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6 **An inter-ocean comparison of coral endemism on seamounts: the case of *Chrysogorgia***

7

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20

20 **ABSTRACT**

21 **Aim** The biogeography of seamount fauna remains poorly known, with less than 1% of the
22 world's seamounts having been investigated. Here, we report data on the geographical
23 isolation of species in the octocoral genus *Chrysogorgia* from south-west Pacific seamounts
24 and slopes, and contrast the results with patterns observed in the north-western Atlantic.

25 **Location** Seamounts of the Norfolk Ridge (NR) and Loyalty Ridge (LR), the slope of New
26 Caledonia, and the Matthew and Hunter Islands, south-west Pacific Ocean, with
27 comparative material from the Pacific and Atlantic oceans.

28 **Methods** The mitochondrial gene *mtMutS* was used to measure diversity within
29 *Chrysogorgia*. Community structure was analysed using rarefaction, multivariate analyses,
30 parsimony analysis of endemism and analysis of molecular variance. The impact of
31 underestimating species richness when using mitochondrial haplotypes was tested using
32 simulations.

33 **Results** 634 colonies and 31 haplotypes were sampled from New Caledonia. Contrary to
34 what was observed in the north-western Atlantic, seamount-scale endemism of south-west
35 Pacific *Chrysogorgia* was substantial (9% and 32% for haplotypes with $n \geq 20$ and $n \geq 2$,
36 respectively). LR sheltered 64% of the New Caledonian haplotype diversity. Assemblages
37 were structured less by habitat type (slope versus seamounts) than by depth. Rarefaction
38 analyses suggested that LR and NR seamounts hold more species than the New Caledonian
39 slope, but additional sampling in the south-western Pacific (133 colonies) revealed that
40 some seemingly geographically restricted haplotypes from New Caledonia have wide
41 geographical distributions, reaching as far as Taiwan.

42 **Main conclusions** The distribution of Pacific *Chrysogorgia* is characterized by high levels of
43 rarity, patchiness and diversity, with the levels of seamount-scale and seamount-chain-
44 scale endemism higher than in the Atlantic. We hypothesize that the contrast between the
45 wide geographical distribution of Atlantic *Chrysogorgia* haplotypes and the higher
46 proportion of endemics in the Pacific is largely explained by differences in depth between
47 the seamounts of these two regions.

48

49 **Keywords**

50 **Atlantic Ocean, marine biogeography, marine connectivity, Octocorallia, Pacific**
51 **Ocean, parsimony analysis of endemism, species delimitation, seamount.**

52

53 **INTRODUCTION**

54 Seamounts, typically defined as undersea mountains that rise above the sea floor, are
55 among the most ubiquitous underwater features in the oceans (Wessel *et al.*, 2010), and
56 constitute one of the largest marine biomes, with a total surface area similar to that of
57 Europe and Russia combined (Etnoyer *et al.*, 2010; Yesson *et al.*, 2011). The geological and
58 hydrographical setting in which seamounts are found makes them a noteworthy system for
59 the study of deep-sea biogeography. Most seamounts are volcanic in origin, and they are
60 commonly characterized by hard substrates and relatively steep slopes, features that are
61 rare in the deep sea (Rogers, 1994). They emerge at island arcs, mid-ocean ridges and in
62 intraplate hotspot settings, forming chains (Wessel, 2007). Because of these geological
63 attributes, seamounts may act as stepping stones between patches of suitable habitats on
64 continental shelves and oceanic ridges, and contribute to pan-oceanic dispersal (Ekman,
65 1953; Hubbs, 1959). On the other hand, hydrographical features such as Taylor caps, local
66 upwelling, jets and eddies (reviewed in Rogers, 1994), and sheer geographical isolation,
67 may significantly impede dispersal between habitat patches (Parker & Tunnicliffe, 1994).

68 One question that has generated great interest and debate among deep-sea
69 biologists is whether the fauna associated with seamounts is highly endemic. The
70 topographical and hydrographical conditions associated with seamounts could contribute
71 to faunal isolation and the accumulation of highly endemic taxa (Hubbs, 1959). Wilson &
72 Kaufmann (1987) provided the first global assessment of levels of endemism on
73 seamounts, and reported that 11.6% of fishes and 15.4% of invertebrates were endemic to
74 individual seamounts or seamount groups. Since this seminal review, many estimates of
75 endemism have been published, ranging from 0 to 100%, reflecting various geographical
76 ranges and sampling efforts (Stocks & Hart, 2007). Most notably, Parin *et al.* (1997)
77 compiled information from 22 seamounts of the Nazca and Sala y Gómez chains in the
78 south-eastern Pacific, and found that 44–51% of fishes and invertebrates were seamount

79 endemics. Richer de Forges *et al.* (2000), summarizing the results of 24 exploration cruises,
80 found that 29–34% of 850 fish and invertebrate species collected from the Norfolk Ridge,
81 Lord Howe and Tasmanian seamounts were potential endemics.

82 From these studies emerged the general paradigm that seamounts harbour high
83 levels of endemism (Rowden *et al.*, 2010a). Even though this paradigm is largely
84 unsupported by recent studies (Samadi *et al.*, 2006; Stocks & Hart, 2007; Hall-Spencer *et*
85 *al.*, 2007; O'Hara, 2007; Lundsten *et al.*, 2009a,b; McClain *et al.*, 2009; Howell *et al.*, 2010),
86 the debate is not closed. Indeed, a minuscule proportion of seamounts have been
87 biologically sampled (less than 1%; Staudigel *et al.*, 2010), and the scarcity of data prevents
88 us from conceptualizing the processes that shape and maintain seamount faunal
89 assemblages (see, for example, reviews by McClain, 2007; Clark *et al.*, 2012). In addition,
90 most current estimates of endemism are based on morphological variation, which can be a
91 highly biased metric of biodiversity. Molecular studies are also subject to biases, in that it
92 can be difficult to establish whether a lack of genetic divergence reflects past or current
93 faunal connectivity (Clark *et al.*, 2010; Miller *et al.*, 2010). It is therefore important to
94 integrate taxonomic and biogeographical approaches when considering questions of faunal
95 isolation (Castelin *et al.*, 2010). Characterizing these faunal assemblages is becoming
96 increasingly important for conservation, as seamounts can be targets of commercial mining
97 and fishing (e.g. Clark *et al.*, 2010; Williams *et al.*, 2010; Schlacher *et al.*, 2014).

98 *Chrysogorgia* Duchassaing & Michelotti, 1864 is a relatively diverse genus of
99 Octocorallia (Cnidaria, Anthozoa). It is globally distributed, and is found both on slopes and
100 on seamounts, where it can be locally very abundant (Watling *et al.*, 2011). The
101 bathymetric range of *Chrysogorgia* is extremely large (Pante *et al.*, 2012a, and references
102 therein), and encompasses the entire depth range of catalogued seamount summits and
103 slopes (Stocks, 2009). In addition, the genus appears to be monophyletic based on current
104 data (Pante *et al.*, 2012a), offering opportunities for specific hypotheses about the
105 historical biogeography of species and species groups to be tested. Finally, the relative
106 congruence between morphotypes and mitochondrial *mtMutS* haplotypes described in four
107 North Atlantic species suggests that endemism can be investigated reliably at the species
108 level (Pante & Watling, 2012). This result was recently confirmed by comparing genome-
109 scale data to *mtMutS* haplotypes (Pante *et al.*, 2014).

110 Based on these characteristics, *Chrysogorgia* offers a model system that is well
111 suited to estimating species endemism at different spatial scales, across the spectrum of
112 seamount environments (e.g. depth range or geological origin) and geographical locations
113 (e.g. latitude or isolation from continental margins) in a phylogenetically comprehensive
114 manner. Here, we investigate the geographical distribution of *Chrysogorgia* species from
115 seamount and non-seamount environments in the south-western Pacific, and contrast the
116 patterns of species distribution with those observed in the north-western Atlantic (Thoma
117 *et al.*, 2009). To the best of our knowledge, this is the first study to look at the seamount-
118 scale endemism of a genus in different ocean basins.

119

120 **MATERIALS AND METHODS**

121 **Sampling and genotyping**

122 Specimens from the New Caledonian exclusive economic zone were collected during the
123 Muséum national d'Histoire naturelle (MNHN) / Institut de Recherche pour le
124 Développement (IRD) *Terrasses* and *ExBoDi* cruises of 2008 and 2011 on the NR, LR,
125 eastern slope of New Caledonia, and Matthew and Hunter Islands (MH) (Figs 1 & 2, and see
126 Appendices S1 & S2 in Supporting Information). The *Terrasses* and *ExBoDi* cruises are part
127 of a long-term research endeavour – the Tropical Deep-Sea Benthos (TDSB) program
128 (Bouchet *et al.*, 2008; details of the cruises are available at
129 <http://expeditions.mnhn.fr/program/tropicaldeep-seabenthos>) – and relied on the
130 combined use of a beam trawl and a dredge to maximize the types of substrates and faunal
131 diversity collected. During the *Terrasses* cruise, 256 *Chrysogorgia* colonies were collected,
132 213 of which were successfully genotyped (see below). An additional 439 and 421 colonies
133 were collected and genotyped, respectively, during the *ExBoDi* cruise. Specimens from
134 other cruises in the Pacific (including the TDSB cruises *BIOPAPUA*, *EBISCO*, *MADEEP*,
135 *Norfolk 2*, *PAPUA NIUGINI*, *Salomon 1*, *Salomon 2*, *SMIB 4* and *TAIWAN2013*) provided
136 additional specimens for biogeographical comparisons ($n = 133$; Appendix S1). For
137 comparison, the study of Thoma *et al.* (2009) in the north-western Atlantic included 24
138 *Chrysogorgia* colonies among 188 octocorals. Sampling maps (Figs 1 & 2) were made with
139 MARMAP (Pante & Simon-Bouhet, 2013; R Core Team, 2014).

140 Specimens were preserved in 80–100% ethanol or RNAlater (Ambion , Austin, TX,
141 USA), or frozen at –80 °C. Protocols for DNA extraction, PCR and sequencing are detailed in
142 Pante *et al.* (2012b). The 5' region of *mtMutS* was PCR-amplified using the primers
143 ND4L2475F and MUT3458R. For specimens with sheared DNA template, internal primers
144 were used (Pante *et al.*, 2012a). Haplotypes were defined as unique *mtMutS* sequences, as
145 described in Thoma *et al.* (2009).

146

147 **Evaluation of putative endemism, haplotype richness and sampling biases**

148 Previous work in the north-western Atlantic that compared genetic variability with
149 morphological data suggested that *mtMutS* haplotypes had the power to resolve species of
150 *Chrysogorgia*, at least at a regional scale (Pante & Watling, 2012), although the number of
151 haplotypes studied (four) was relatively small. It is therefore possible that, among our
152 Pacific samples, a single haplotype may represent multiple species of *Chrysogorgia*,
153 reducing our power to detect narrow geographical ranges (e.g. Baco & Cairns, 2012). To
154 test whether unrecognized species diversity significantly affects our estimates of
155 connectivity between island slopes and seamounts, we performed computer simulations in
156 which haplotypes were split into two species of equivalent biogeography (Appendix S2).

157 To test the hypothesis that seamounts and island slopes harbour different species,
158 we analysed the site × haplotype matrix using non-metric multidimensional scaling (NMDS;
159 Kruskal, 1964a,b) and analysis of similarities (ANOSIM; Clarke, 1993). Sites are groups of
160 stations as presented in Fig. 2 and Appendix S1. We also grouped sites into five regions
161 (Fig. 2) to perform hierarchical clustering. Jaccard's index was used to compute distance
162 matrices from presence/absence data, because dredging and trawling are semiquantitative
163 sampling methods that may not capture the true abundance of organisms. Analyses were
164 performed in R using the package VEGAN 2.2-1 (Oksanen *et al.*, 2015).

165 To test the hypothesis that seamounts harbour more endemics than island slopes,
166 we looked for species that were limited to individual seamounts and seamount chains. We
167 completed this qualitative survey by parsimony analysis of endemism (PAE; Rosen &
168 Smith, 1988). This method relies on parsimony to infer the relationship among sites, based
169 on their shared haplotypes. Sampling sites were grouped by region (slope, NR, southern LR,

170 northern LR and MH), for which species occurrence was coded as 0 (absent), 1 (present at
171 one site) or 2 (present at more than one site). A 'zero vector' containing no species was
172 included in the region \times haplotype data matrix to polarize characters (Morrone, 1994). The
173 most parsimonious tree was searched using nearest-neighbour interchange
174 rearrangements, and 1000 independent replicates were run. The consistency index (CI)
175 and retention index (RI) were calculated to evaluate how well the haplotype distribution
176 data fitted the most parsimonious tree (i.e. the degree of homoplasy). PAE was performed
177 in R using the package PHANGORN (Schliep, 2011).

178 To test the hypothesis that seamount communities are richer than island-slope
179 communities, haplotype richness was estimated using sample-based rarefaction, because
180 the total numbers of individuals and stations sampled varied among localities (Gotelli &
181 Colwell, 2001). Estimated species richness (as computed in Colwell *et al.*, 2012) was scaled
182 both using samples (Colwell *et al.*, 2012) and using individuals (Gotelli & Colwell, 2001), in
183 order to ease interpretation. Computations were performed in ESTIMATES 9.0 (Colwell,
184 2013). No rarefaction analysis was performed on the north-western Atlantic data, because
185 specimen collection during dives was non-random. Similarly, data from NR collected on
186 TDSB cruises prior to the *Terrasses* cruise (Bouchet *et al.*, 2008) were not used in the
187 rarefaction analysis, because their sampling of *Chrysogorgia* was more qualitative than
188 quantitative.

189 Finally, we tested whether *mtMutS* haplotypes that share a distributional pattern
190 (specialist on seamounts or island slopes, or generalist) are phylogenetically close. To do
191 so, we inferred the phylogenetic relationships of all the known Pacific haplotypes by
192 building a median-joining haplotype network (<http://popart.otago.ac.nz/>, Bandelt *et al.*,
193 1999). We also ran one-level analyses of molecular variance (AMOVA; Excoffier *et al.*, 1992)
194 in ARLEQUIN 3.5 (Excoffier & Lischer, 2010) on the data from the *Terrasses* and *ExBoDi*
195 cruises to partition the molecular variance (1) among seamount and slope groups and (2)
196 among depth groups (Kimura two-parameter distance matrix, gamma null, 10,000
197 permutations; Kimura, 1980).

198

199 **RESULTS**

200 ***Chrysogorgia* biogeography on seamounts and slope of New Caledonia**

201 *Chrysogorgia* was found on the slope of New Caledonia, on the NR and LR, and on the slope
202 of MH, over most of the geographical and bathymetric range sampled during the *Terrasses*
203 and *ExBoDi* cruises. Out of 261 stations sampled (99 and 162 for *Terrasses* and *ExBoDi*,
204 respectively; Appendix S2), 74 recovered *Chrysogorgia*, 49 (66%) of which were sampled
205 by dredging, reflecting the preference of *Chrysogorgia* for hard substrates. This proportion
206 was consistent across slope and seamount stations. Over the 74 stations containing
207 *Chrysogorgia* colonies, 31 haplotypes were detected from 71 stations (specimens from
208 three stations could not be sequenced), eight of which were represented by single colonies
209 (Appendix S1). Most haplotypes (52%) were represented by fewer than 10 specimens; 33
210 of the 71 stations contained multiple haplotypes. The most diverse stations (CP3898 and
211 DW3855 on LR) contained 10 haplotypes. Most haplotypes were found in the 200–600 m
212 depth range, a bathymetric zone that has been extensively sampled (Fig. 3).

213 Of the 31 haplotypes, five were found exclusively on the slope, 16 exclusively on
214 seamounts (19 if MH is included), and only six haplotypes were shared between the slope
215 and the seamounts of the NR and LR (seven including MH); 20 haplotypes were sampled on
216 LR, 9 of which were sampled nowhere else during the *Terrasses* and *ExBoDi* cruises. Only
217 five haplotypes were found on both seamount chains. Seamount-level endemism was
218 detected for 14 haplotypes, but five of these were observed only once each. Only three
219 relatively well-sampled haplotypes were each restricted to one seamount (haplotypes 11,
220 24 and 27 on LR; $n \geq 20$). Haplotype 11 was sampled at especially great depths (750–
221 990 m); if this taxon were indeed restricted to these depths, it could explain why we did
222 not observe it elsewhere, most stations being shallower. Haplotypes 24 and 27, in contrast,
223 were restricted to one seamount but were within the depth range of most sampling
224 stations (240–345 m).

225 The abundances of the seven haplotypes shared between slopes and seamounts
226 varied widely. To investigate whether species distributed across these habitats are found in
227 different densities, we calculated the proportion of stations containing each of the seven
228 haplotypes for slopes and seamounts, and sorted these proportions into vectors of high-

229 density and low-density occurrences. If haplotypes shared between these environments do
230 not differ in their relative abundances, we expect the difference between these vectors to
231 be non-significant. This was not the case (paired Wilcoxon signed rank test: $V = 0$, $P =$
232 0.016). For example, haplotype 23 was found at 5 of the 42 seamount stations where
233 *Chrysogorgia* was collected and only at one station (out of 29) on the slope.

234 Seamount regions did not group together under hierarchical clustering. Rather, the
235 slope region clustered with seamounts of the northern LR and MH, whereas the assemblage
236 of the NR and southern LR grouped together. NMDS recovered a weak association of sites
237 based on habitat (i.e. seamounts versus slope) (Fig. 4; ANOSIM R -statistic = 0.02, $P = 0.367$),
238 and a stronger association of sites of similar depth (< 400 m, 400–600 m, ≥ 600 m; ANOSIM
239 R -statistic = 0.22; $P = 0.048$).

240 Rarefaction curves suggest that seamounts are more haplotype-rich than the south-
241 eastern slope of New Caledonia (Fig. 5). We observed 12 haplotypes in 181 individuals
242 from 101 slope stations. For comparison, rarefaction of the seamount data recovered 18
243 haplotypes from 180 individuals, and 23 haplotypes from 101 stations. These richness
244 estimates are relatively well supported statistically, as little (individual-scaled rarefaction)
245 or no (sample-scaled rarefaction) overlap in 95% confidence intervals was observed. This
246 pattern (seamounts being richer than the slope) is largely driven by the richness observed
247 on southern LR seamounts (a total of 17 haplotypes). No rarefaction curve reached an
248 asymptote, suggesting that more haplotypes would be discovered with additional sampling.

249 The most parsimonious tree produced by the PAE (score of 45, CI = 0.89, RI = 0.5)
250 nested groups mostly according to geography (Fig. 6). PAE lumped stations on NR and the
251 southern LR together, this clade comprising 11 of the 31 detected haplotypes (35%). The
252 slope was sister to this clade, forming a group sheltering 17 endemics, i.e. over half of the
253 total haplotype richness. Haplotype 3 was the only haplotype to be shared across all five
254 regions, and seven haplotypes (2, 8, 9, 10, 16, 19 and 23) were shared by different clades
255 (homoplastic haplotypes). Even though there are haplotypes shared between slope and
256 seamounts, the haplotype network showed some evidence of evolutionary subdivision
257 between these two groups (Fig. 7). This qualitative result was confirmed by the AMOVA,
258 which suggests that the amount of genetic variance partitioned between groups (8.5%) is
259 larger than expected by chance ($P = 0$). However, the amount of genetic variance explained

260 by depth stratification was 3.4 times greater (variance component, 28.8%; $P = 0$; see
261 Appendix S3).

262

263 **Regional and global haplotype distributions**

264 As reported in Thoma *et al.* (2009), the geographical distribution of haplotypes across the
265 New England Seamounts (NES) and Corner Seamounts (CS) was accompanied by wide
266 faunal connections with the Azores, the bathyal slope of the Bahamas, and Hawaii. Some
267 haplotypes collected during the *Terrasses* and *ExBoDi* cruises had wide distributions within
268 the Pacific, but none of them were observed in the Atlantic. For example, eight haplotypes
269 occurring in New Caledonia were collected in Papua New Guinea (PNG) (haplotypes 5, 7, 8,
270 9, 10, 16, 22 and 30; Pante *et al.*, 2012b). Three of these (haplotypes 7, 10 and 30) were
271 collected on Sanguma Seamount (5.42° S, 154.02° E), the others coming from the PNG
272 island slopes. None of these haplotypes were restricted to a single seamount peak, but four
273 were restricted to seamounts (haplotypes 7, 10, 16 and 30; haplotype 22 being found
274 exclusively on the slope, and haplotypes 5, 8 and 9 on both slope and seamounts).

275 Haplotype 7, restricted to the seamounts of NR and LR, was also sampled on Nova Bank
276 Seamount (780 km west of New Caledonia; 330–340 m depth), from a depth zone
277 consistent with the bathymetric range observed on NR for this haplotype (300–390 m),
278 deeper on a seamount off Taiwan (517–573 m), and on slopes and Sanguma Seamount in
279 PNG (369–860 m). Similarly, a single colony of haplotype 12 was collected during the
280 *Terrasses* and *ExBoDi* cruises. We found a specimen with an identical *mtMutS* sequence and
281 congruent morphology from the south-west of the Kermadec Ridge (north-east of New
282 Zealand). This haplotype is an example of a rare but widespread species. Interestingly,
283 haplotype 9 appeared to have a very restricted distribution on the south-eastern slope of
284 New Caledonia, but a specimen with an identical *mtMutS* sequence and with congruent
285 gross morphology was sampled in the Solomon Islands during a TDSB cruise. This
286 haplotype was also sampled in Hawaii (Middle Bank) and the Aleutian Islands (Alaska). The
287 broad geographical distribution of some haplotypes points to the crucial role of sampling in
288 assessing endemism. Haplotype 9, for instance, was the fourth most frequently collected
289 taxon in New Caledonia, and was exclusively sampled on the south-western slope of the

290 Isle of Pines ($n = 45$) and MH ($n = 1$). This haplotype was, however, also sampled in the
291 Solomon Islands, over 1500 km from the Isle of Pines.

292

293 **DISCUSSION**

294 **Correspondence between haplotypes and nominal species**

295 A major issue for studies of coral biogeography and connectivity, this one included, is the
296 difficulty of separating historical from contemporary connectivity. Wide geographical
297 distributions could reflect either strong dispersal capabilities or ancient connections
298 between ocean basins. We recently used genome-wide SNP (single nucleotide
299 polymorphism) data to evaluate the hypothesis that mitochondrial *mtMutS* haplotypes can
300 reliably represent species-level lineages, and found good congruence (67%) between
301 *mtMutS*-based species delimitation and genomic divergence (Pante *et al.*, 2014). Specimens
302 characterized by haplotypes 2, 8 and 13 may belong to a single species. Conversely, the
303 New Caledonian specimens with haplotype 7 were phylogenetically distinct from the ones
304 sampled in PNG, suggesting that colonies bearing this haplotype may belong to at least two
305 species. Nevertheless, our simulation data (Appendix S2) suggest that, at the community
306 level, underestimation of species richness due to lack of genetic resolution only has a
307 moderate impact on the overall measure of faunal connectivity between slopes and
308 seamounts. In addition, the apparent lack of geographical structuring on the NES and CS
309 (Thoma *et al.*, 2009) is in sharp contrast with the data from New Caledonia. Our data are
310 therefore useful in a comparative biogeographical framework.

311

312 ***Chrysogorgia* on seamounts and slope**

313 The apparent lack of endemism of chrysogorgiid corals on Atlantic seamounts is consistent
314 with recent biogeographical and molecular studies of other seamount fauna (reviewed in
315 Clark *et al.*, 2010; Rowden *et al.*, 2010a; Schlacher *et al.*, 2010). The overall consensus is
316 that Pacific seamounts do not harbour significantly more endemic species than other,
317 equivalent deep-sea habitats (Samadi *et al.*, 2006; O'Hara, 2007; Rowden *et al.*, 2010b). For
318 instance, no endemism was detected among bamboo corals based on mitochondrial
319 sequence data (Smith *et al.*, 2004). Similarly, Miller *et al.* (2010) recently reported on the

320 genetic connectivity among nine species of corals (six scleractinians and three
321 antipatharians) and found weak evidence for isolation by distance and barriers to dispersal
322 between seamount peaks in the south-western Pacific. Our results are in contrast with
323 those patterns, as up to 29% of *Chrysogorgia* haplotypes sampled more than once could be
324 restricted to a single seamount. Durand Reef in particular appeared to be a hotspot of
325 diversity and endemism, with 14 haplotypes, half of which were observed nowhere else.
326 The difference between our study and the studies of Smith *et al.* (2004) and Miller *et al.*
327 (2010), may lie in the overall depth range surveyed; Miller and colleagues used specimens
328 collected between 110 and 2136 m (median 542 m, mean 721 m), covering a much deeper
329 range than we have here (70–1180 m; median 456 m, mean 497 m). The haplotypes
330 reported by Smith *et al.* (2004) were also mostly restricted to waters deeper than 500 m,
331 some extending as deep as 3000 m. These observations are consistent with the wide
332 geographical distribution observed in the Atlantic, where sampling was mostly performed
333 at depths between 1500 and 2000 m. In fact, Pante & Watling (2012) noted that none of the
334 *Chrysogorgia* species previously detected on the slope of the north-western Atlantic were
335 detected on the NES and CS, and that the sampling depth of these two species pools barely
336 overlapped (see Fig. 14 in Pante & Watling, 2012).

337

338 **Geographical distribution structured by depth**

339 The effect of depth on the distribution (reviewed in Etter & Rex, 2010) and genetic
340 structure (e.g. France & Kocher, 1996; Zardus *et al.*, 2006; Cho & Shank, 2010; Jennings *et*
341 *al.*, 2013) of deep-sea organisms has long been known, and is gaining recognition for corals
342 (Eytan *et al.*, 2009; Baco & Cairns, 2012; Quattrini *et al.*, 2013, 2015; Doughty *et al.*, 2014).
343 Environmental conditions such as pressure, temperature, dissolved oxygen and habitat
344 heterogeneity (to name a few; Gage & Tyler, 1991) can change significantly with depth,
345 resulting in vertical zonation of benthic communities. These effects are, however, still little
346 characterized for seamount fauna. McClain *et al.* (2010), investigating the structure of
347 invertebrate and fish communities on Davidson Seamount in the north-eastern Pacific,
348 found that assemblage composition, rather than diversity or density, changed with depth
349 (1246–3656 m). In particular, they reported that octocorals showed significant species

350 turnover between depths, which accounted for a significant proportion of the variation
351 observed. In our study, differences in geographical and bathymetric haplotype
352 distributions might be due to differences in the environmental setting, such as the sampled
353 depth regimes, which overlapped only slightly (deepest NR/LR station: 1130 m; shallowest
354 NES/CS station: 823 m). Etter *et al.* (2005) showed that genetic differentiation decreases
355 with increasing depth in populations of deep-sea bivalves. Likewise, Bradbury *et al.* (2008)
356 found a positive correlation between depth and pelagic larval duration, and a negative
357 correlation between depth and amounts of genetic structure in marine fishes. Our results
358 may therefore suggest that the stratification of *Chrysogorgia* haplotypes decreases with
359 depth. This hypothesis, which implies that environmental conditions are less structuring at
360 deeper depths, cannot be rigorously tested across ocean basins with the data at hand, but
361 preliminary observations from our data suggest more complex patterns, because the
362 deepest haplotypes observed on the LR and NR are not necessarily the most geographically
363 widespread (e.g. haplotypes 12, 30 and 31, although sampling was less intensive below
364 800 m) and some shallow haplotypes are widely distributed (e.g. haplotypes 3 and 4; Fig. 3,
365 Appendix S1). The stratification of haplotypes may therefore decrease below a depth of
366 1130 m; this could be tested by deeper sampling on the LR and NR.

367

368 **Regional and global haplotype distributions**

369 *Chrysogorgia* species pools from the Atlantic and Pacific Oceans seem to be characterized
370 by different distributional ranges and diversity patterns. The *Terrasses* and *ExBoDi*
371 haplotypes that were found outside the New Caledonian exclusive economic zone were
372 mostly limited to the south-west Pacific region (from Taiwan to the Kermadec Ridge, a
373 range of approximately 59° of latitude and 61° of longitude; with the exception of
374 haplotype 9, the distribution of which extends to Hawaii). In contrast, all chrysogorgiid
375 genera (*Chrysogorgia*, *Iridogorgia*, *Radicipes* and *Metallogorgia*) sampled on the Atlantic
376 NES and CS contain haplotypes that are represented in the Pacific (Thoma *et al.*, 2009). In
377 other words, the Atlantic chrysogorgiids appear to have an overall geographical range that
378 is wider than that of New Caledonian chrysogorgiids. On the other hand, Pacific
379 *Chrysogorgia* were characterized by high levels of patchiness, rarity and haplotypic

380 diversity. Rarity and patchiness were observable at two levels. At the local scale, the
381 number of colonies sampled at a single station was highly variable. For instance, at stations
382 with *Chrysogorgia*, abundance varied from 1 to 109 colonies, with an average of 9 and a
383 standard deviation of 18. At the regional scale, some haplotypes categorized as rare in New
384 Caledonia were nevertheless sampled very far apart, such as in New Zealand, Papua New
385 Guinea or Taiwan. These patterns of rarity and patchiness of deep New Caledonian fauna
386 have also been observed in gastropods (Castelin *et al.*, 2011). These observations suggest
387 that the sampling effort necessary to accurately describe the distribution of *Chrysogorgia*
388 haplotypes in the Pacific is far greater than in the Atlantic. Nevertheless, sampling over 760
389 Pacific specimens provided data that emphasize the importance of depth, rarity and
390 patchiness in structuring these communities, both on seamounts and on oceanic slopes.

391

392 **ACKNOWLEDGEMENTS**

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394 *Chrysogorgia*, as well as to our colleagues at the MNHN, IRD, the University of Louisiana at
395 Lafayette and the University of Hawaii. We thank two anonymous referees for their
396 comments. Detailed acknowledgements on sampling and funding information are given in
397 Appendix S2.

398

399

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Excel table of *Chrysogorgia* specimens with biogeographical and haplotype information.

Appendix S2 Supplemental text.

Appendix S3 Median-joining network for Pacific *Chrysogorgia* haplotypes, plotted by depth and geography.

BIOSKETCH

Eric Pante and **Scott C. France** work on the evolution, biogeography and systematics of marine organisms, particularly deep-sea corals. **Sarah Samadi** and her group investigate faunal connectivity among benthic organisms of the deep tropical western Pacific Ocean.

Author contributions: E.P., S.C.F. and S.S. conceived the ideas; E.P., S.C.F. and S.S. (among others) collected the specimens; E.P., D.G. and C.C. generated the genetic data; E.P. analysed the data and wrote the paper; all authors approved the final version.

Editor: David Bellwood

611 **FIGURE CAPTIONS**

612 **Figure 1** World map with the two major sampling locations and the sampling locations of
613 specimens used in biogeographical comparisons. Samples used in previous studies are
614 plotted using different symbols. NES, New England Seamounts; CS, Corner Seamounts.

615 **Figure 2** Bathymetric map of New Caledonia and parts of the Norfolk and Loyalty ridges. All
616 stations sampled during the *Terrasses* and *ExBoDi* cruises are plotted as grey squares.
617 Stations containing at least one *Chrysogorgia* colony are marked by black circles. Isobaths
618 are plotted every 500 m from 100 to 3000 m. Slope stations were divided into three
619 geographically discrete areas for biogeographical analyses. The feature labelled '6756' is a
620 nameless seamount (Allain *et al.*, 2008) adjacent to the New Caledonian slope. Although a
621 *Chrysogorgia* specimen was collected from this seamount, it could not be genotyped. LR,
622 Loyalty Ridge; NR, Norfolk Ridge.

623 **Figure 3** Geographical (top) and bathymetric (bottom) distributions of the 31 haplotypes
624 sampled during the *Terrasses* and *ExBoDi* cruises. Minimum and maximum depths were
625 calculated based on the minimum and maximum depths of trawling and dredging stations
626 that contained *Chrysogorgia*. The colour of each bar represents the number of colonies
627 sampled for each haplotype (*n*; see key in the bottom left corner). Haplotype number is
628 provided on top of each bar. LR, Loyalty Ridge; NR, Norfolk Ridge; MH, Matthew and Hunter
629 Islands.

630 **Figure 4** (a) Hierarchical cluster analysis and (b) non-metric multidimensional scaling
631 (NMDS) based on Jaccard's dissimilarity between regions and sites. For NMDS, the symbol
632 size is proportional to the number of haplotypes recorded at each site, and different
633 symbols represent different mean depths (light grey, seamounts; dark grey, slope). Site
634 names and depth ranges (m) are provided next to each symbol.

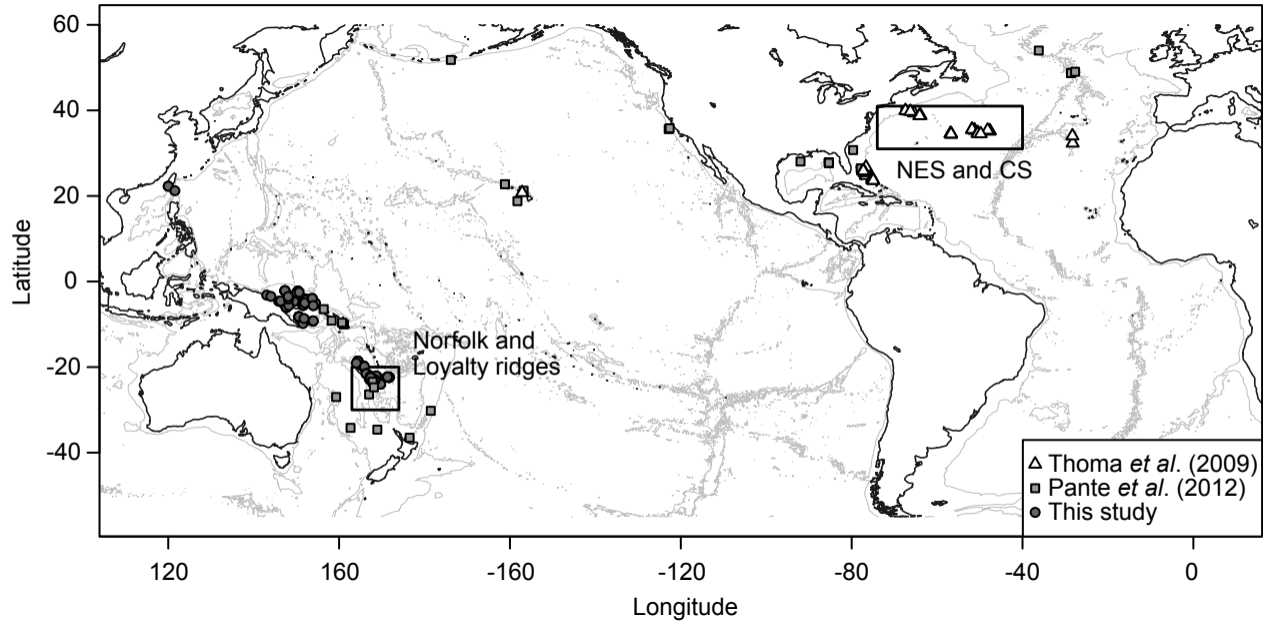
635 **Figure 5** Haplotype richness on the south-eastern New Caledonian slope and seamounts of
636 the Norfolk Ridge (NR) and Loyalty Ridge (LR). Left: individual-scaled rarefaction curves.
637 Right: sample-scaled rarefaction curves. Upper panels: rarefied haplotype richness for all
638 regions. Lower panels: rarefied haplotype richness for seamounts and slopes, with 95%
639 confidence envelopes. For each group, the total observed number of haplotypes is given in
640 parentheses.

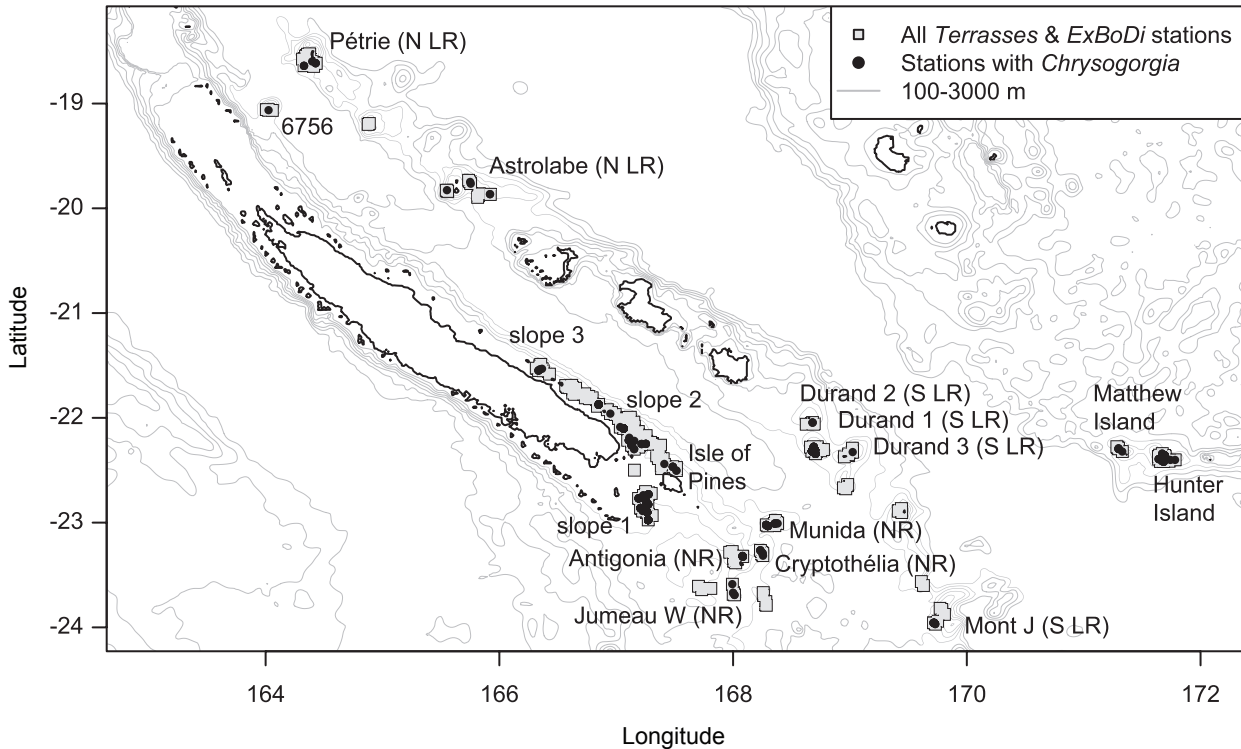
641 **Figure 6** Parsimony analysis of endemcity (PAE). The dots placed on branches of the tree
642 represent haplotypes endemic to a clade (synapomorphic haplotypes), which can be
643 defined by one or several regions.

644 **Figure 7** Median-joining network for all known Pacific *Chrysogorgia* haplotypes (left) and
645 Venn diagram showing the haplotype distribution among Pacific regions (right). Network:
646 mutational steps are represented by hashes on network branches; circle size is
647 proportional to sample size. A detailed list of sampling locations and networks drawn
648 according to depth and geography are available in Appendices S1 & S3 of Supporting
649 Information.

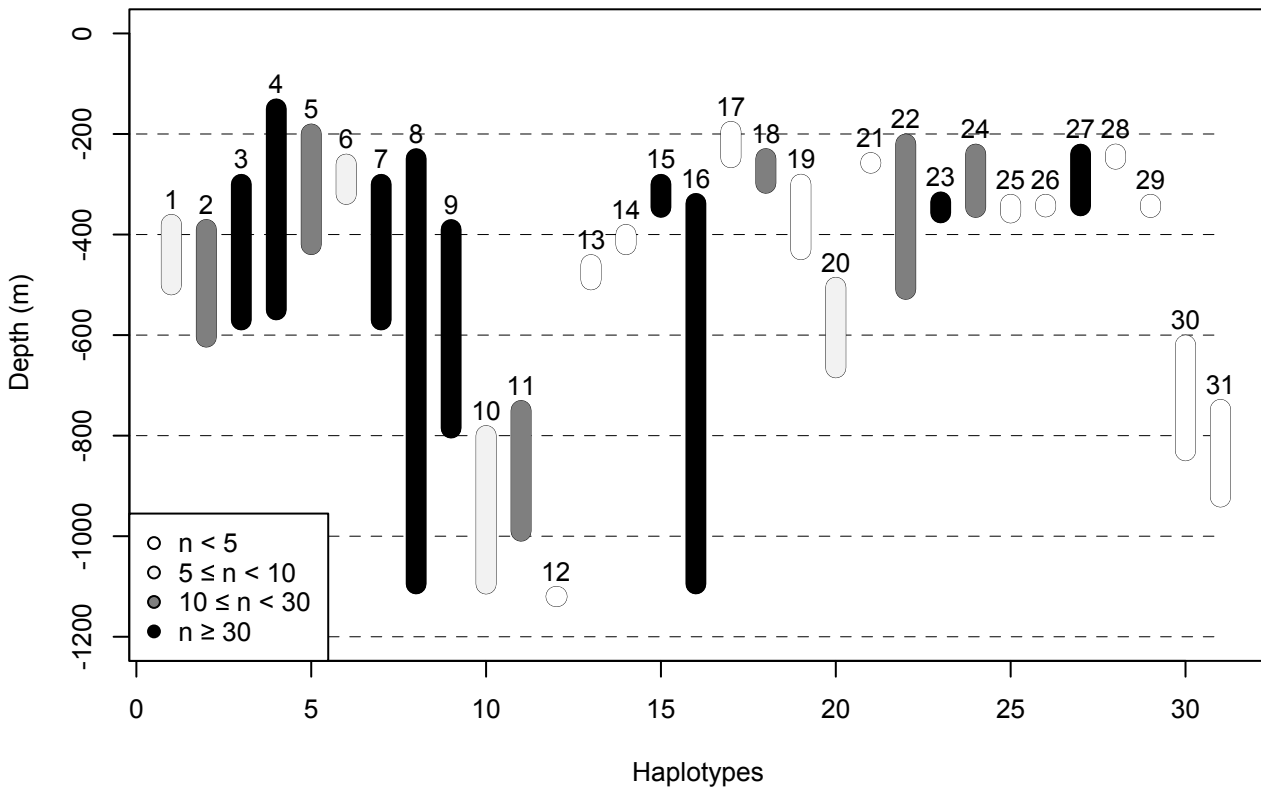
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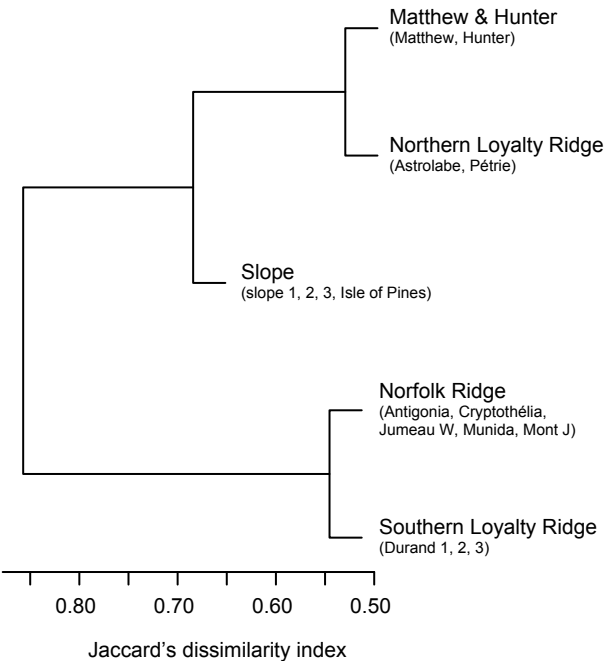




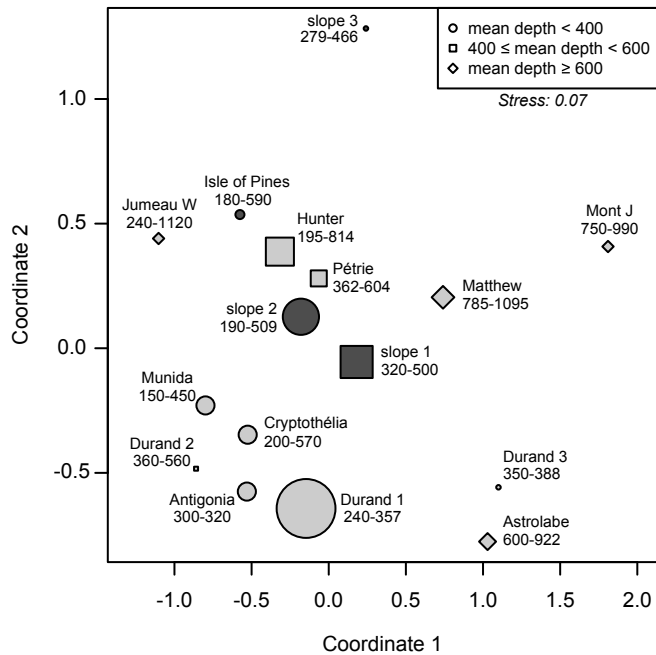
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
N LR	x	x						x											x											x	x
S LR		x	x	x		x				x	x				x	x								x	x	x	x	x	x	x	
NR		x	x	x	x	x						x			x																
MH		x	x					x	x	x						x	x	x	x	x											
Slope	x	x	x	x	x			x	x				x	x									x	x	x						



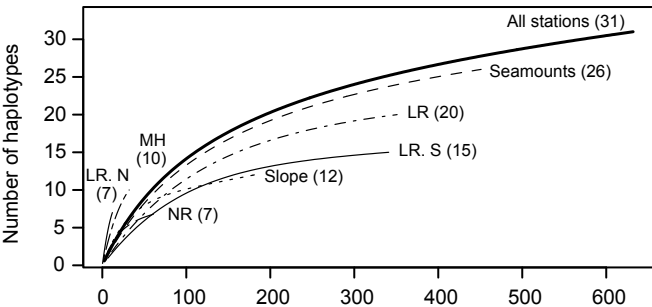
(a)



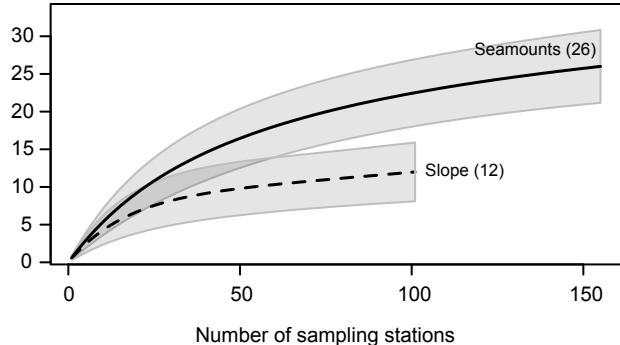
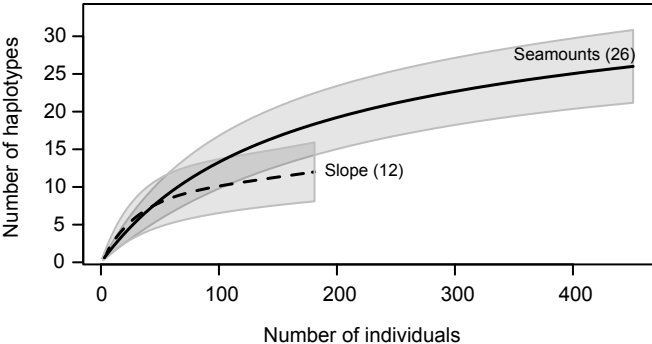
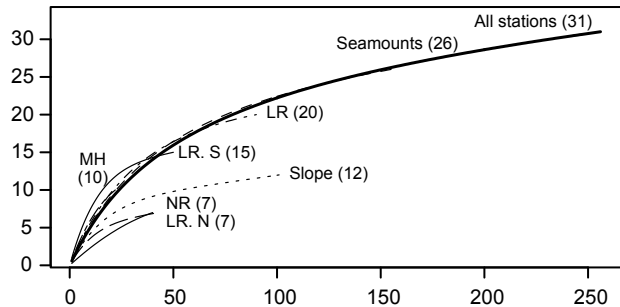
(b)

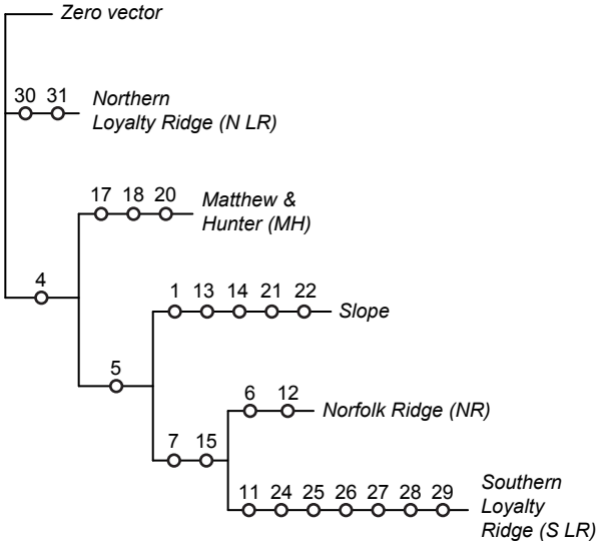


Individual-scaled rarefaction



Sample-scaled rarefaction





(a)

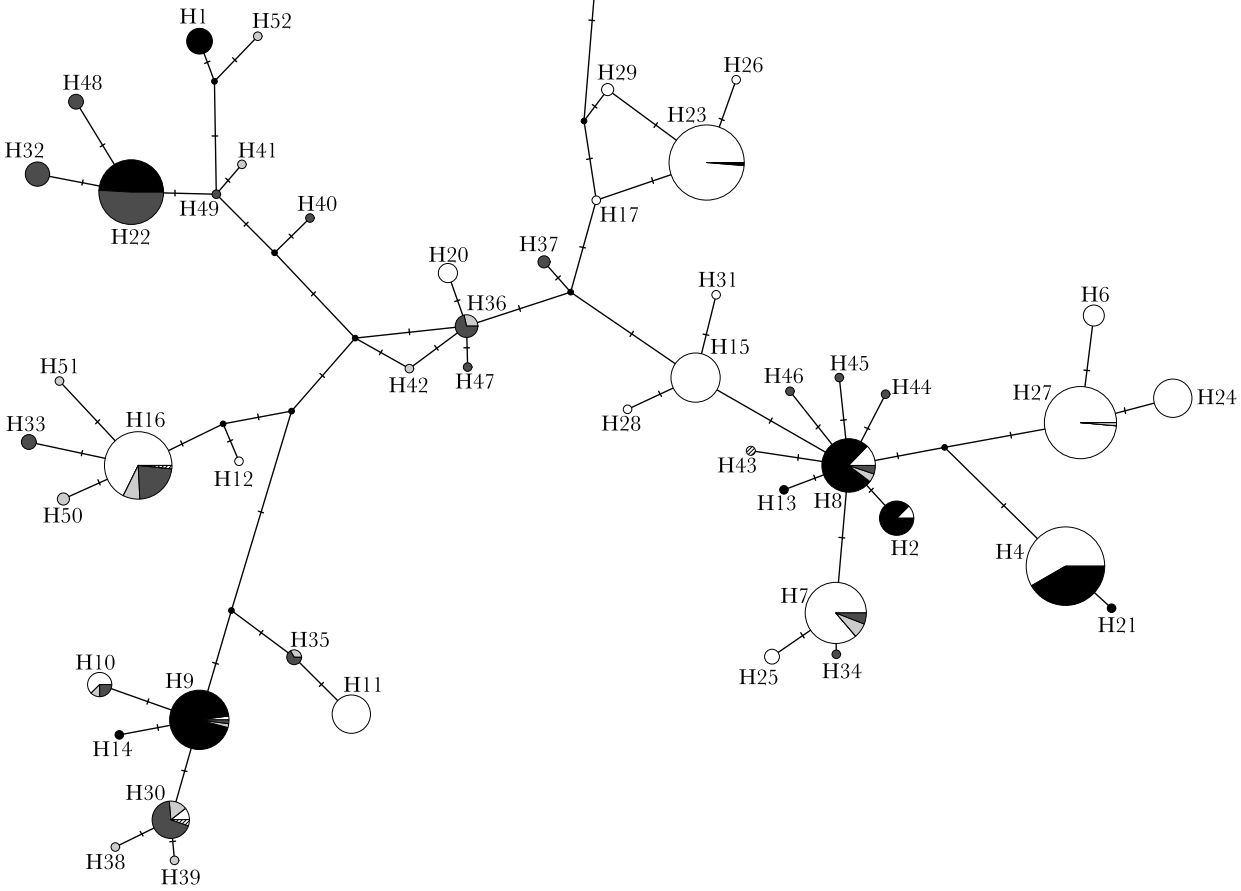
○ New Caledonian seamount

● Other Pacific seamount

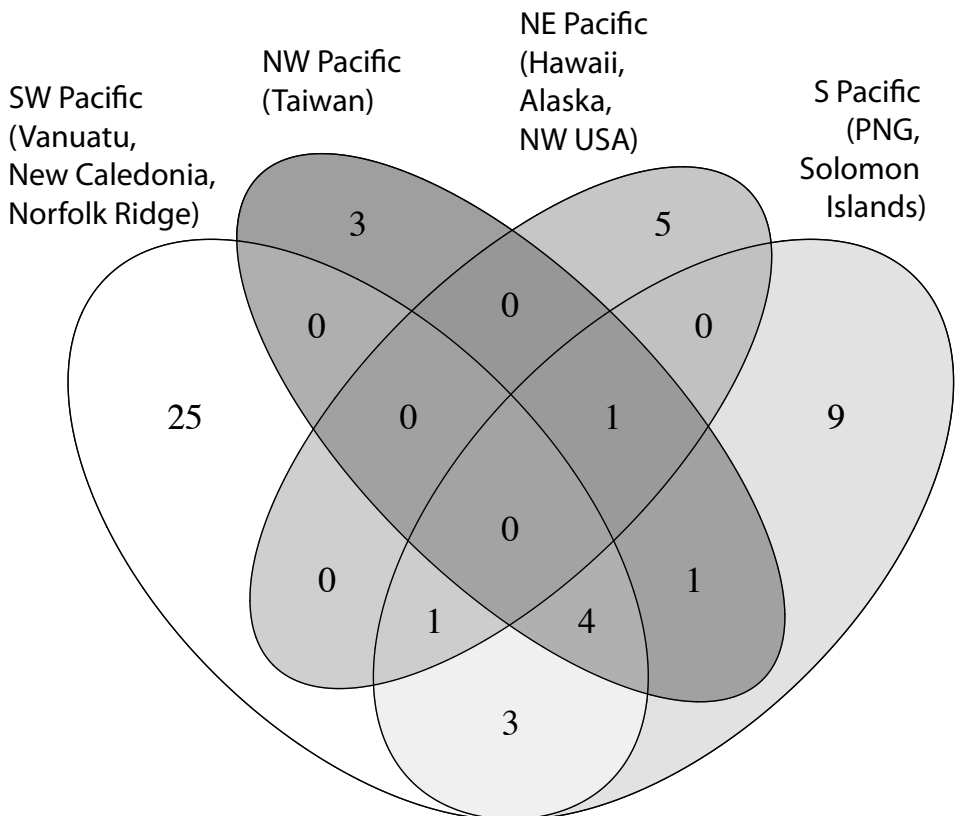
● New Caledonian slope

● Other Pacific slope

● Other Pacific feature (e.g. bank)



(b)



SUPPORTING INFORMATION

An inter-ocean comparison of coral endemism on seamounts: the case of *Chrysogorgia*

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APPENDIX S2 Supplemental text.

Study area: geology, oceanography, and associated fauna

The south-west Pacific Norfolk Ridge (NR) is approximately 1500 km long and 200 km wide, and connects the south-eastern tip of New Caledonia to the north-western tip of New Zealand. The seamounts along this ridge have, on average, summit depths between 700 and 1000 m towards the north-east, and between 250 and 500 m towards the south-west. Some seamount summits are particularly shallow, such as Antigonina Seamount, which peaks at 57 m depth (Allain *et al.*, 2008). The Loyalty Ridge (LR) runs parallel to the NR, and harbours many deep seamounts (summit depths 750–1000 m). The NR and LR are separated by a sedimentary basin that is 2500 m deep and 70 km wide (Dupont *et al.*, 1995). A total of 57 underwater features were catalogued from the New Caledonian exclusive economic zone (Allain *et al.*, 2008), including 17 seamounts more than 1 km tall. Most seamounts are shorter, and can be considered guyots (Castelin, 2010).

Sub-surface currents around New Caledonia are mainly influenced by the South Equatorial Current (SEC), which flows westward and passes between New Caledonia and the Solomon Islands (Kessler & Cravatte, 2013, and references therein). The SEC is composed of several narrow currents, or jets, two of which pass by New Caledonia (the

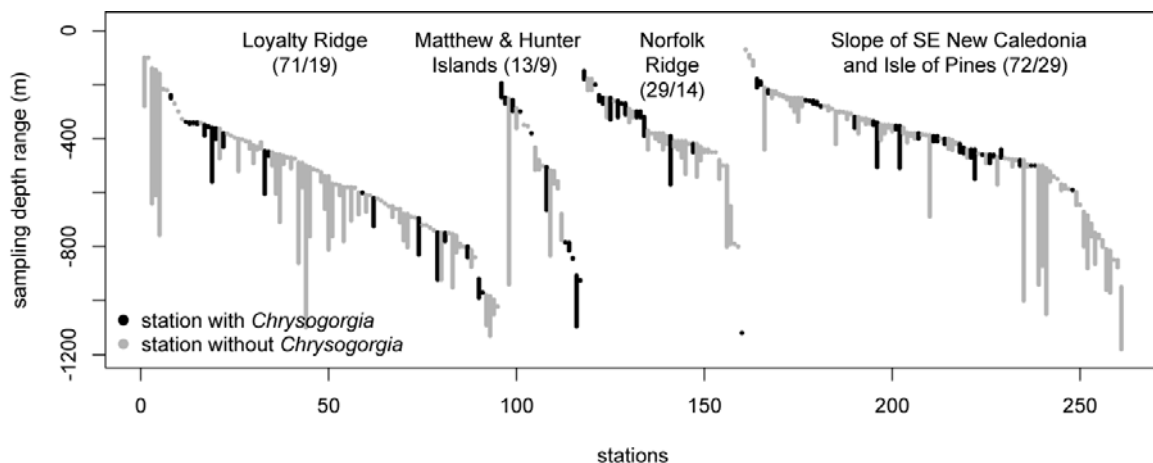


Figure S1 Bathymetric range of sampling stations for the *Terrasses* and *ExBoDi* cruises. Vertical segments connect the shallower and deeper sampling depths for each station. Shade represents the presence (black) or absence (grey) of *Chrysogorgia* at each station. The numbers of stations with/without *Chrysogorgia* are provided in parentheses for each group.

westward Northern Caledonian Jet, NCJ, and Southern Caledonian Jet, SCJ). These jets split from the South Fiji Jet at the southern tip of Vanuatu. The NCJ first flows north-west along the Loyalty Ridge, and continues west as it passes the northern tip of New Caledonia. The SCJ leaves the southern tip of Vanuatu to go over the Norfolk Ridge and, further west, over the Lord Howe Rise (see Fig. 6 in Kessler & Cravatte, 2013).

The taxonomy of *Chrysogorgia* in this zone is very poorly known. Whereas 25 species are known from the Malay Archipelago, only one species was documented from New Caledonia (Bayer & Stefani, 1988), and there are no records of *Chrysogorgia* specimens identified to the species level within a 1300-km radius of this location. We are in the process of testing species hypotheses using genomic markers (Pante *et al.*, 2014) and plan to formally describe *Chrysogorgia* species from the SW Pacific area. In the following sections, we will refer to the south-western slope of New Caledonia as ‘the slope’.

Correspondence between haplotypes and nominal species

A single nominal species of *Chrysogorgia* (*C. admete*, Bayer & Stefani, 1988) is currently known from the area (type locality: south-eastern slope of New Caledonia). We attempted, without success, to amplify *mtMutS* from the holotype of this species. Preliminary observations suggest that colony morphology correlates well with genetic identity within the region, and that *mtMutS* haplotypes might therefore represent evolutionary units that are close to the species level. Specimens belonging to haplotype 12 are among the rare pinnate colonies ever collected. It is, however, genetically distinct from the only pinnate *Chrysogorgia* species described to date (*C. pinnata* Cairns, 2007), suggesting that this specimen belongs to an undescribed species.

Evaluation of putative endemism, haplotype richness and sampling biases

Computer simulation methods

To test whether unrecognized species diversity significantly affects our estimates of connectivity between island slopes and seamounts, we performed computer simulations in which haplotypes were split into two species of equivalent biogeography. For example, if a haplotype present both on slopes and on seamounts represents two species instead of one, these two species may both be present on seamounts and slopes. Alternatively, one of them may be present in both environments, whereas the second is (1) absent from both environments, (2) present on slopes but not seamounts, or (3) present on seamounts but not slopes. We used the presence–absence matrix built for slopes and Norfolk Ridge stations (16 haplotypes in common) to perform simulations in R. We split 1–16 haplotypes (sampled at random without replacement) into two species each. The presence/absence pattern of the two ‘new’ species are chosen at random, but always match the original haplotype biogeography. The modified matrices therefore contained 17–32 species. Jaccard’s dissimilarity index (JI) was recalculated for the modified matrix, and 1000 replicates were performed for each condition (total of 16×1000 simulations).

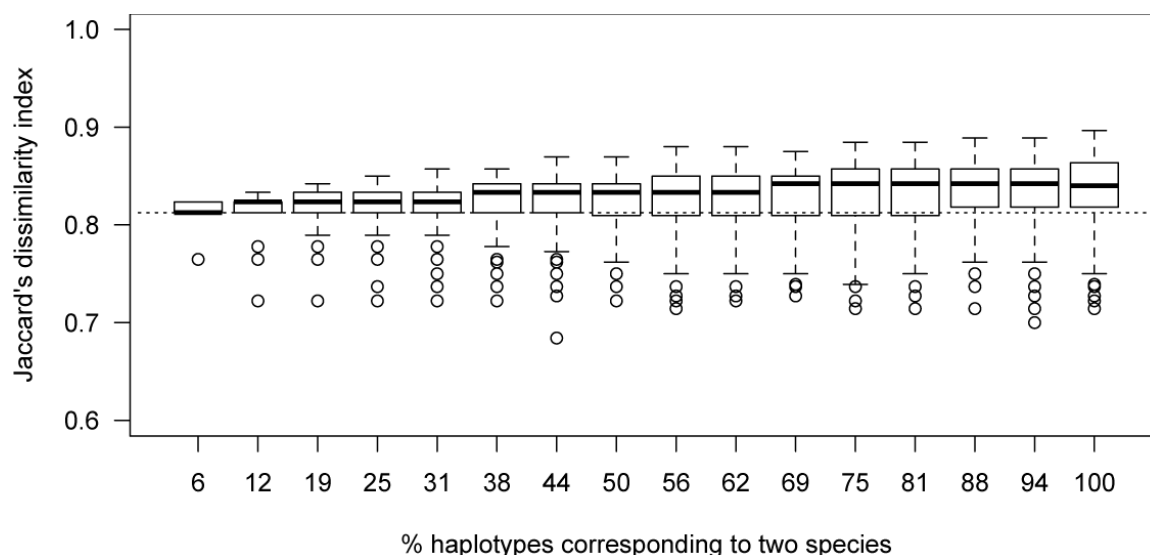


Figure S2 Results of the species simulation study comparing the slope of New Caledonia and the seamounts from the northern end of the Norfolk Ridge. Distributions (represented as box-and-whisker plots) of Jaccard's dissimilarity index (JI) when haplotypes (from 1 to 16) are split into two species of equivalent biogeography. The horizontal dashed line represents the observed value of JI for 16 haplotypes. The thick black line represents the median of simulated data. Boxes include data from the first to the third quartile, and vertical bars represent the non-outlier range. Outliers are defined as values > 1.5 the interquartile range.

Results of computer simulations

Computer simulations aiming at artificially splitting haplotypes into two putative species show an increase in median JI with increasing number of species (i.e. slopes and seamounts become more dissimilar as the number of species increases), and an increase in the variance of JI with increasing number of species (see Fig. S2). These increases are, however, moderate: when all haplotypes are split into two species (total of 32 species), JI varies between 0.73 and 0.89, with a median of 0.84. The observed JI of 0.81, calculated on the empirical data based on 16 haplotypes, is included in the simulated interquartile range of most simulation sets (11 / 16 sets; overall interquartile range for all 16,000 simulations: 0.81–0.84).

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Appendix S3: Median-joining network for Pacific *Chrysogorgia* haplotypes, plotted by depth (top) and geography (bottom).

