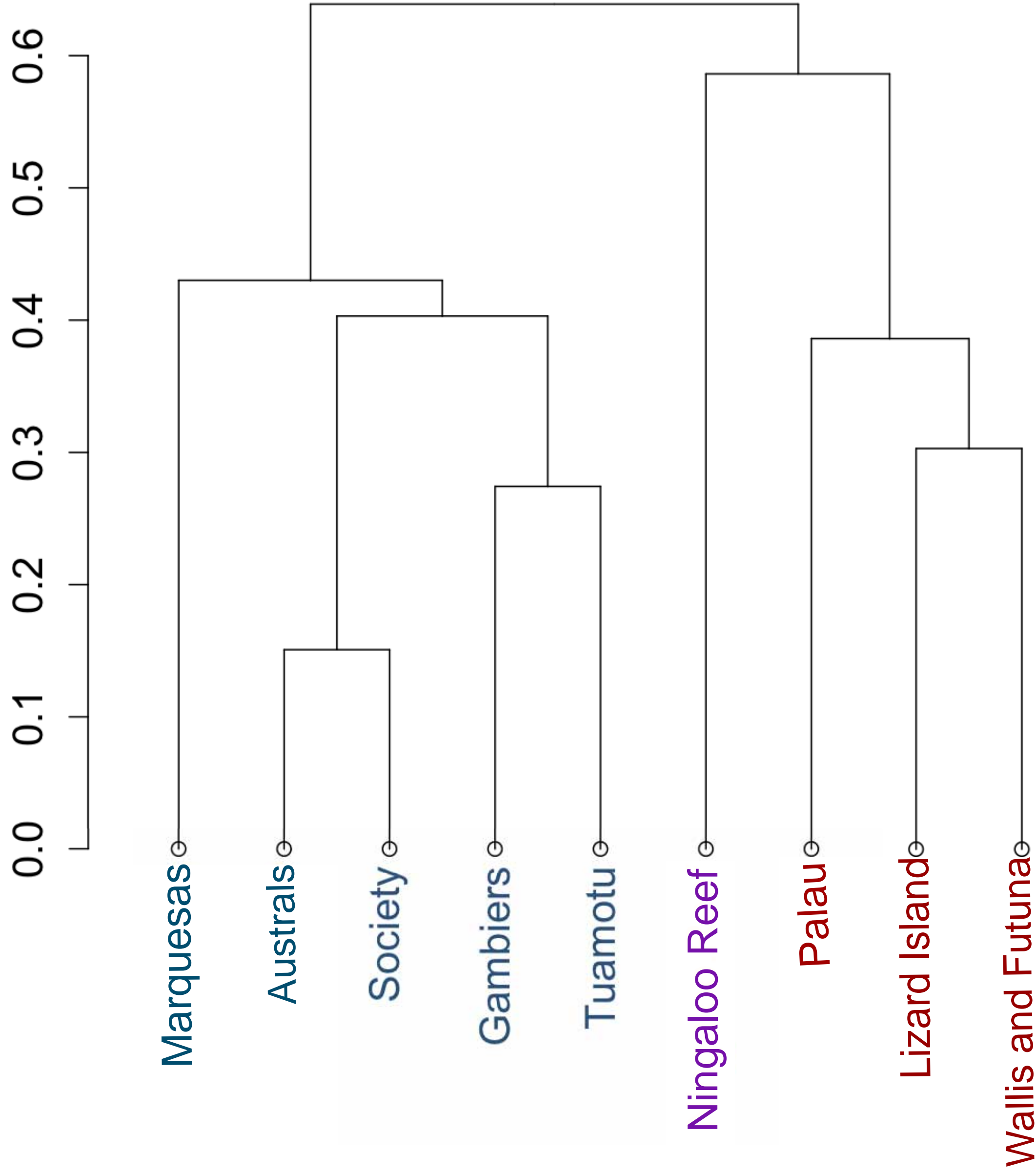
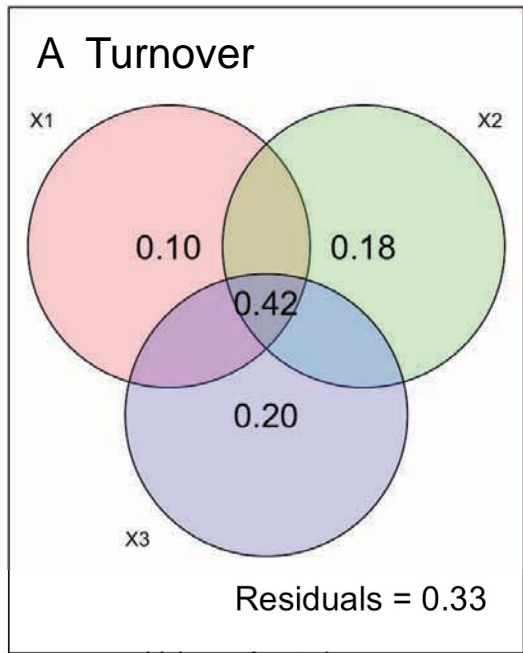
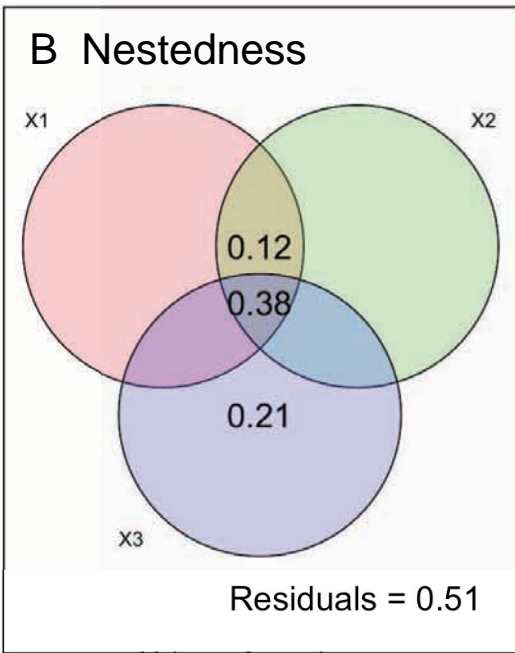


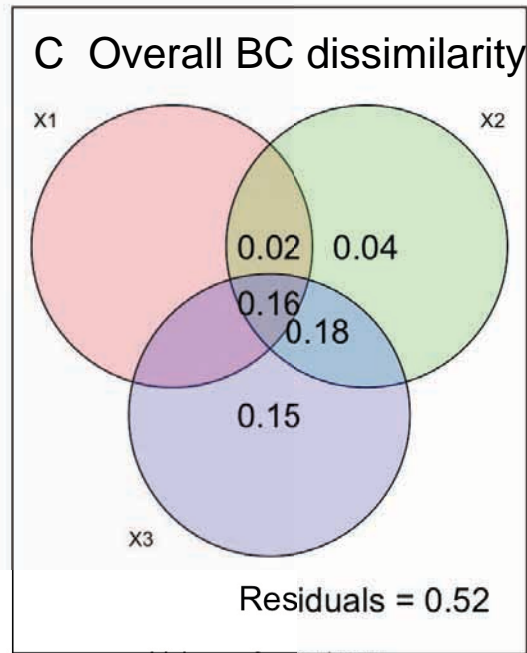
Figure 5 revised



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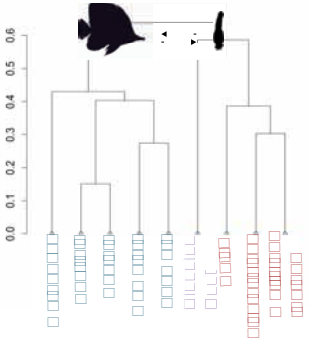


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Biogeography of butterflyfish dactylogyrds



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.