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# Mesophotic coral ecosystems of French Polynesia are hotspots of alpha and beta generic diversity for scleractinian assemblages

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## Abstract

**Aim:** Revealing how diversity varies across the depth gradient is key for understanding the role of mesophotic coral ecosystems in the functioning of coral reefs. We quantitatively examined how alpha and beta generic diversity of scleractinian coral assemblages vary across a wide depth gradient for coral reefs.

**Location:** Sixteen sites in eight islands of three archipelagos in French Polynesia.

**Methods:** We studied generic diversity patterns of scleractinian corals, as derived from the analysis of photo-quadrats, across the seafloor from shallow to lower mesophotic depths (6–120 m) and on a wide geographic scale. Our sampling considered quantitative coral cover to explore the patterns of alpha and beta components of diversity across depth and horizontal space.

**Results:** We show that in French Polynesia, mesophotic coral ecosystems host higher alpha and beta generic diversity than shallow reefs despite decreasing coral cover with depth. The variation of coral genus richness across the depth gradient is mainly driven by a mid-domain effect with a peak at 40 m depth. At the same time, we found that the differences in coral genera across islands (spatial beta-diversity) increased steadily along the depth gradient.

**Main conclusions:** Our findings report the first quantitative results of coral cover and diversity from mesophotic coral ecosystems in French Polynesia and also present one of the few existing studies to examine the broad breadth of the mesophotic depth gradient. We demonstrate that mesophotic depths can host unexpectedly high generic richness of scleractinian coral assemblages. At the same time, we showed that increasing depth increases the differences in generic diversity composition across islands, whereas shallow reefs are similar in between. While a single island could conserve shallow regional biodiversity, mesophotic depths containing the richest diversity

Valeriano Parravicini and Laetitia Hédouin contributed equally as joint senior authors.

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require site-specific measures, suggesting that considering these mesophotic depths in conservation is necessary to maintain regional diversity.

#### KEYWORDS

coral genus biodiversity, coral reefs, diversity patterns, mid-domain effect, quantitative ecology, regional diversity, scleractinian diversity

## 1 | INTRODUCTION

Mesophotic Coral Ecosystems (MCEs) are the deeper counterpart of shallow reef ecosystems. They are characterized by the presence of light-dependent corals from the order Scleractinia and occur in the tropical and subtropical oceans between 30 and 150 m depth, in the twilight ocean's photic zone (Ginsburg, 2007). Our knowledge of the diversity and community composition of coral reefs decreases steadily with increasing depth (Bongaerts et al., 2019; Pyle & Copus, 2019). This decrease is due to the many technical and logistical challenges involved in quantitative sampling beyond compressed air SCUBA (self-contained underwater breathing apparatus) diving frontiers at mesophotic depths (Kahng et al., 2014; Sinniger et al., 2016). However, advancements in underwater and diving technologies (including Remoted Operated Vehicles and closed-circuit rebreathers; Pyle, 2019) enabled the discovery that MCEs are more widespread and biodiverse in terms of coral diversity than previously expected (Englebert et al., 2017; Muir & Pichon, 2019; Muir et al., 2018; Rocha et al., 2018). Given the contribution of the mesophotic zone to the total area of reef ecosystems (Bridge et al., 2013; Eyal & Pinheiro, 2020; Laverick et al., 2018; Pyle & Copus, 2019), it is crucial to understand the biological diversity and composition of coral assemblages across the depth gradient, from the upper to the lower limits of photosynthetic Scleractinia. Also, there is a need to comprehend how these gradients vary across locations in this depth zone. The interest in finding such patterns lies on revealing key depths for conservation planning.

A quantitative understanding of the complementary patterns of biodiversity is a major prerequisite for testing ecological predictions and implementing conservation planning (Ferrier, 2002; Gaston, 2000; He, & Legendre, 2002; MacArthur, 1965; MacArthur & Wilson, 2016; Parravicini et al., 2013; Wang & Loreau, 2014). "Alpha ( $\alpha$ -diversity)" measures biological diversity within a community (Whittaker et al., 2001) and is useful in identifying biodiversity gradients. In contrast, the variation in composition between communities is called "beta ( $\beta$ -diversity)" or dissimilarity (Jost, 2007; Meynard et al., 2011; Tuomisto, 2010).  $\beta$ -diversity measures how many taxa are shared between communities or compositional changes from one reference point to another (Azalee et al., 2015; Harrison et al., 1992; Nekola & White, 1999). These indices allow the study of diversity gradients and assessments of species turnover across horizontal and vertical depth gradients (Fontana et al., 2020; da Silva et al., 2018; Swenson et al., 2011; Wang et al., 2012).

Thus far, the patterns of  $\alpha$ - and  $\beta$ -diversity of scleractinian corals across the entire depth gradient, from the upper to the lower limit of the photic zone, are little known and specific to a few locations. Diversity patterns of corals and fish have primarily focussed on the spatial variation in shallow communities with less attention to depth gradients (Bellwood & Hughes, 2001; Bellwood et al., 2005; Kusumoto et al., 2020; McDevitt-Irwin et al., 2021). Still, certain studies targeted depth gradients. Among others, some focused on fish (Beaman et al., 2016; Brokovich et al., 2008; Liddell et al., 1997; Rocha et al., 2018) and some on corals (Beaman et al., 2016; Englebert et al., 2017; Laverick et al., 2018; Madin et al., 2016; Muir & Pichon, 2019; Muir et al., 2018; Tamir et al., 2019). However, most studies, especially on corals, were based on qualitative observations, depth distribution ranges and literature. To the best of our knowledge, excluding bibliographic meta-analysis merging observations from studies with different depths and sites, only a few surveys quantitatively assessed coral richness gradients from the shallows to mesophotic depths beyond 30 m. These showed that coral richness increased to a certain depth, between 10 and 40 m across locations, and then decreased. These surveys were between 1 and 40 m depths (Bouchon, 1983), 1 and 50 m (Roberts et al., 2019; Roberts, Keith, et al., 2019), 1 and 60 m (Sheppard, 1980), 5 and 85 (Laverick et al., 2017), and only two studies beyond 100 m depth, for example, between 5 and 100 m (Tamir et al., 2019) and between 1 and 120 m (Liddell & Ohlhorst, 1988). Consequently, our understanding of reef functioning and conservation decisions is mainly based on data coming only from shallow coral reefs (Cinner et al., 2016; Hedley et al., 2016), with too few exceptions considering MCEs (e.g. lionfish control measures; Loya et al., 2019). This may be seen as a reasonable strategy because, as a general rule, coral cover decreases with depth (Hoeksema et al., 2017; Kahng et al., 2010; Laverick et al., 2017, 2020). However, if the goal is preserving coral diversity, which correlates with coral reef health and functioning of the whole reef system (Baskett et al., 2010; Benkwitt et al., 2020; Duffy, 2009), the potential contribution of MCEs should be accounted for.

The determination of gradients in  $\alpha$ -diversity is fundamental to understanding the ecological contribution of MCEs. At the same time, the assessment of vertical  $\beta$ -diversity along the depth gradient indicates potential taxonomic overlaps (or turnover) among coral assemblages at different depths (Laverick et al., 2018; Semmler et al., 2017). For instance, quantifying taxonomic turnover across the depth gradient is essential to test for a potential role of MCEs as a deep reef refuge (Bongaerts et al., 2010, 2019; Bongaerts & Smith, 2019).

Finally, the study of spatial  $\beta$ -diversity at given depths will inform the commonness and rarity of compositionally different communities within each site across depths and between different sites also across depths at regional scales. For all these reasons, the delineation of coral diversity patterns along the entire depth gradient seems critical to evaluate the inclusion of MCEs in future conservation planning (He, & Legendre, 2002; Kukkala & Moilanen, 2013; Margules & Pressey, 2000; McIntosh et al., 2017; Socolar et al., 2016).

In the present study, we assessed the diversity patterns of scleractinian corals along the depth gradient (bathymetric slope) and across spatial (geographic) scales in French Polynesia. We used a quantitative database (i.e. 2880 photo-quadrats from 6 to 120 m depth, from 16 sites of eight islands with distances from 45 up to 2000 km apart, covering sites across a total area of  $\sim 1,500,000$  km<sup>2</sup>) at the genus level, where sampling effort was equal (same number of photo-quadrats) all along the depth gradient. Our aims were to (1) map the depth profiles of coral cover, generic richness ( $\alpha$ -diversity) and generic dominance; (2) reveal the generic depth distribution; (3) assess the diversity patterns across the depth gradient to display overlaps and turnover in communities between depths ( $\beta$ -diversity within one site across depths); and (4) assess the spatial diversity patterns to display similarity and uniqueness between sites with depth ( $\beta$ -diversity at a given depth across sites).

## 2 | METHODS

Studying MCEs is challenging because of technical diving constraints (Pyle, 2019). Given our regional objectives, we selected the photo-quadrat technique as the best sampling strategy (Hill & Wilkinson, 2004). This passive high-definition image processing methodology allowed us to (1) keep a systematic sampling effort (Chen et al., 2021; Margules & Pressey, 2000) at any depth, independently of decompression diving limitations and (2) assess the genus diversity patterns of reef-building corals at any depth with the same observational bias. Using photo-quadrats allowed us to quantitatively assess coral communities down to 120 m depth but constrained us to accept collecting data at the genus level. We accepted this loss of taxonomic resolution because visual identification of corals to the species level remains complex in the field even through direct inspection. Additionally, previous studies have used similar generic diversity indexes to quantify  $\beta$ -diversity on coral assemblages (Ateweberhan & McClanahan, 2016) and to successfully inform conservation and management strategies (Darling et al., 2019; Hughes et al., 2018).

### 2.1 | Sampling

As part of the DEEPHOPE scientific expedition, we analysed 2880 photo-quadrats (0.75 × 0.75 m) from eight islands (Bora Bora, Makatea, Gambier, Moorea, Rangiroa, Raroia, Tahiti and Tikehau) from three archipelagos of French Polynesia collected from August

2018 to September 2019 (Figure S1; Table S1). All sites were located on outer slopes, and on each island, two sites were selected randomly within the constraints imposed by the logistics of technical diving. We collected these quadrats at the isobaths of 6, 20, 40, 60, 90 and 120 m depths in collaboration with the Under The Pole team using TRIMIX Closed Circuit Rebreather. We randomly placed four line transects of ten metres at each working depth at both sides of a reference point. We photographed ten quadrats on each line (leaving a constant of 25 cm in between quadrats to avoid superposition), resulting in at least 40 photo-quadrats at each depth. We analysed 30 randomly selected quadrats from the available pictures at each depth using the software Photoquad (Version 1.4; Trygonis & Sini, 2012). Photographs were taken with a Nikon D810 camera in Nautican Housing, with a 16mm lens, a 37.09-pixel high-definition resolution and two Keldan strobes. For each photo-quadrat, we quantified (i) the presence-absence of all scleractinian coral genera to account for rare and small genera and (ii) percentage coverage of scleractinian coral genera, as the proportion of points falling on each coral genus colony in a random stratified sampling point cloud of 75 points in each quadrat. When coral genera could not be identified, for instance, in juvenile corals, we classified them as “non-identified” scleractinian coral, and in cases of lack of visual taxonomic criterion, to the family level (e.g. some Fungiidae genera such as *Fungia*, *Danafungia* and *Lithophyllon* but not *Sandalolitha*, *Herpolitha* or *Pleuractis*). Generic identification was done following coral identification guides (Bosselle et al., 2014; Kelley, 2016) and previous training and supervision from taxonomic experts, who also carried out preliminary on-board identifications. Hereafter, we called the presence-absence data “composition” and the percentage of the coral cover data “coral cover” or “genus cover.” We chose 75 points following recommendations of the available literature on photo-quadrats (Roelfsema et al., 2021; Van Rein et al., 2011), and previous tests to confirm quadrats were thoroughly analysed. Total generic richness at each site and depth was the sum of all unique genera among 30 quadrats (i.e. the presence-absence of all genera for a constant sampling size of 16.8 m<sup>2</sup> of reef). The total percentage of coral cover at each quadrat was the proportion of points that fell on a scleractinian coral. The total percentage of coral cover at each site and depth was the mean (with standard error) among all 30 quadrats.

### 2.2 | Comparing diversity metrics at genus versus species level

To test whether genus level patterns of diversity were representative of species-level patterns, we calculated Pearson and Spearman correlations between these two taxonomic levels in three external open-access published databases (Roberts, Bridge, et al., 2019; Roberts, Keith, et al., 2019; Rocha et al., 2018; Figure S2). For all cases, we found high correlations  $>0.95$ , demonstrating that the genus level was highly representative of species level. Accordingly, we considered our results at the genus diversity patterns as a proxy

for the species diversity patterns (Balmford et al., 1996; Heino & Soininen, 2007).

### 2.3 | Depth variation in coral cover, $\alpha$ -diversity, dominance and distribution

We tested the relationship between coral cover and depth using Bayesian regression models (Table S2). In the model, the response variable was coral cover (as the proportion of points falling on a coral according to the total number of points (trials)). The predictor was depth as a numeric variable. The model specified random intercepts for each site (1|site) and used the Binomial family with the R package “brms” (Bürkner, 2017). The model converged ( $R^2 = .542$ ,  $R_{hat} = 1$ ) with two chains accounting for 4000 iterations after discarding 1000 iterations. In the special case of generic richness, we tested for a mid-domain effect (MDE) to explain the humped relationship with depth. The mid-domain effect is defined as the peak of richness where the increasing overlap of species is found towards the centre (Colwell & Lees, 2000). For the test, we used a simulation ( $n = 10,000$ ) Range Cohesion Model for Ordered Data computed with the R package “rangemodelR” (Colwell, 2008; Gotelli et al., 2009). Finally, we mapped the average relative genus dominance in community structure with depth and the depth distribution of coral genera based on presence-absence within and across locations to help to interpret our results.

### 2.4 | Depth variation of communities (vertical $\beta$ -diversity)

In order to evaluate the vertical  $\beta$ -diversity among depths, we computed complementary indices between all depths in each site (Anderson et al., 2006; Legendre & De Cáceres, 2013). We calculated two dissimilarity indices: Jaccard dissimilarity accounting only for genus presence-absence (i.e. each genus has the same weight; Baselga, 2012; Koleff et al., 2003) and Bray-Curtis dissimilarity accounting for genus cover (i.e. each genus has a different weight according to percentage coverage; Baselga, 2017). If dissimilarity in genera is high, dissimilarity in species can only be higher. Jaccard is close to 0 when communities host the same genera, and it increases when the proportion of unique genera to one of the two communities increases. Bray-Curtis dissimilarity is close to 0 when communities are dominated by the same genera and tends to 1 when the most abundant genera are different. Yet, both indices account for differences in richness (i.e. two communities cannot share more genera than the minimum number of genera present in both communities) and genus cover. Thus, we computed for each of these  $\beta$ -diversity indices the contribution of its turnover component (i.e. independent from differences in richness or genus cover; Baselga, 2010, 2013, 2017; Baselga & Orme, 2012) as the ratio between turnover and dissimilarity (Toussaint et al., 2014). A turnover ratio close to 1 means pure turnover, indicating that the dissimilarity is driven only by the

replacement of genera along the depth gradient (without changes in richness). Conversely, a turnover ratio close to 0 implies no turnover, indicating that the dissimilarity is driven only by differences in richness (poorest communities hosting a subset of the genera present in the richest ones). We plotted the average results, for all our sites, with a heat map representing the values between different depths.

### 2.5 | Spatial variation of communities (spatial $\beta$ -diversity)

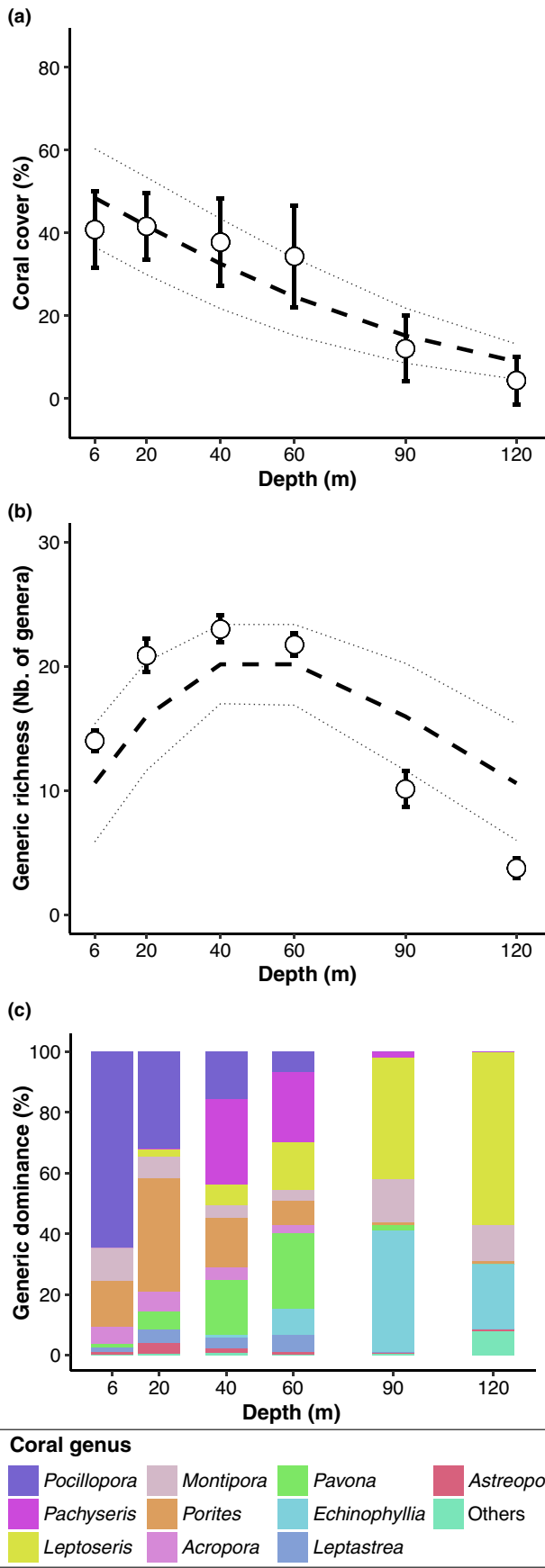
We measured the values of spatial  $\beta$ -diversity for each depth and the contribution of the turnover component with the same methodology used for the depth dissimilarity gradient. Next, we tested the multivariate homogeneity and dispersion of spatial  $\beta$ -diversity at the different given depths (Anderson, 2006; Anderson et al., 2006) and the effect of depth using  $p$ -values with the R package “vegan” (Oksanen et al., 2013). We then applied linear regressions (Linear Models, LM) to test and quantify the variation of  $\beta$ -diversity with increasing depth. Additionally, we tested if the geographical distance between sites could explain dispersion patterns at the different depths using Mantel tests (Legendre & Legendre, 2012; Oksanen et al., 2013). Finally, we performed a non-metric multidimensional scaling (NMDS; Kruskal, 1964a, 1964b) with the R package “vegan” (Oksanen et al., 2013) and presented ordination results to visualize spatial generic composition differences between locations for given depths. We created convex hull polygons by depth, the area of which reflected  $\beta$ -diversity. We made all analyses (which statistical significance level of  $p$ -values was .05) and figures with RStudio (Version 1.3.959). Data and scripts are available in [Data Availability Statement](#).

## 3 | RESULTS

### 3.1 | Depth profiles of coral cover, generic richness and dominance

In general, and considering all locations, the percentage of coral cover decreased on average with depth (Bayesian [Population-Level effect = Depth]:  $\beta$ -slope =  $-0.02$ , l-95% CI =  $-0.02$ , u-95% CI =  $-0.02$ ,  $R_{hat} = 1.0$ , conditional  $R^2 = .542$  and marginal  $R^2 = .383$ ), and the fitted values of the model were similar to the observed ones (Figure 1a). However, despite this general trend, a few locations presented higher coral cover at mesophotic depths than shallow waters (e.g.  $81 \pm [SE = 7.7]\%$  of coral cover at 40 m vs.  $41.2 \pm 1.9\%$  at 6 m in Raroia;  $74.5 \pm 3.1\%$  at 60 m vs.  $55.2 \pm 3.4\%$  at 6 m in Gambier). Also, we sometimes found very high coral cover at lower mesophotic depths such as  $68.2 \pm 1.7\%$  in Bora Bora at 60 m;  $35.4 \pm 6.9\%$  and  $52.8 \pm 5.1\%$  in Makatea and Gambier, respectively, at 90 m; or  $42.0 \pm 4.2\%$  in Gambier at 120 m (Figure S3).

Generic richness displayed a humped relationship with depth, peaking at 40 m (between 20 and 60 m; Figure 1b). This pattern fits



**FIGURE 1** Coral depth gradient profiles. (a) Coral cover with depth. White dots indicate the mean values for all islands with 95% confidence intervals. Dashed lines indicate predicted values for the Bayesian regression model and dotted lines the standard deviations from the posterior distribution. Spatial variability of coral cover with depths across islands and sites is available in Figure S3. (b) Generic richness with depth. White dots indicate the mean values for all islands with standard errors. Dashed lines indicate predicted values for the mid-domain effect model and dotted lines are interquartile values of Q2.5 and Q97.5. Spatial variability of generic richness with depth across islands and sites is available in Figure S4. (c) Generic dominance of the main genera in community structure with depth. Main genera are considered if relative genus cover was above 5% at the site and depth. Relative percentages are the average within locations for each depth. Standard errors are not displayed, but spatial variability across locations is available in Figure S5. It displays that while particular genera largely dominate at some depths, other depths show a more balanced generic distribution

with that expected according to the mid-domain effect. Indeed, our simulations show that the generic richness of corals rarely deviates from the null expectation (Figure 1b). There were slight deviations between islands in the peak and limits of the mid-domain richness (Figure S4), but the observed maximum generic richness was always inside the upper mesophotic zone (40 m depth).

The generic dominance in coral community structure is distributed unequally along the depth gradient. While, on average, *Pocillopora* dominated the relative coral genus assemblages with over 70% at 6 m depth, other genera such as *Pachyseris* were less dominant with 31% and 28% at 40 and 60 m, respectively, or *Leptoseris* with 42% at 90 m depth. The sum of the top three dominant genera was over 92.2% at 6 m, 78.4% at 20 m, 65.1% at 40 m, 63.2% at 60 m, 91.5% at 90 m and 89.7% at 120 m (Figure 1c). The absence of dominant genera at 20, 40 and 60 m promoted more diverse communities. Genus dominance at certain depths was also evident within locations, but showed some spatial variability because the dominance of genera was not equally distributed across sites (Figure S5).

We identified 34 different coral genera across all the study sites. The depth distribution analysis showed that most of these genera were present below 30 m, especially at 40 m inside the mesophotic range (Figure 2). For instance, *Leptoseris*, *Porites* and *Montipora* were present in the entire depth range studied, qualifying as depth generalist genera. *Pocillopora*, a dominant genus of shallow reefs, was generally present down to 60 m depth and *Pachyseris*, a typical genus of mesophotic assemblages (Bongaerts et al., 2021), was present from 20 to 90 m. However, if we consider a threshold of multiple occurrences ( $\geq 15$  or 50), some rare genera had a slightly reduced depth distribution range (Figure S6). Finally, the depth zonation within sites showed less overlap but still showed that generalist coral genera can be present at all depths at particular locations (Figure S7).



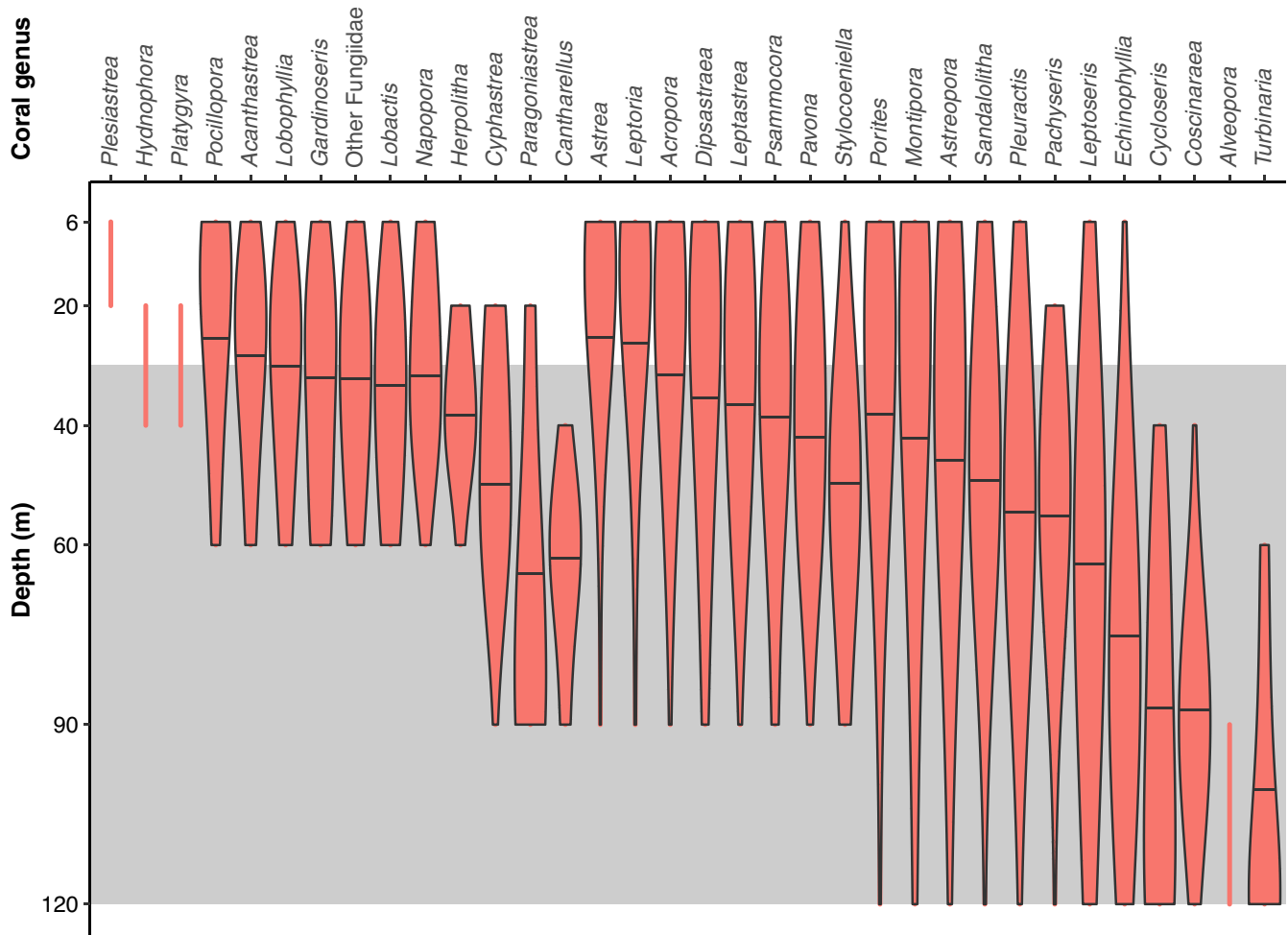


FIGURE 2 Depth distribution of the different genera pooled for the 16 study sites of French Polynesia. “Other Fungiidae” represents genus such as *Fungia*, *Danafungia* and *Lithophyllon* that could not be visually identified. Violin plots show presence–absence and quantiles the mean of the density estimate. The grey background highlights the mesophotic depth range as traditionally delimited (30–150 m). Depth overlaps are higher considering a single presence–absence than considering  $\geq 15$  observations or  $\geq 50$  observations (Figure S6) and pooling all sites together than separating between locations (Figure S7)

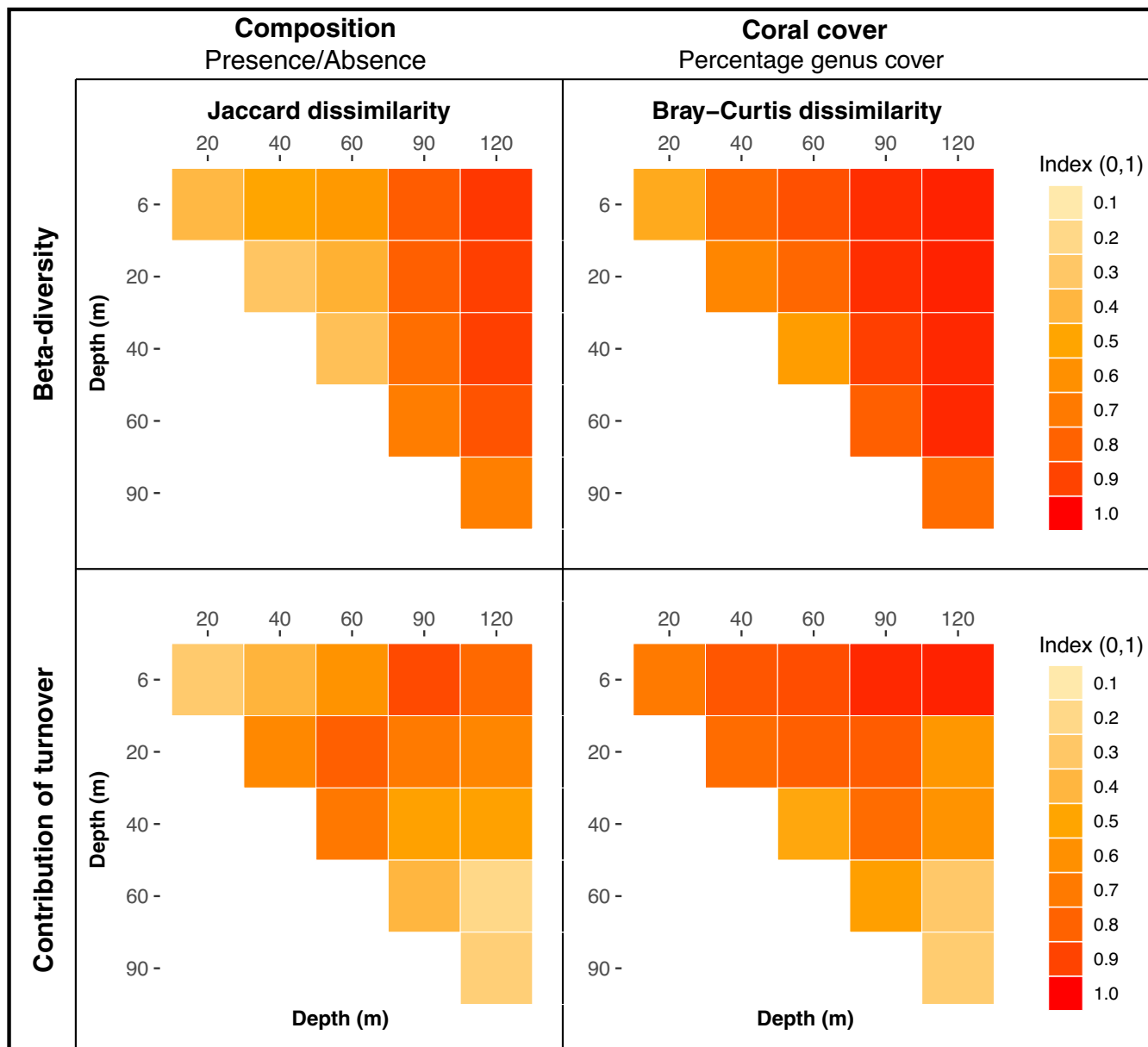
### 3.2 | Dissimilarity along the depth gradient

Both Jaccard (i.e. composition) and Bray–Curtis (i.e. coral cover) dissimilarity indices increased with differences in depth (Figure 3). The high dissimilarity between distant depths was explained mainly by turnover, meaning very few genera were shared between shallowest and deepest depths. The lower dissimilarity within shallow waters (6 and 20 m) and within deep waters (90 and 120 m) was paired with a lower contribution of the turnover, meaning that beyond differences in richness, both depths contained shared genera with the richest depths. Intermediate depths with the highest generic richness (20, 40 and 60 m) had lower dissimilarities (Jaccard  $< 0.6$ ) with shallow (6 m) assemblages than with deep mesophotic (90 and 120 m) assemblages (Jaccard  $> 0.8$ ). The contribution of turnover to the dissimilarity between shallow and mid-depth and between mid-depth and deep assemblages was moderate (0.4–0.6). Hence, distant depths had lower generic richness and hosted, unique genera in between, but genera also present in the

intermediate depths. Thus, intermediate depths shared genera with both shallow (6 m) and deep (90 and 120 m) assemblages (Figure 3; Figure S5).

### 3.3 | Spatial diversity patterns at different depths

We found an increase in  $\beta$ -diversity with depth in both the Jaccard (i.e. composition) and Bray–Curtis (i.e. coral cover) dissimilarity. This increase is represented by the sequentially larger area of the convex hull polygons in the NMDS plot along the depth gradient (Figure 4). While shallow-water communities were relatively similar between sites (small  $\beta$ -diversity), mesophotic assemblages were relatively unique at each site (high  $\beta$ -diversity). The visual impression in the increase of  $\beta$ -diversity with depth was statistically significant for Bray–Curtis (LM regressions: Jaccard =  $0.0022 \times \text{Depth} + 0.336$ ,  $R^2 = .58$ , Sig. = 0.1; and Bray–Curtis =  $0.0027 \times \text{Depth} + 0.5192$ , Sig. = 0.001,  $R^2 = .75$ ), but



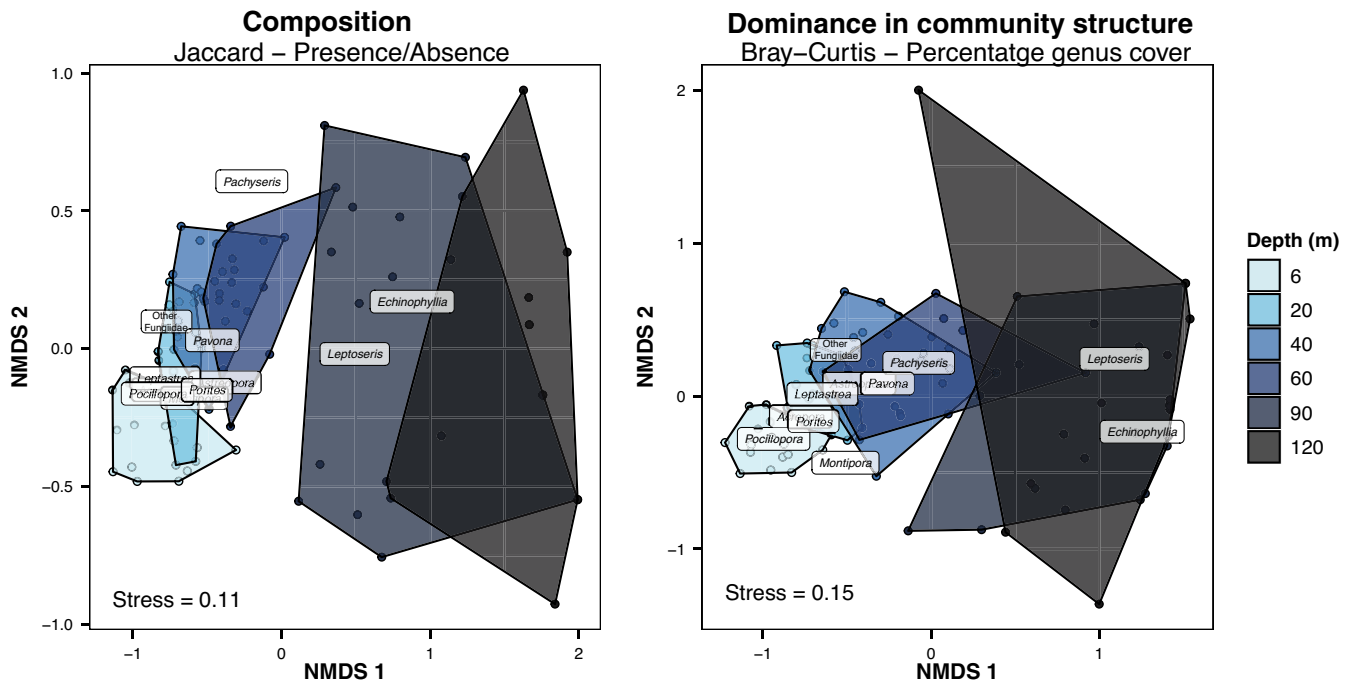
**FIGURE 3** Heat map displaying the vertical  $\beta$ -diversity along the depth gradient and the turnover within sites between depths. (Left) Jaccard dissimilarity for the presence-absence (i.e. composition) and the ratio of turnover. (Right) Bray-Curtis dissimilarity for the coral cover (i.e. percentage genus cover) and turnover ratio.  $\beta$ -diversity (0–1) near 1 means coral assemblages have different genera (or different dominant genera for Bray-Curtis) between the compared depths, while 0 means having the same genera. The contribution of turnover to dissimilarity (0–1) close to 1 means the dissimilarity is driven only by the replacement of genera along the depth gradient (i.e. without changes in richness). Conversely, close to 0 means the dissimilarity is driven only by differences in richness (i.e. poorest communities hosting a subset of the genera present in the richest one). Individual genus depth distributions are available for all and separate islands in [Figure 2](#) and [Figures S6](#) and [S7](#)

somehow consistent for composition and coral cover data. Geographical distance explained the high  $\beta$ -diversity with depth because we found significant correlations for mesophotic reefs (Jaccard at 60 m, Mantel.stat.r (Mantel) = 0.393, Sig. = 0.026 and at 120 m, Mantel = 0.466, Sig. = 0.01; and Bray-Curtis at 60 m, Mantel = 0.324, Sig. = 0.006, at 90 m, Mantel = 0.375, Sig. = 0.01 and at 120 m, Mantel = 0.359, Sig. = 0.022) but not in shallow waters (Sig. > 0.05; except for Bray-Curtis at 6 m, Mantel = 0.629, Sig. = 0.001; [Figure S8](#)).

#### 4 | DISCUSSION

The present study suggests that the depths between 20 and 60 m host a high ( $\alpha$ -diversity) and unique ( $\beta$ -diversity) generic diversity for scleractinian corals in French Polynesia. Our findings raise the importance of these depths for conservation based on the patterns of coral genus diversity obtained by the quantitative analysis of standardized photo-quadrats. Quantitative coral assemblage studies with identical sampling effort at each depth, which is an essential





**FIGURE 4** Spatial  $\beta$ -diversity patterns at different depths. (Left) dissimilarity in composition (Jaccard computed on generic presence-absence). (Right) dissimilarity in dominance in the coral community structure (Bray-Curtis computed on percentage of coral genera). Spatial  $\beta$ -diversity is reflected in the size of the hull polygons. Genus labels are present only for coral genera with a percentage cover higher than 5%. Points indicate the different sites for the given depth. The increase in spatial  $\beta$ -diversity means that while shallow waters between sites are homogeneous (similar in genus composition and genus cover), mesophotic depths are unique (in composition and genus cover including for the dominant genera)

prerequisite for studying diversity patterns (Chen et al., 2021) and over such a wide depth range (6–120 m), are rare worldwide in MCE literature (Bongaerts et al., 2019; Roberts, Bridge, et al., 2019; but see: Liddell & Ohlhorst, 1988; Tamir et al., 2019), and novel for French Polynesia (Pichon, 2019).

Overall, our patterns revealed that the depths around 40 m host the highest richness ( $\alpha$ -diversity) of coral genera. According to our analysis, this is mainly due to a mid-domain effect (MDE) along the depth gradient, where the richness and overlap converge towards the centre (Colwell & Lees, 2000), similarly to available studies on fish communities (Brokovich et al., 2008). More precisely, the peak in the richness of coral genera seems to be generated by the range overlap of assemblages typical of shallow and deep communities. This high richness mid-domain is present despite the fact that, in general, coral cover decreased with depth as previously expected for light-dependent scleractinian corals (Kahng et al., 2010; Kahng & Kelley, 2007; Laverick et al., 2020). Also, our results showed that coral cover generally decreased with depth, but at some sites, it was as high or even higher in the 40 and 60 m zone than on the shallows (e.g. 81% at 40 m or 70% at 60 m; Figure S3). These high cover values are unexpected for the light dependency of scleractinian corals (Kahng et al., 2019) but similar to other locations in the Indo-Pacific at such depths (Hopley et al., 2007; Kahng & Kelley, 2007). In any case, the importance here is that the role of the communities between 20 and 60 m may be a zone of transition between shallow and mesophotic coral genus communities as supported by the  $\beta$ -diversity

pattern across the depth gradient, which highlights a moderate overlap of this mid-zone with communities at both 6 and 120 m depth.

A hypothesis to explain the humped relationship between genus richness and depth could be that the sum of disturbances seems to be relatively more intense and frequent (chronic) at shallow depths than in MCEs (Smith et al., 2019), especially for global disturbances such as thermal bleaching events (Baird et al., 2018; Pérez-Rosales, Rouzé, et al., 2021). However, our patterns are similar across multiple locations (Figure S3) and comparable with previous studies conducted elsewhere with quantitative techniques but on narrower depth gradients (Bouchon, 1978; Laverick et al., 2017; Liddell & Ohlhorst, 1988; Loya, 1972; Roberts, Bridge, et al., 2019; Roberts, Keith, et al., 2019; Sheppard, 1980; Tamir et al., 2019). For instance, our findings at 40 m are similar to Tamir et al. (2019) in surveys down to 100 m in the Red Sea. Slightly deeper than 30 m, found by Loya (1972) in the Red Sea, where sampling stopped, Bouchon (1978) in La Reunion Islands, in surveys down to 40 m, and Liddell and Ohlhorst (1988) in Jamaica, in surveys down to 120 m. On the contrary, our findings are deeper than Roberts, Bridge, et al. (2019) and Roberts, Keith, et al. (2019) at 20 m in Papua New Guinea, in surveys down to 50 m depth, Sheppard (1980) also at 20 m in the Chagos Archipelago, in surveys down to 60, and finally, Laverick et al. (2017) at 10 m in Honduras, in surveys down to 85 m depth. Moreover, the analyses of available time series in French Polynesia (SO CORAIL, Polynesia Mana) reveal that generic coral richness in shallow waters did not decline

substantially in the last 15 years, despite important changes in the composition of coral assemblages (Figure S9; Moritz et al., 2021; Pérez-Rosales, Brandl, et al., 2021; Tsounis & Edmunds, 2016). Similar to the time series with *Pocillopora* emerging as the new dominant genus (from <50% in 2005 to >70% in 2018 of coral composition), we also found this particular dominance in shallow waters (between 30 and 90% at 6 m; Figure 1c). However, we did not find this dominance in mesophotic depths, with *Pocillopora* contributing between 0% and 50% of composition at 40 and 60 m, potentially allowing extra space for a higher richness. Therefore, we suggest that the deeper peak of genus richness found in this study compared to that reported in the literature for other locations might be attributed to (i) the optimal conditions for light-dependent corals in the crystal clear waters of French Polynesia (Pichon, 2019; Pichon et al., 2021); (ii) a slight bias between genus and species-level analyses (but see Methods—*Comparing diversity metrics at genus vs species level*); (iii) the wide depth range considered in our study or (iv) the higher diversity allowed because of the lack of more highly competitive genus.

The spatial analysis along the reef slope reveals an increase in  $\beta$ -diversity with depth. This increase suggests that when comparing sites, shallow-water assemblages are similar in composition but deeper assemblages, at mesophotic depths, differ from site to site. This mismatch in  $\beta$ -diversity patterns between shallow and mesophotic depths challenges our perception of conservation needs. The low  $\beta$ -diversity in shallow waters suggests that the protection of a single location, if large enough, may be effective in protecting regional diversity. In contrast, for the high  $\beta$ -diversity of mesophotic coral ecosystems, we may need the protection of multiple sites because each site at these depths seems unique. Such a mismatch adds complexity to the Single Large Or Several Small (SLOSS) debate about establishing Marine Protected Areas (Diamond, 1975; Fahrig, 2017, 2020), with the same ecosystems requiring different protection strategies at different depths. This finding also suggests that we could protect all coral genera present along the depth gradient by deciding the protected locations according to the condition of these transition zone.

Our approach based on photo-quadrats has intrinsic limitations, the most evident being the relatively coarse taxonomic resolution. However, diving constraints limit our capacity to perform sampling techniques that require extended time at mesophotic depths (Pyle, 2019). The method of photo-quadrats represents one of the best compromises to obtain standardized sampling effort and adequate replication across the depth gradient (Hill & Wilkinson, 2004). In addition, we showed that genus and species levels are highly correlated (Figure S2); Heino & Soininen, 2007; Jimenez et al., 2010), and we carefully considered results only when correct for both taxonomic levels. We emphasize the need for caution with the interpretation of similarity patterns at the genus level because whether these also hold at the species or genetic level is unclear (Bongaerts et al., 2017, 2021). In any case, potential misidentifications, regardless of the taxonomic level, were systematic because all quadrats were analysed by a

single observer, and therefore, they should not modify the general patterns we found. Even at the genus level and specific to the fore reefs of French Polynesia, our results are pioneering and increase the knowledge of understudied MCEs (Turner et al., 2019), setting the starting point for future studies in this little-known region of the Southern Central Pacific. Lastly and most importantly, our photo-quadrats strategy corrected the associated problems of uneven sampling design studies (i.e. built from depth distributions of observations and scientific literature) with significant differences in sampling effort between well-studied shallow depths and poorly studied mesophotic depths (Bongaerts et al., 2019; Pyle & Copus, 2019). Additionally, all our interpretations came from the complementarity of  $\alpha$ - and  $\beta$ -diversity (with composition and coral cover) patterns that highlight the robustness of our results.

In this study, we provide new perspectives that if we seek to preserve the regional coral genus biodiversity of shallow and mesophotic reefs in French Polynesia, the depths between 20 and 60 m are an important area from a systematic conservation perspective (Kukkala & Moilanen, 2013; Margules & Pressey, 2000; McIntosh et al., 2017; Myers et al., 2000). Indeed, this zone hosts the highest coral generic richness and the coral genus assemblages typical of both ranges, the shallow and deep; thus, it could act as a safeguard of biodiversity. In conclusion, we suggest that conservation planning for coral reefs cannot ignore and should account for MCEs (Bridge et al., 2013; Kahng et al., 2016; Pyle & Copus, 2019; Soares et al., 2020) and consider multiple locations because each is spatially unique in their coral composition. The high  $\alpha$ - and  $\beta$ -diversity of mesophotic coral ecosystems highlights how they may be crucial for preserving coral biodiversity and coral reef ecosystems as a whole. This is particularly relevant in the light of ever-increasing human pressures and climate change effects, which seem to be less severe with increasing depth.

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## CONFLICT OF INTEREST

All authors had no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

All analyses, scripts and data necessary to replicate this study are at Github: [https://github.com/gonzalopr/Diversity\\_with\\_Depth](https://github.com/gonzalopr/Diversity_with_Depth) and

at Dryad Data: <https://datadryad.org/stash/dataset/doi:10.5061/dryad.rjdfn2zc7>

## PEER REVIEW

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## BIOSKETCH

Our team of researchers has benefited from diving and logistic assistance provided by the Under The Pole team to study the Mesophotic Coral Ecosystems of French Polynesia. Under the project name DEEPHOPE (Agence Nationale de la Recherche), our interdisciplinary team combined taxonomists, geneticists, biologists, ecologists, etc., to test—in the present manuscript—the patterns of scleractinian coral genus diversity across an unprecedented depth range.

**Gonzalo Pérez-Rosales** is an oceanographer, marine biologist and quantitative ecologist. After a BSc in Marine Science—Oceanography in the Canary Islands, he moved to Australia and became astonished by the world of Coral Reefs. He finished an MSc in Biodiversity and Environmental Management of Coral Reefs between France and French Polynesia. Currently, he is a PhD candidate entitled *Diving deep on the reef slopes in French Polynesia: new insights into mesophotic coral ecosystems* at the CRIOBE. His ultimate goal is to provide empirical research and tools for science-based conservation planning for the future of the oceans and coral reefs with global changes.

Author contributions: G.P.-R. and V.P. conceived the research study with inputs from M.P., S.V., H.R., P.B. and L.H.; G.P.-R., U.T.P.C., M.P. and H.R. collected the data; G.P.-R. analysed the data with guidance from V.P. and inputs from S.V.; G.P.-R. drafted the manuscript; all authors revised and approved the manuscript; L.H. obtained the funding.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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