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

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Abstract :

Aim

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

Location

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

Methods

The mitochondrial gene mtMutS was used to measure diversity within Chrysogorgia. Community structure was analysed using rarefaction, multivariate analyses, parsimony analysis of endemicity and analysis of molecular variance. The impact of underestimating species richness when using mitochondrial haplotypes was tested using simulations.

Results

Six hundred and thirty-four colonies and 31 haplotypes were sampled from New Caledonia. Contrary to what was observed in the north-western Atlantic, seamount-scale endemism of south-west Pacific Chrysogorgia was substantial (23% and 39% for haplotypes with n20 and n2, respectively). LR sheltered 64% of the New Caledonian haplotype diversity. Assemblages were structured less by habitat type (slope versus seamounts) than by depth. Rarefaction analyses suggested that LR and NR seamounts hold more species than the New Caledonian slope, but additional sampling in the south-western Pacific (133

colonies) revealed that some seemingly geographically restricted haplotypes from New Caledonia have wide geographical distributions, reaching as far as Taiwan.

Main conclusions

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

Keywords : Atlantic Ocean, marine biogeography, marine connectivity, Octocorallia, Pacific Ocean, parsimony analysis of endemicity, seamount, species delimitation

INTRODUCTION

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

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

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

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

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

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

MATERIALS AND METHODS

Sampling and genotyping

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

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

Evaluation of putative endemism, haplotype richness and sampling biases

Previous work in the north-western Atlantic that compared genetic variability with morphological data suggested that *mtMutS* haplotypes had the power to resolve species of *Chrysogorgia*, at least at a regional scale (Pante & Watling, 2012), although the number of haplotypes studied (four) was relatively small. It is therefore possible that, among our Pacific samples, a single haplotype may represent multiple species of *Chrysogorgia*, reducing our power to detect narrow geographical ranges (e.g. Baco & Cairns, 2012). 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 (Appendix S2).

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

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

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

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

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

RESULTS

Chrysogorgia biogeography on seamounts and slope of New Caledonia

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

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

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

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

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

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

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

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

Regional and global haplotype distributions

As reported in Thoma *et al.* (2009), the geographical distribution of haplotypes across the New England Seamounts (NES) and Corner Seamounts (CS) was accompanied by wide faunal connections with the Azores, the bathyal slope of the Bahamas, and Hawaii. Some haplotypes collected during the *Terrasses* and *ExBoDi* cruises had wide distributions within the Pacific, but none of them were observed in the Atlantic. For example, eight haplotypes occurring in New Caledonia were collected in Papua New Guinea (PNG) (haplotypes 5, 7, 8, 9, 10, 16, 22 and 30; Pante *et al.*, 2012b). Three of these (haplotypes 7, 10 and 30) were collected on Sanguma Seamount (5.42° S, 154.02° E), the others coming from the PNG island slopes. None of these haplotypes were restricted to a single seamount peak, but four were restricted to seamounts (haplotypes 7, 10, 16 and 30; haplotype 22 being found exclusively on the slope, and haplotypes 5, 8 and 9 on both slope and seamounts). Haplotype 7, restricted to the seamounts of NR and LR, was also sampled on Nova Bank Seamount (780 km west of New Caledonia; 330–340 m depth), from a depth zone consistent with the bathymetric range observed on NR for this haplotype (300–390 m), deeper on a seamount off Taiwan (517–573 m), and on slopes and Sanguma Seamount in PNG (369–860 m). Similarly, a single colony of haplotype 12 was collected during the *Terrasses* and *ExBoDi* cruises. We found a specimen with an identical *mtMutS* sequence and congruent morphology from the south-west of the Kermadec Ridge (north-east of New Zealand). This haplotype is an example of a rare but widespread species. Interestingly, haplotype 9 appeared to have a very restricted distribution on the south-eastern slope of New Caledonia, but a specimen with an identical *mtMutS* sequence and with congruent gross morphology was sampled in the Solomon Islands during a TDSB cruise. This haplotype was also sampled in Hawaii (Middle Bank) and the Aleutian Islands (Alaska). The broad geographical distribution of some haplotypes points to the crucial role of sampling in assessing endemism. Haplotype 9, for instance, was the fourth most frequently collected taxon in New Caledonia, and was exclusively sampled on the south-western slope of the

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

DISCUSSION

Correspondence between haplotypes and nominal species

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

Chrysogorgia on seamounts and slope

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

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

Geographical distribution structured by depth

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

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

Regional and global haplotype distributions

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

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

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591

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

FIGURE CAPTIONS

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

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

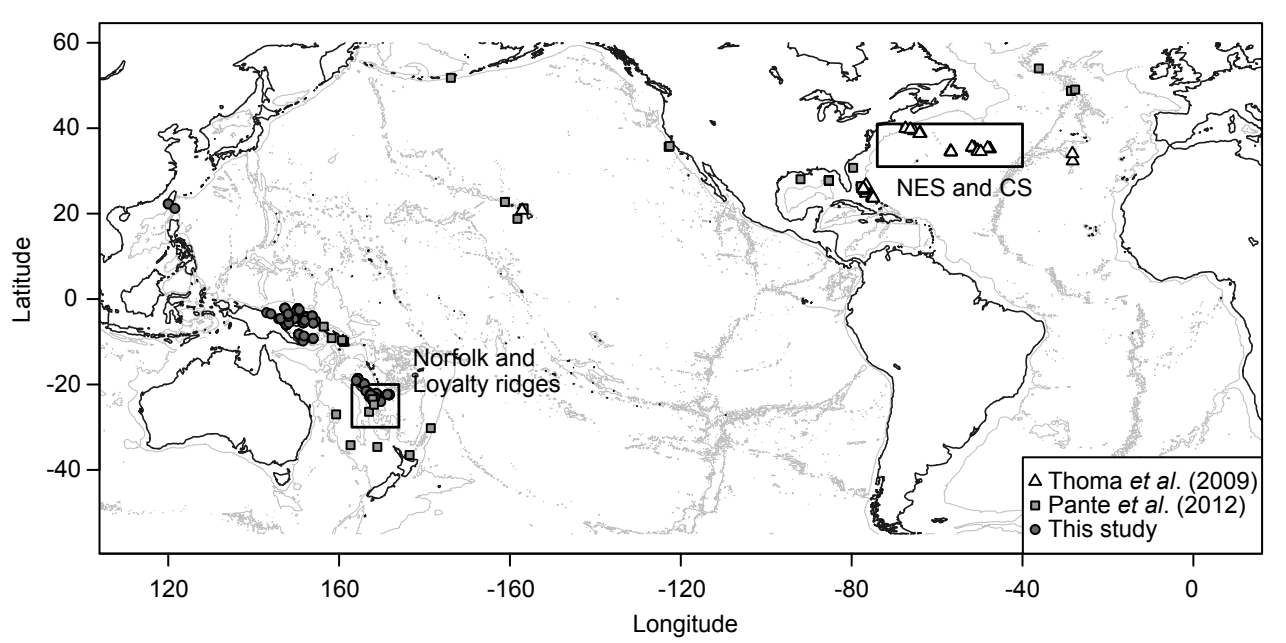
Figure 3 Geographical (top) and bathymetric (bottom) distributions of the 31 haplotypes sampled during the *Terrasses* and *ExBoDi* cruises. Minimum and maximum depths were calculated based on the minimum and maximum depths of trawling and dredging stations that contained *Chrysogorgia*. The colour of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

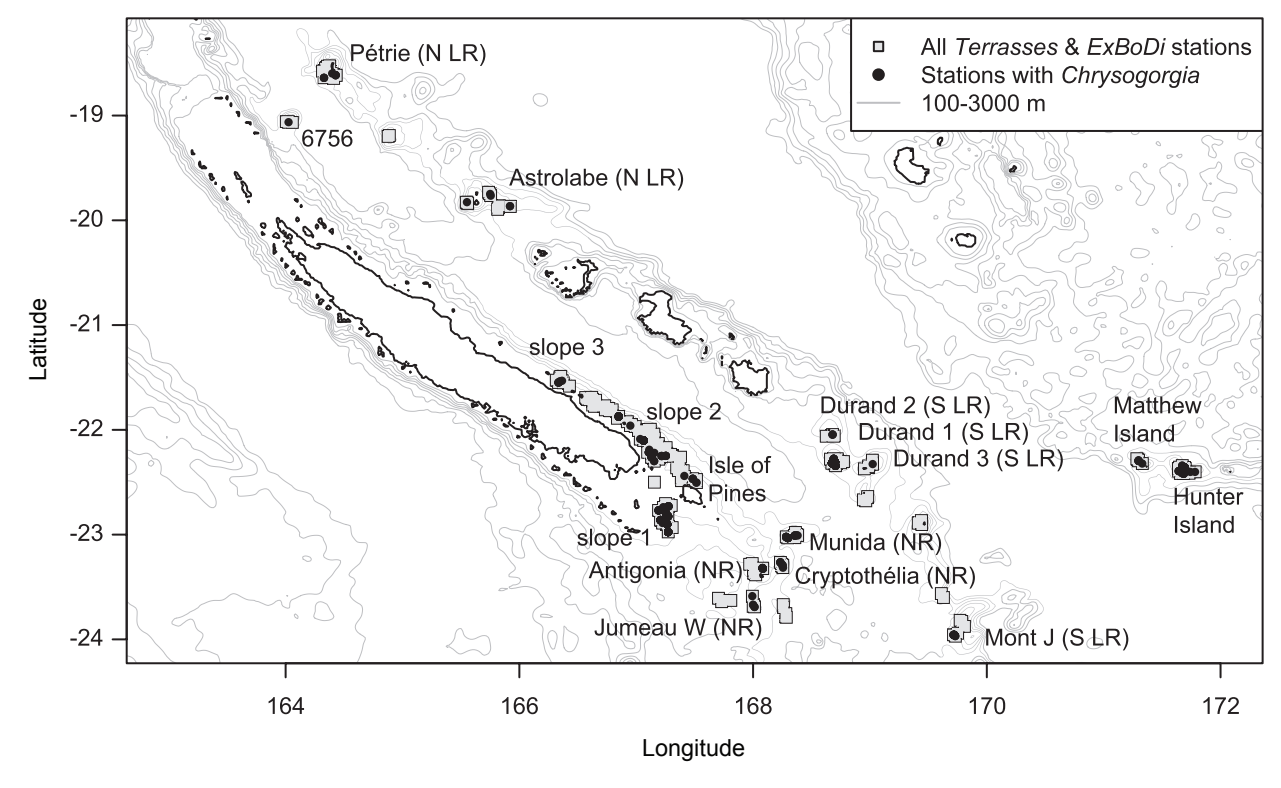
Figure 4 (a) Hierarchical cluster analysis and (b) non-metric multidimensional scaling (NMDS) based on Jaccard's dissimilarity between regions and sites. For NMDS, the symbol size is proportional to the number of haplotypes recorded at each site, and different symbols represent different mean depths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

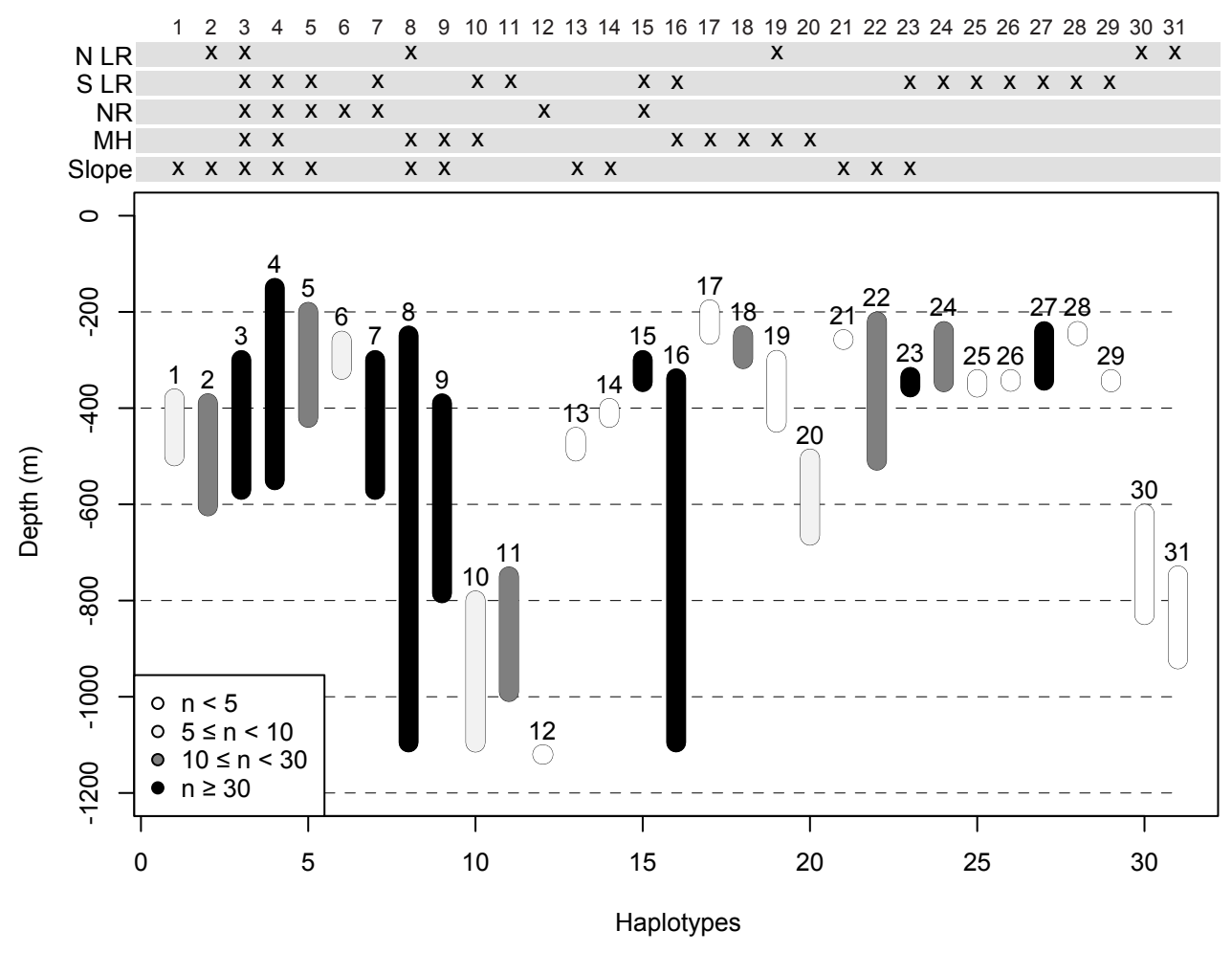
Figure 5 Haplotype richness on the south-eastern New Caledonian slope and seamounts of the Norfolk Ridge (NR) and Loyalty Ridge (LR). Left: individual-scaled rarefaction curves. Right: sample-scaled rarefaction curves. Upper panels: rarefied haplotype richness for all regions. Lower panels: rarefied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

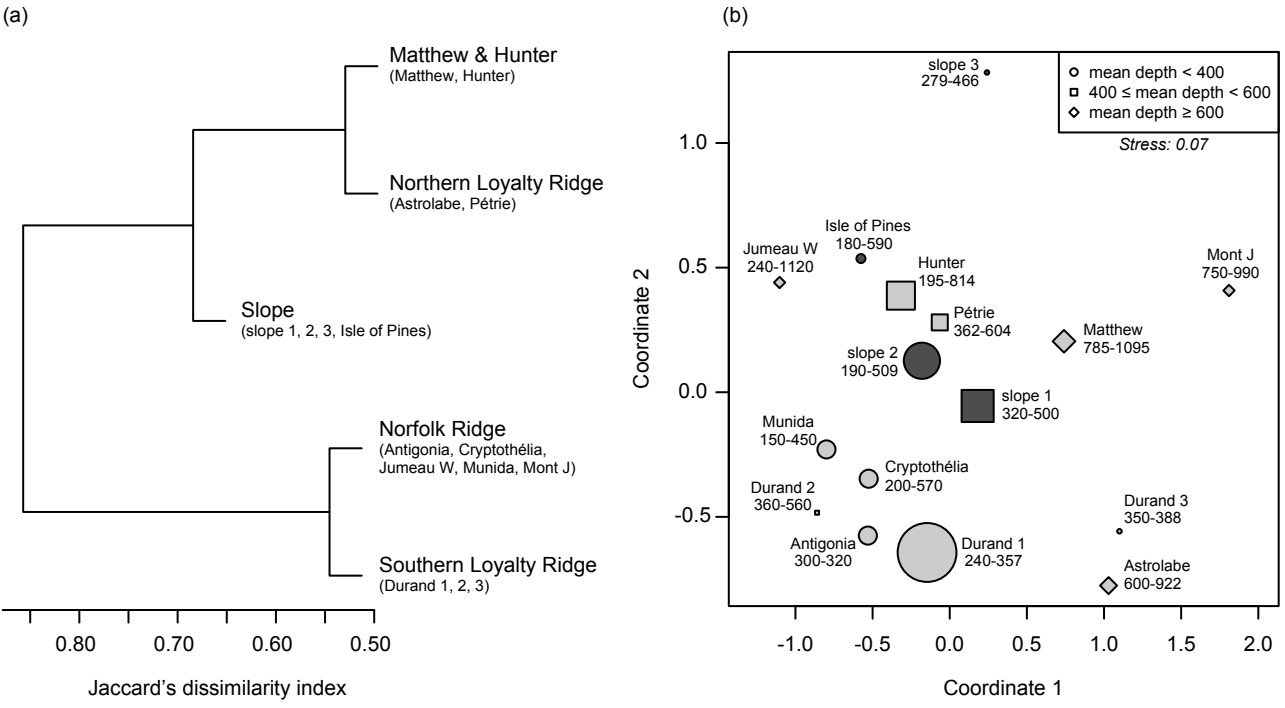
Figure 6 Parsimony analysis of endemicity (PAE). The dots placed on branches of the tree represent haplotypes endemic to a clade (synapomorphic haplotypes), which can be defined by one or several regions.

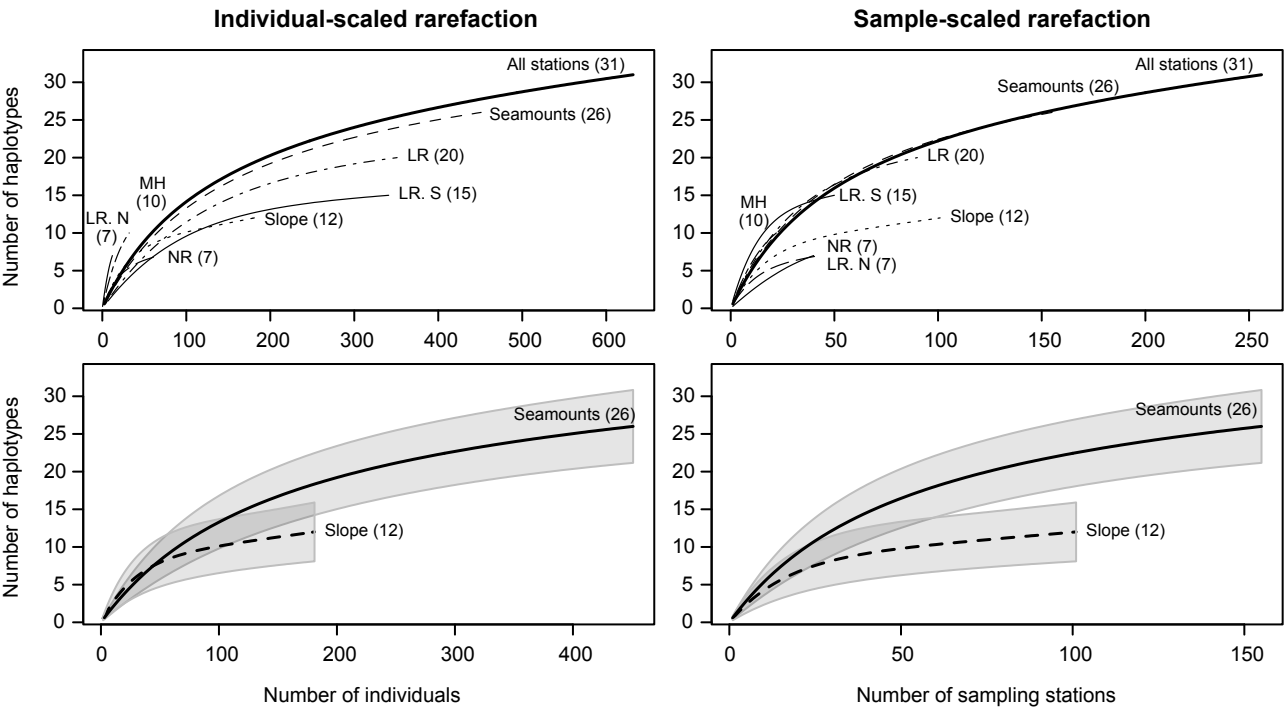
Figure 7 Median-joining network for all known Pacific *Chrysogorgia* haplotypes (left) and Venn diagram showing the haplotype distribution among Pacific regions (right). Network: mutational steps are represented by hashes on network branches; circle size is proportional to sample size. A detailed list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

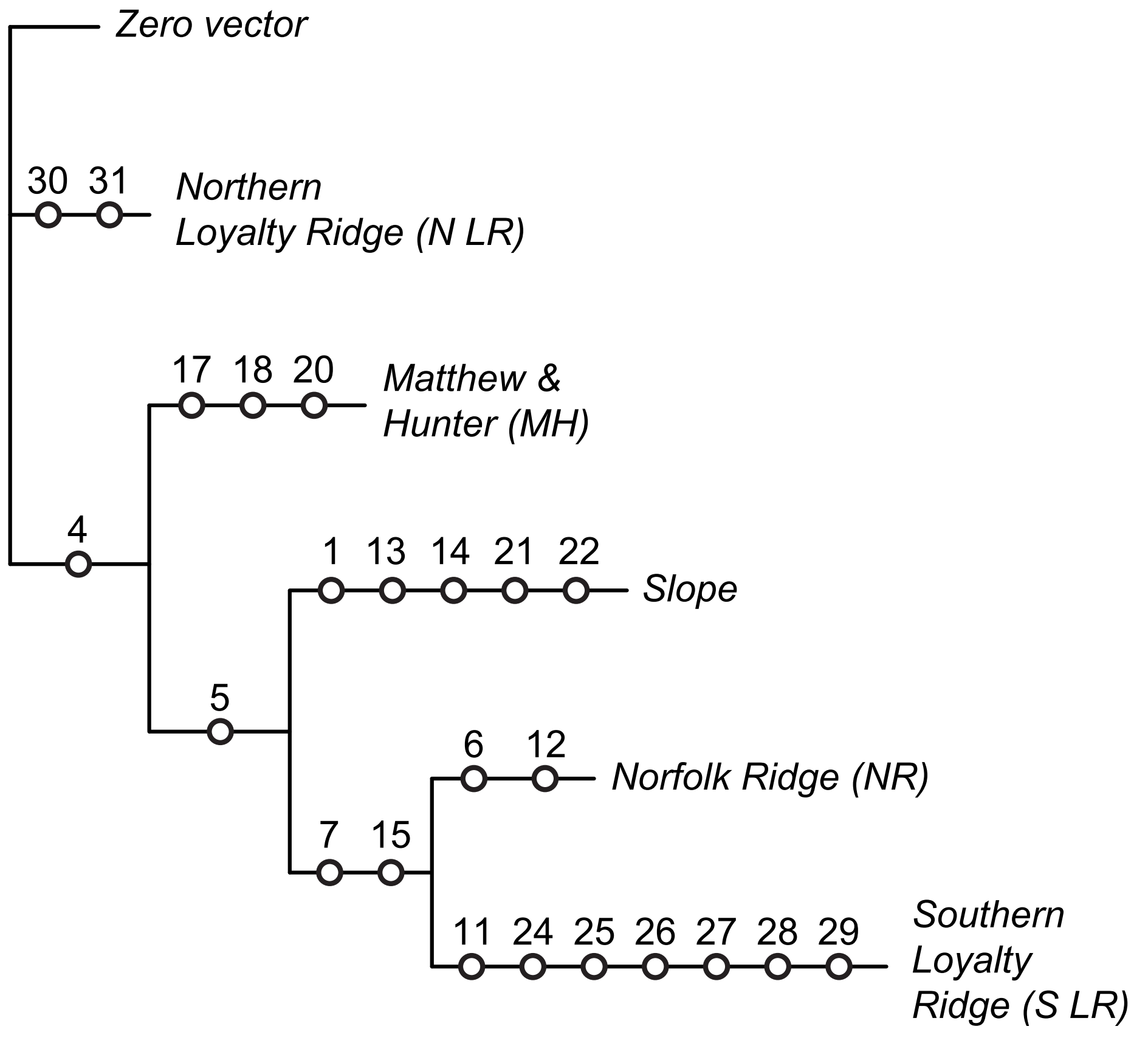

60
40
20
0
-20
-40
Latitude
120
160
-160
-120
-80
-40
0
Longitude
NES and CS
Norfolk and
Loyalty ridges
Thoma et al. (2009)
Pante et al. (2012)
This study

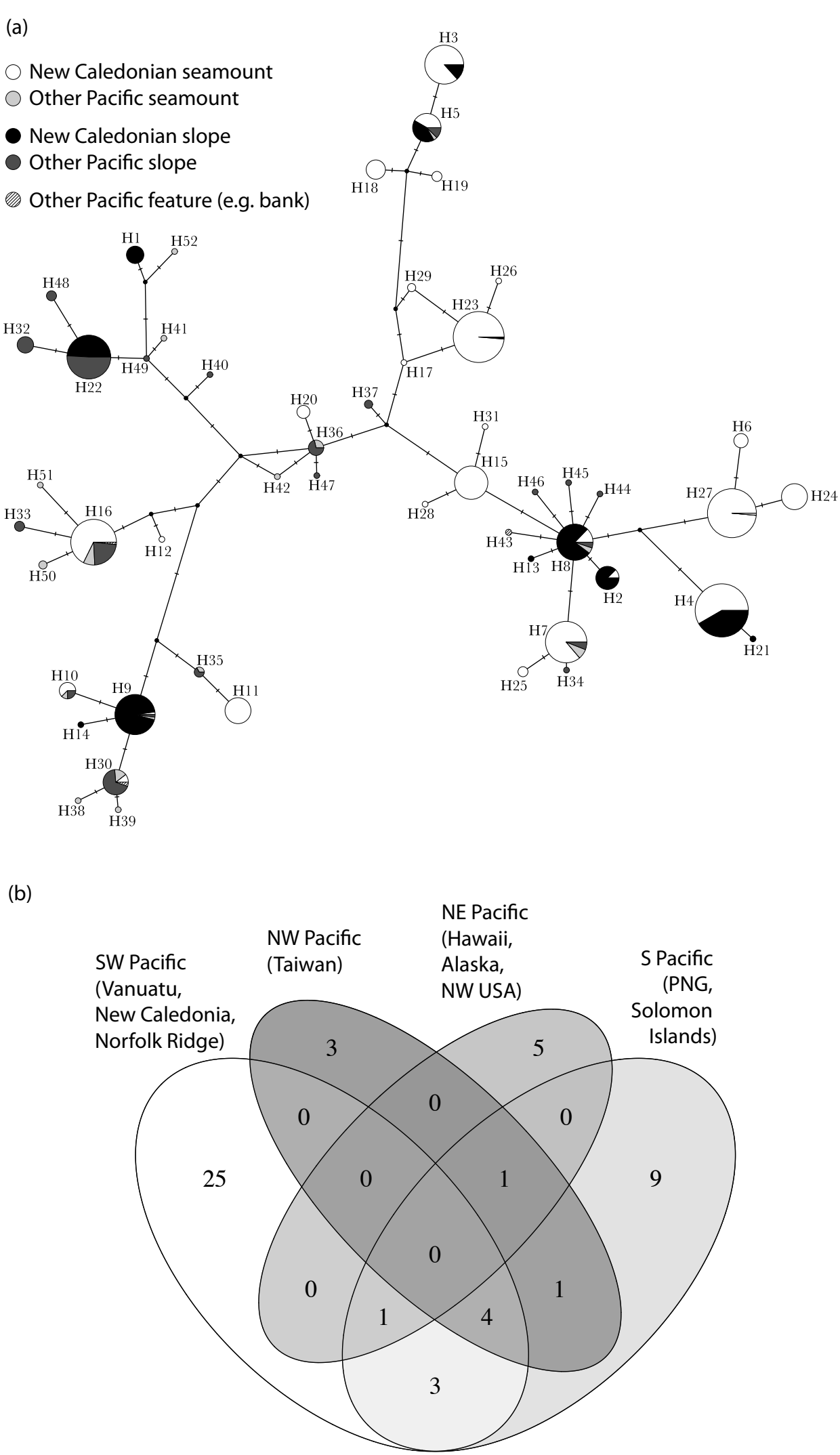

All *Terrasses* & *ExBoDi* stations
Stations with *Chrysogorgia*
100-3000 m
Pétrie (N LR)
6756
Astrolabe (N LR)
slope 3
slope 2
slope 1
Isle of Pines
Durand 2 (S LR)
Durand 1 (S LR)
Durand 3 (S LR)
Matthew Island
Hunter Island
Munida (NR)
Antigonia (NR)
Cryptothélia (NR)
Jumeau W (NR)
Mont J (S LR)
-19
-20
-21
-22
-23
-24
Latitude
164
166
168
170
172
Longitude


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
S LR
NR
MH
Slope
Depth (m)
0
-200
-400
-600
-800
-1000
-1200
n < 5
5 ≤ n < 10
10 ≤ n < 30
n ≥ 30
0
5
10
15
20
25
30
Haplotypes


(a)
Matthew & Hunter
(Matthew, Hunter)
Northern Loyalty Ridge
(Astrolabe, Pétrie)
Slope
(slope 1, 2, 3, Isle of Pines)
Norfolk Ridge
(Antigonia, Cryptothélia,
Jumeau W, Munida, Mont J)
Southern Loyalty Ridge
(Durand 1, 2, 3)
0.80
0.70
0.60
0.50
Jaccard's dissimilarity index
(b)
mean depth < 400
400 ≤ mean depth < 600
mean depth ≥ 600
Stress: 0.07
slope 3
279-466
Isle of Pines
180-590
Jumeau W
240-1120
Hunter
195-814
Mont J
750-990
Pétrie
362-604
Matthew
785-1095
slope 2
190-509
slope 1
320-500
Munida
150-450
Cryptothélia
200-570
Durand 2
360-560
Durand 3
350-388
Antigonia
300-320
Durand 1
240-357
Astrolabe
600-922
Coordinate 2
1.0
0.5
0.0
-0.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
Coordinate 1


Individual-scaled rarefaction
Sample-scaled rarefaction
Number of haplotypes
All stations (31)
Seamounts (26)
LR (20)
LR. S (15)
Slope (12)
MH (10)
LR. N (7)
NR (7)
Number of individuals
Number of sampling stations


Zero vector
30 31
Northern
Loyalty Ridge (N LR)
17 18 20
Matthew &
Hunter (MH)
4
1 13 14 21 22
Slope
5
6 12
Norfolk Ridge (NR)
7 15
11 24 25 26 27 28 29
Southern
Loyalty
Ridge (S LR)


(a)
New Caledonian seamount
Other Pacific seamount
New Caledonian slope
Other Pacific slope
Other Pacific feature (e.g. bank)
H3
H5
H18
H19
H1
H52
H48
H29
H26
H23
H32
H41
H49
H22
H40
H17
H20
H37
H36
H31
H6
H51
H42
H47
H15
H46
H45
H44
H27
H24
H33
H16
H28
H43
H12
H13
H8
H2
H4
H50
H7
H21
H35
H10
H9
H11
H25
H34
H14
H30
H38
H39
(b)
SW Pacific
(Vanuatu,
New Caledonia,
Norfolk Ridge)
NW Pacific
(Taiwan)
NE Pacific
(Hawaii,
Alaska,
NW USA)
S Pacific
(PNG,
Solomon
Islands)
3
5
0
0
0
25
0
1
9
0
0
1
1
4
3

Journal of Biogeography

SUPPORTING INFORMATION

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

Eric Pante, Scott C. France, Delphine Gey, Corinne Cruaud, and Sarah Samadi

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 Antigonia 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

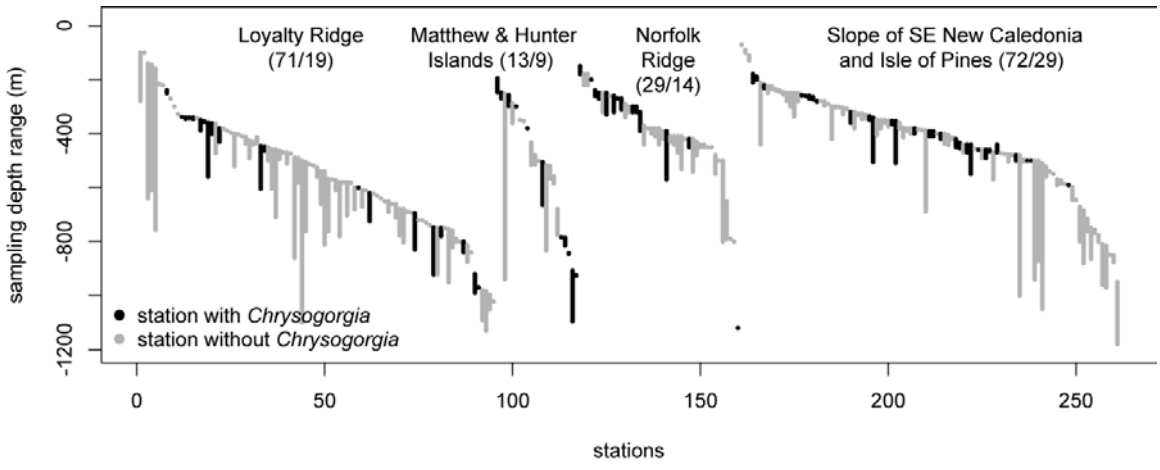


Figure S1 Bathymetric range of sampling stations for the *Terrasses* and *ExBoDi* cruises. Vertical segments connect the shallower and deeper sampling depths for each station. Shade represents the presence (black) or absence (grey) of *Chrysogorgia* at each station. The numbers of stations with/without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

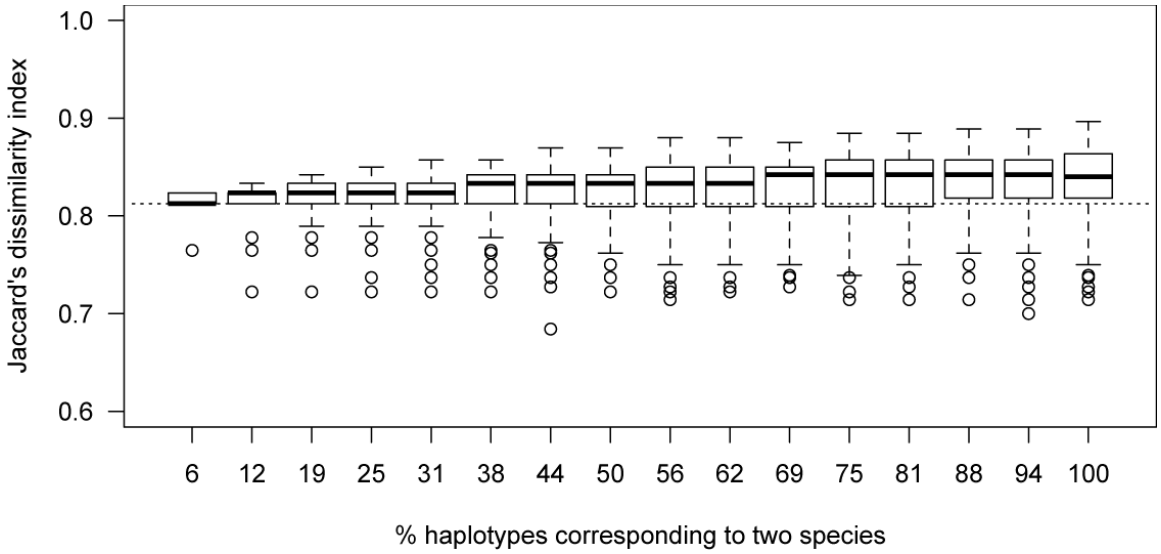


Figure S2 Results of the species simulation study comparing the slope of New Caledonia and the seamounts from the northern end of the Norfolk Ridge. Distributions (represented as box-and-whisker plots) of Jaccard's dissimilarity index (JI) when haplotypes (from 1 to 16) are split into two species of 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).