Niche differences in co-occurring cryptic coral species (*Pocillopora* spp.)

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Abstract

Cryptic species that are morphologically similar co-occur because either the rate of competitive exclusion is very slow, or because they are not, in fact, ecologically similar. The processes that maintain cryptic local diversity may, therefore, be particularly subtle and difficult to identify. Here, we uncover differences among several cryptic species in their relative abundance across a depth gradient within a dominant and ecologically important genus of hard coral, *Pocillopora*. From extensive sampling unbiased towards morphological characters, at multiple depths on the fore reef around the island of Mo'orea, French Polynesia, we genetically identified 673 colonies in the *Pocillopora* species complex. We identified 14 mitochondrial Open Reading Frame haplotypes (mtORFs, a well-studied and informative species marker used for pocilloporids), which included at least six nominal species, and uncovered differences among haplotypes in their relative abundance at 5, 10, and 20 m at four sites around the island. Differences in relative haplotype abundance across depths were greater than differences among sites separated by several kilometers. The four most abundant species are often visibly indistinguishable at the gross colony level, yet they exhibited stark differences in their associations with light irradiance and daily water temperature variance. The pattern of community composition was associated with frequent cooling in deeper versus shallower water more than warmer temperatures in shallow water. Our results indicate that these cryptic species are not all ecologically similar. The differential abundance of *Pocillopora* cryptic species across depth should promote their coexistence at the reef scale, as well as promote resilience through response diversity.

Keywords: Depth, internal waves, niche partitioning, Mo'orea, temperature variance

Introduction

Understanding the mechanisms that give rise to, and maintain, biodiversity allows for better predictions of how communities respond to natural and anthropogenic disturbance (Levin and Lubchenco 2008). Molecular phylogenetic studies frequently identify the co-occurrence of cryptic species (Bickford et al. 2007; Bongaerts et al. 2021), which would not be expected to coexist if they were truly ecologically similar and competing for the same limiting resource (Zhang et al. 2004; McPeek and Gomulkiewicz 2005). Studying co-occurring cryptic species provides the opportunity to discover biological differences among cryptic species beyond morphological characters, and how such differences arise and influence community response to environmental change.

Niche partitioning among cryptic species may be particularly subtle, and difficult to identify in natural communities. Much of the theory of species coexistence is based on competition, where species coexist via the relative strength of two fundamental classes of mechanisms (Chesson 2000): equalizing and stabilizing processes. Processes that equalize frequency-independent fitness differences between species slow competitive exclusion. Compared to non-cryptic species, cryptic species are likely to be ecologically more similar, so may co-occur simply because the rate of competitive exclusion is slow enough to permit them to persist for substantial periods of time before one species eventually dominates (McPeek and Gomulkiewicz 2005). Species coexist in the long-term due to stabilizing processes, where competition causes species to limit themselves more than their competitors (i.e., intraspecific competition > interspecific competition). Niche, or resource, partitioning is an important and common stabilizing mechanism (Chesson 2000), in addition to asynchronous fluctuations in population dynamics (Snyder and Chesson 2004), environmental fluctuations (De Meester et al.

2011; Montero-Pau et al. 2011), differences in dispersal (Berkley et al. 2010; Bode et al. 2011; Boulay et al. 2014; Daly et al. 2021) and density-dependent mate competition (Levitan 2004; Zhang et al. 2004). Importantly, equalizing effects modify the magnitude of stabilizing effects needed for coexistence. If cryptic species, being morphologically indistinguishable, are ecologically similar, there will be smaller fitness differences between them and less niche partitioning will be required to promote their coexistence (Mayfield and Levine 2010). Thus, only very subtle niche differences among cryptic species are required for their coexistence.

Scleractinian corals, the foundation species that build diverse coral reefs, are notorious for containing high species diversity and cryptic species (Knowlton et al. 1992; Pinzón et al. 2013; Schmidt-Roach et al. 2013; Richards et al. 2016; Gélin et al. 2017; Bongaerts et al. 2021; Prada and Hellberg 2021). Explanations for why such species commonly co-occur at fine scales, such as on the same reef, remain elusive. Part of the problem is that the few studies on cryptic species distribution have focused mostly on one morphological type across environmental gradients (e.g., Levitan et al. 2011, Warner et al. 2015, De Palmas et al. 2018, Johnston et al. 2018). However, the highly plastic morphology exhibited by scleractinians allows species to modify their skeletal structure in response to changes in environmental conditions (Todd 2008), which allows genetically identified species to shift between morphospecies (Paz-García et al. 2015a). That is, while a morphological species can contain multiple genetic species (Edmunds et al. 2016; De Palmas et al. 2018), individuals from the same genetic species can also look like individuals from different morphological species (Pinzón et al. 2013; Marti-Puig et al. 2014; Paz-García et al. 2015a; Edmunds et al. 2016; Gómez- Corrales and Prada 2020). Thus, studying the co-occurrence of cryptic species across environmental gradients requires that samples collected for genetic analysis in order to identify species be sampled without regards to

morphology. Furthermore, environmental gradients across depths in particular, are hypothesized to be an important factor causing divergence among scleractinian cryptic marine species (Knowlton et al. 1992; Prada and Hellberg 2021).

At Mo'orea, French Polynesia, *Pocillopora* colonies dominate the fore reef substratum, and multiple morphologies commonly co-occur and include both geographically widespread and endemic species (Forsman et al. 2013). *Pocillopora* species on the fore reef are all species that are considered to reproduce via broadcast spawning (Bouwmeester et al. 2011; Schmidt-Roach et al. 2012). The brooding species, *P. damicornis* and *P. acuta*, have not been seen or sampled on the fore reef of Mo'orea (Burgess et al. 2021). Gross colony morphology is an unreliable indicator of species (Marti-Puig et al. 2014; Paz-García et al. 2015b), but species can be identified genetically (Flot et al. 2008; Schmidt-Roach et al. 2014; Gélin et al., 2017; Johnston et al. 2017).

The near complete loss of live coral (<5% cover at all fore reef sites around Mo'orea) after several major disturbances ending in 2010 (Adam et al. 2011), and subsequently high *Pocillopora* recruitment and colony growth into vacant space in the following years (Tsounis and Edmunds 2016), provides a unique context with which to examine the role of depth in structuring *Pocillopora* community composition because observed abundance patterns nine years later will reflect the net outcomes of recruitment, growth, and survival, and not differences in disturbance history. Our goals were to: 1) sample *Pocillopora* without regards to morphology and quantify the relative abundance of cryptic genetic lineages across depths at multiple sites on the fore reef around Mo'orea, and 2) identify the relative contribution of different aspects of the temperature and light regimes in potentially explaining differences in community composition across depths and sites. We hypothesized that the relative abundance of cryptic species would differ across

depths. We also hypothesized that the community composition would differ more among depths within sites than they would vary among sites separated by several kilometers if environmental conditions vary across depths more than across sites. Differences in the relative abundance of cryptic species across depths would allow ecologically similar species to co-exist at the reef scale by increasing the potential effect of intraspecific competition on population size compared to interspecific competition, or simply because of different responses among cryptic species to environmental conditions.

Materials and Methods

Description of the Pocillopora *species complex.*

Corals in the genus *Pocillopora*, which dominate reefs throughout much of the Indo-Pacific, contain separately evolving, genetically distinct lineages that are 'hidden' by morphological similarity and plasticity. *Pocillopora* species can be delineated using the mitochondrial open reading frame marker (mtORF, a gene which may play a role in the adaptive response to environmental changes in pocilloporids (Banguera-Hinestroza et al. 2019)) (Johnston et al. 2017), with the exception of *P. meandrina* and *P. eydouxi*, which can be differentiated via a restriction fragment length polymorphism (RFLP) assay of the Histone 3 region (Johnston et al. 2018). The ability to use the mtORF marker and the RFLP assay to delineate species is based on previous analyses comparing multiple genomic markers. In previous phylogenetic analyses, Johnston et al. (2017) found strong concordance between holobiont metagenomic data, transcriptomic data, near complete mitochondrial genomes, and 430 unlinked biallelic SNPs, and identified mtORF haplotype 1a - *P. eydouxi*, haplotype 1a - *P. meandrina*, haplotype 2 (*P.* cf. *effusus*), haplotype 3b (belonging to *P. verrucosa*), haplotype 6a

(*P. ligulata*), haplotype 4 (*P. damicornis*), and haplotype 5 (*P. acuta*) as nominal species. The strong concordance between these datasets and a time-calibrated phylogeny of mitochondrial protein coding regions provide clear evidence of reciprocal monophyly with no evidence for hybridization or incomplete lineage sorting for all but the two youngest sister species, *P. damicornis* and *P. acuta* (which do not occur in our dataset) (Johnston et al. 2017). Using the mtORF marker, Pinzón et al. (2013) identified haplotype 8a as a distinct lineage and Gélin et al. (2017) identified mtORF haplotype 8a as a nominal species using two mitochondrial markers, a nuclear marker, and 13 microsatellites. mtORF haplotype identification follows Pinzón et al. (2013) and Forsman et al. (2013), and species names associated with each mtORF haplotype follows Schmidt-Roach et al. (2014).

Sampling design

In August 2019, we sampled *Pocillopora* colonies from three depths (5, 10, and 20m) at each of four sites (sites 1, 2, 4, and 5) on the fore reef of Mo'orea (Fig. 1). Site locations and names correspond to that used by the Mo'orea Coral Reef Long-Term Ecological Research (MCR-LTER) program (Holbrook et al. 2018). At each site, the sampling locations for each depth were separated by horizontal distances in the order of 10's of meters. At each depth at each site, 10-15 50 × 50 cm quadrats were randomly placed on the reef along the target depth contour until approximately 50 colonies had been sampled. Tissue from all *Pocillopora* colonies within the quadrat was sampled. Unlike previous studies, we did not target specific morphologies (Edmunds et al 2016; De Palmas et al 2018). The number of *Pocillopora* colonies sampled at each depth at each site ranged from 37 to 83 (Table 1). Tissue was collected from a total of 673 *Pocillopora* colonies. Tissue (~ 5 mm diameter) was collected using small bone clippers, stored

in salt-saturated dimethyl sulfoxide (DMSO) buffer (Gaither et al. 2011), and transported to Florida State University for further processing.

Genetic analysis and identification of genetic lineages

Genomic DNA was extracted from tissues using Chelex 100 (Bio-Rad, USA). Samples were incubated in 150 μL of 10% Chelex 100 for 60 mins at 55°C followed by 15 mins at 95°C. The supernatant was then used for PCR amplification using the mitochondrial Open Reading Frame (mtORF) marker (Flot & Tillier, 2007). For the two species that cannot be differentiated using this marker, *P. meandrina* and *P. eydouxi*, we used a restriction fragment length polymorphism (RFLP) gel-based assay to distinguish the two following Johnston et al. (2018). In GENEIOUS v.9.1.8 (Biomatters), forward mtORF sequences (855bp) were aligned and samples were identified to haplotype based on previously published sequences of mtORF haplotypes, using the naming conventions in Forsman et al. (2013) and Pinzón et al. (2013). We used the R software package *pegas* (Paradis 2010) to construct the haplotype network.

Environmental data

We derived seven environmental variables related to sea water temperature and light regimes at each site and depth (Fig. 1b – g):

1) the mean of the maximum daily sea water temperature from June to November ('Max Daily Temp (Jun-Nov)'),

2) the mean of the maximum daily sea water temperature from December to May ('Max Daily Temp (Dec-May)'),

3) the mean of the minimum daily sea water temperature from December to May ('Min Daily Temp'),

4) the mean of the daily sea water temperature variance from December to May ('Temp Variance [Mean]'),

5) the maximum of the daily sea water temperature variance from December to May ('Temp Variance [Max]'),

6) the mean photosynthetically active radiation (PAR) from December to February ('Mean Light'), and

7) the minimum PAR from December to February ('Min Light').

The sea water temperature regimes at 10 m and 20 m were quantified based on the *in situ* time series (2005 – 2019) collected at 2 min intervals as part of the MCR-LTER program (http://mcrlter.msi.ucsb.edu/data/variable/) using Seabird Electronics SBE39 and SBE56 temperature recorders (0.002 °C accuracy, 0.0001 °C resolution, < 10 s response time) mounted onto plates directly affixed to the reef surface. Sea water temperatures for 5 m depth, where there were no loggers, were derived for each site based on SST and the diurnal and semi-diurnal variance observed at 2-min intervals in the backreef at 2 m and the fore reef at 10 m. Daily average sea water temperatures at each depth was closely related to sea surface temperature (SST), with SST explaining between 90-94%, 92-94%, 91-93%, 86-87%, and 78-80% of the daily temperature variation at 2, 10, 20, 30 and 40 m, respectively. This allowed the derivation of daily average sea water temperatures for 5 m depths at each site based on strong (r^2 of 0.988-0.995) relationships describing changes in the SST-in situ relationships across depths. Daily average sea water temperatures at 5 m were interpolated onto a 2-min grid and realistic variability superimposed based on the time series of semi-diurnal and diurnal variability

observed at 2 m and 10 m at each site focusing on variations between 1 hr and the local inertial period of 40 hrs (Wyatt et al. 2020).

PAR was derived for each site and depth based on satellite estimates of surface PAR (Frouin et al. 2003) and the diffuse attenuation coefficient for PAR (K_d(PAR); (Morel et al. 2007)) available from the European Space Agency GlobColour datasets over the period April 2016 to April 2020 (http://www.globcolour.info/). Daily PAR and K_d(PAR) values were obtained around Mo'orea at a 1/24° resolution (approximately 6 x 6 km), with site specific values based on the average of the nearest 4 pixels (approximately 12 x 12 km). Depth specific PAR values (PAR_Z) were then determined at 5, 10, and 20 m water depths at each site based on the site-specific PAR and K_d(PAR): $PAR_Z(z) = PAR.e^{-K_d(PAR).z}$.

A climatology was calculated for the time series of temperature and light at each site and depth, which closely resembled bimodal normal distributions corresponding to summer and winter seasons. Analyses focused on the summer-time temperature (December to May) and light (December to February) regimes because we were specifically interested in how maximum daily temperatures and the variance in temperature, which are both greatest in the summer months, would serve as potential factors structuring *Pocillopora* communities. We also included the mean of the maximum daily sea water temperature from June to November because it was the main winter metric that differed among sites and depths in dissimilar ways to the summer metrics.

Statistical analyses

Statistical analyses were performed in R v3.6.2 (R Core Team, 2019). We used binomial generalized linear mixed models with base R function 'glm' to determine if *Pocillopora* relative

abundance differed by depth at each site. Distance-based Redundancy Analysis (db-RDA) was used to analyze variation in the composition of *Pocillopora* haplotypes among depths and sites (Legendre & Andersson, 1999; Legendre & Gallagher, 2001) using the *vegan* package in R (Oksanen et al. 2019). db-RDA is a Redundancy Analysis (RDA) that analyzes the relationship between principal coordinates, estimated using Bray-Curtis dissimilarity matrices on the raw species data (proportion of samples from each species within each site and depth), and the explanatory, or constraining, variables. In the first model, depth and site were the constraining variables. In the second model, the seven environmental variables were the constraining variables. The effects of the constraining variables were determined using a nonparametric permutation test with 99999 permutations. Marginal tests of each factor indicate the unique effect of each factor conditional on the presence of the other factor in the model. Ordination biplots were used to visualize results and aid in interpretation.

Results

Genetic identification

Of the 673 *Pocillopora* samples, 14 mtORF haplotypes were identified, which include at least six previously identified nominal species (Fig. 2). The majority of sampled colonies were from two different species: *P. meandrina* (haplotype 1a, n = 273) and haplotype 10 (n = 187). At Mo'orea, *P. meandrina* is often visibly indistinguishable from *P. verrucosa* and haplotype 10 in the field based on gross morphology but differs by at least 20 (2%) mtORF base pairs (Fig. 2). Haplotype 10 is most genetically similar to haplotypes previously described as *P. verrucosa* (3a, n = 7; 3b, n = 22; 3f, n = 3, and 3h, n = 2) (Schmidt-Roach et al. 2014), but still differs by 5 – 8 bp. Haplotype 10 has only been documented at Mo'orea and surrounding islands (Forsman et al.

2013; Mayfield et al. 2015; Edmunds et al. 2016; Gélin et al. 2017). Haplotype 8a (n = 72) is most genetically similar to *P. meandrina* and *P. eydouxi* (haplotype 1a, n = 53), differing by 7 bp. Haplotype 2 (n = 6) and haplotype 11 (n = 38) differ by 4 bp. Haplotype 11 is also closely related to haplotype 6a (*P. ligulata*), differing by only two base pair substitutions (mtORF sequences 99.8% identical over 855bp; Fig. 2), but is morphologically most similar to *P. eydouxi*. Haplotype 9 (n = 3), previously documented from Mo'orea (Forsman et al. 2013), differs by 1 bp from *P. meandrina* and *P. eydouxi* (haplotype 1a). All but four haplotypes have been documented from previous mtORF analyses of *Pocillopora.* They include three haplotypes that each differed from *P. meandrina* and *P. eydouxi* (haplotype 1a) by one bp (haplotype 1c, n = 3; haplotype 1d, n = 1; haplotype 1e, n = 2), and one haplotype that differed from haplotype 11 by one bp (n = 1).

Depth distribution

The relative abundance of the most abundant species (*P. meandrina*, haplotype 10, and haplotype 8a) differed among depths (Fig. 3). For example, at 5m depth, 49% to 73% of *Pocillopora* colonies were *P. meandrina*, and only 0% to 5% were haplotype 10, depending on the site. At 20m depth, only 0% to 21% of *Pocillopora* colonies were *P. meandrina*, whereas 44% to 81% of colonies were haplotype 10. At site 4, the relative abundance of *P. meandrina* did not differ between 5 and 10 m, but the species was not present in our sampling at 20 m. Site 4 was also the only site at which haplotype 11 was sampled at all depths. For the less abundant species (haplotype 11, *P. eydouxi*, and *P. verrucosa* haplotype 3b), there were little to no differences in their relative abundances across depths (Fig. 3). *P. eydouxi* was relatively rare but was the only species in our collection that was sampled from all sites and depths.

Community composition

The composition of *Pocillopora* haplotypes varied across depths, but not among sites (Table 2, Fig. 4a). In the analysis using depth and site as the constraining variables, the first dbRDA axis explained 79.72% of the variation in community dissimilarity and was most associated with differences across depths. The *Pocillopora* community at 5 m was characterized by relatively high abundance of *P. meandrina*. The *Pocillopora* community at 20 m was characterized by relatively high abundance of haplotype 10. The second dbRDA axis explained 6.67% of the variation in community dissimilarity and was associated with differences across sites. In the analysis constrained using the environmental variables (Fig. 4b), the *Pocillopora* community at 20 m was associated with higher daily temperature variance, lower minimum daily temperatures in December – May, and lower maximum daily temperatures in June - November. Maximum daily temperature in December – May, on the other hand, was more associated with community differences between the north shore (Site 1 and 2, higher maximum daily temperature) vs the southern shore (Site 4 and 5, lower maximum daily temperature) than it was between depths. The *Pocillopora* community at 5 m was associated with higher mean and minimum daily light.

Discussion

Cryptic species, because of their morphological similarity, are often considered to be ecologically similar, so would not be expected to exhibit stable coexistence if competing for the same limiting resource. However, empirical explanations for why exactly cryptic species commonly co-occur in a particular circumstance remain elusive (Zhang et al. 2004; McPeek and

Gomulkiewicz 2005; De Meester et al. 2011; Montero-Pau et al. 2011). From extensive sampling around the island of Mo'orea and at multiple depths, we genetically identified 673 colonies in the *Pocillopora* species complex, without limiting sampling towards certain morphological characters, and uncovered differences among haplotypes in their relative abundance at each depth. Most of the dominant haplotypes are known to be evolutionarily distinct genetic lineages, or genetic species (Gélin et al. 2017; Johnston et al. 2017; Schmidt-Roach et al. 2014). We found that differences in species composition across depths within a site across 10's of meters were greater than differences among sites separated by several kilometers. Consistent with internal-wave cooling found at Mo'orea (Wyatt et al. 2020), we also show that the temporal variance in sea water temperatures increased with depth and were more associated with the *Pocillopora* community composition at 20 m than were maximum daily temperatures.

Species must co-occur to directly interact, but the degree of co-occurrence does not necessarily reflect the degree to which species interact (Blanchet et al. 2020). Therefore, while we have identified differences among cryptic species in their relative abundance across a depth gradient, and associations with environmental variables that co-vary with depth, we cannot yet determine whether such ecological differences are driven by species interactions (e.g., competition) or difference in the response of species to abiotic environmental conditions, or both. For example, the observed depth patterns could be influenced by larval habitat selection and post-settlement mortality, both of which could be determined by the presence of other species as well as the abiotic environment (Mundy and Babcock 1998, Baird et al. 2003, Hunt and Scheibling 1997, Penin et al. 2010). Furthermore, the depth segregation of species could be facilitated by dispersal limitation of negatively buoyant eggs in benthic boundary layers (Hirose et al. 2000; Schmidt-Roach et al. 2012), and the relatively fast development of larval motility

(only 8 hrs in *P. eydouxi* (Hirose et al. 2000) compared with up to 96 hrs in acroporid corals (Miller and Ball 2000)).

Divergent selection between adjacent habitats can both form new species and maintain closely related species, despite the lack of physical barriers preventing the dispersal of marine larvae among habitats (Rocha et al. 2005; González et al. 2018; Whitney et al. 2018). Changes in environmental conditions associated with depth gradients have been hypothesized to serve as axes of speciation in corals (Carlon and Budd 2002; Bongaerts et al. 2010, 2013, 2021; Levitan et al. 2011; Prada and Hellberg 2013, 2021). At Mo'orea, the four most abundant *Pocillopora* species, which are often visibly indistinguishable at the gross colony level, exhibited stark differences in their relative abundance across depths – *P. meandrina* and haplotype 8a were often more abundant at 5 m than at 10 m and 20 m, while haplotype 10 and *P. verrucosa* haplotype 3b were more abundant at 20 m than at 10 and 5 m (Fig. 3). In Taiwan, De Palmas et al. (2018) targeted sampling of the "*P. verrucosa* morphotype," and also found that samples genetically identified as *P. verrucosa* (haplotypes 3a, 3b, 3f, 3g, 3h) were more prevalent on deeper reefs (23 – 45 m), while *P. meandrina* and haplotype 8a were more prevalent on shallow reefs (7 – 15 m). Haplotype 10 is most closely related to *P. verrucosa* haplotype 3b (Fig. 2) yet, although more dominant, shares the same depth distribution, which would be inconsistent with an expectation of speciation by depth. However, *P. verrucosa* haplotype 3b has a widespread distribution (documented from the Galapagos to the Red Sea (Pinzón et al., 2013; Sawall et al., 2015)), while haplotype 10 has only been documented from French Polynesia (Forsman et al. 2013; Mayfield et al. 2015; Gélin et al. 2017). The apparent endemicity of haplotype 10 to French Polynesia is consistent with the hypothesis that this haplotype diverged from *P. verrucosa* in this region, but

because these lineages share similar niche space with respect to depth, the conditions that led to their divergence require further investigation.

The sampling of clones was unlikely in our study. Brooding *Pocillopora* species (e.g., *P. damicornis* and *P. acuta*) are known to produce asexual larvae (Combosch and Vollmer 2013; Torda et al. 2013), but we did not observe any of the brooding *Pocillopora* species on the fore reef of Mo'orea. Clonal stands of broadcast spawning *Pocillopora* species have been observed in the Gulf of California and in the Galapagos as a result of branch fragmentation and reattachment, and not the release of clonal larvae (Pinzón et al. 2012; Baums et al., 2014). However, we did not find visible evidence for branch reattachment to the reef via fragmentation at any of our sites. In contrast to the large monospecific stands that form in the Tropical Eastern Pacific, individual *Pocillopora* colonies are distinct and can be easily distinguished on the fore reef of Mo'orea, which is aided by the fact that colonies are all less than ~10 years old (Adam et al. 2011). Furthermore, Magalon, Adjeroud, & Veuille (2005) found no genetic evidence of clones when sampling colonies displaying the "*P. meandrina* morphology" on Mo'orea and throughout French Polynesia.

Differences in the relative abundance of species across a fairly narrow depth range (5 – 20 m) indicates that there are biological differences among cryptic species. Therefore, these cryptic species are not ecologically similar (see also Burgess et al. (2021)) and should not be grouped and analyzed as a single group, as is commonly done (Darling et al. 2013; Pratchett et al. 2013; Tsounis and Edmunds 2016). Our results indicate that *P. meandrina* and haplotype 8a are genetically and ecologically divergent from haplotype 10 and *P. verrucosa* haplotype 3b, yet these four haplotypes cannot be reliably identified in the field based on morphology (Fig. 3). Additionally, *P. eydouxi* is morphologically indistinguishable from haplotype 11, but exhibited a

different depth distribution pattern. All six of these haplotypes are morphologically indistinguishable when small (<approx. 25 cm diameter). To properly capture biodiversity patterns, sampling needs to be stratified by depth, not just occur horizontally across different locations, and should not rely on morphological characters to identify genetically and ecologically different species.

Depth differences in the community composition of *Pocillopora* were associated with temperature and light regimes. *P. meandrina* and haplotype 8a dominated shallower locations with higher light irradiance, higher daily temperature minimums, and lower temperature variance (Fig. 4). Haplotype 10 and *P. verrucosa* haplotype 3b dominated deeper locations with lower irradiance, lower daily temperature minimums, and higher temperature variance. The increased temperature variance, and lower daily temperature minimums, with depth is a signature of the internal wave climate and the increased extent to which internal waves bring cooler water to deeper sections of the reef slope (Wyatt et al. 2020). Depth distributions of *P. meandrina*, haplotype 8a, haplotype 10, and *P. verrucosa* haplotype 3b therefore seem more sensitive to frequent cooling in deeper water than to periodic heating more likely in shallower water due to increased solar irradiance. The current distribution of haplotype 11, however, does appear to reflect the impacts of more prolonged heating. In 2019, a prolonged ocean heating event (several weeks) caused widespread coral bleaching in *Pocillopora* at Mo'orea, with subsequent mortality much higher for haplotype 11 than any of the other *Pocillopora* species (Burgess et al. 2021). Heat accumulation and bleaching mortality was also greatest at site 1 and 2, intermediate at site 5, and the least at site 4, which might explain the differences in the *Pocillopora* community among sites seen in Fig 4. These data suggest that the niche space of haplotype 11 is more constrained by heat stress than that of the other cooccurring species. The lack of differentiation

in abundance by depth or site observed for *P. eydouxi* indicates that this species has a broader niche space with respect to depth than other co-occurring *Pocillopora* species.

Any differences in the *Symbiodiniaceae* community hosted by each *Pocillopora* haplotype could also be associated with their depth specificity. *Pocillopora* species typically host Symbiodiniaceae from a single genus, but under certain conditions are capable of shuffling their symbiont communities in response to environmental changes (McGinley et al. 2012; Rouzé et al. 2019). Both brooding and broadcast spawning *Pocillopora* vertically transmit their photosynthetic symbionts (Glynn et al. 1991; Schmidt-Roach et al. 2012; Massé et al. 2013; Johnston et al. 2020), and there is some evidence that *Symbiodiniaceae* associations differ between *Pocillopora* species (Cunning et al. 2013; Brener-Raffalli et al. 2018).

Finally, the identification of differences among cryptic species in their relative abundance across depths has important implications for response diversity (*sensu* Elmqvist et al. 2003). Response diversity can maintain ecosystem states when species sharing similar ecological functions, afforded by their similar morphology, differ in their response to perturbations, such that the temporary loss of one species is compensated by less impacted species (Chapin et al. 1997; Yachi and Loreau 1999). We have previously shown differences among cryptic *Pocillopora* species at Mo'orea in their response to a recent bleaching event (Burgess et al. 2021). However, response diversity enhances resilience only when there are niche differences and spatial variation in the relative abundance among species (Baskett et al. 2014). Our results here, therefore, strengthen the case for response diversity as an explanation for the seemingly unusual patterns of recovery in *Pocillopora* known for Mo'orea (Kayal et al. 2018; Edmunds et al. 2019).

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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Data Accessibility:

R scripts and data used to perform analyses and prepare figures are available at Dryad (link provided upon acceptance).

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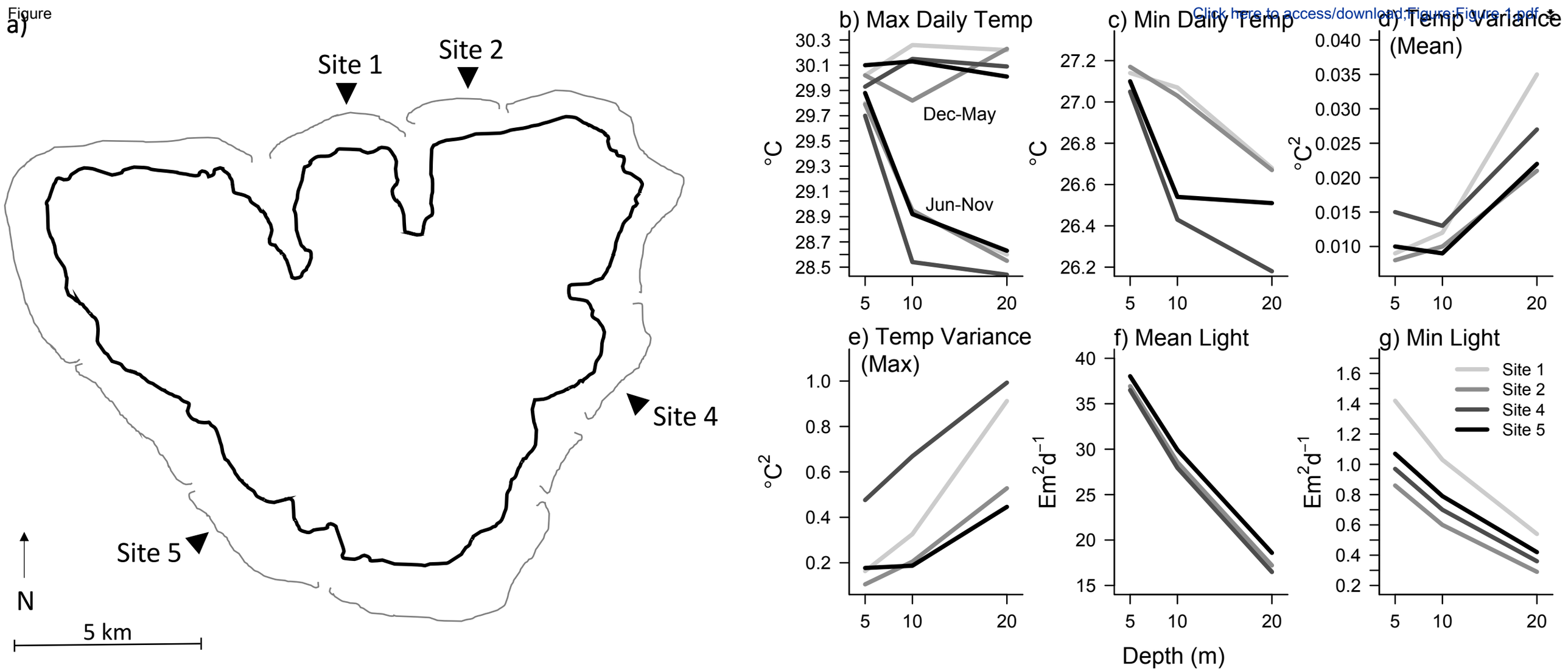
Figure 1: a) Map of Mo'orea, French Polynesia (-17°32′S -149°50′W), showing location of sites where *Pocillopora* samples and environmental data were collected. At each site, *Pocillopora* samples were collected from 5 m, 10 m, and 20 m. b) - g) Summary of the environmental data showing the relationship between environmental variables and depth at each site (shaded lines). All data are for summer-time temperature (December to May) and light (December to February) regimes, unless otherwise indicated.

Figure 2: Haplotype network of the mitochondrial ORF region (855 bp) for 673 *Pocillopora* samples collected from the fore reef of Mo'orea, French Polynesia. Each black dot represents one base pair difference. Species and haplotype identification follows Forsman et al. (2013), Pinzón et al. (2013), and Schmidt-Roach et al. (2014). Haplotypes 3a, 3b, 3f, and 3h have been identified as *P. verrucosa* (Schmidt-Roach et al. 2014). Haplotypes without a species name associated with them have not been formally identified yet. The size of each circle represents the relative abundance of each haplotype found at Mo'orea across four sites and three depths.

Figure 3: Proportion of *Pocillopora* species/haplotype (rows, examples provided on the right) at 5, 10, and 20 m depths at each site on the fore reef of Mo'orea in August 2019. Each bar denotes the number of samples of that species divided by the total number of colonies sampled at that depth and site. Black bars denote 95% confidence intervals based on the variance of a binomial sampling distribution (i.e., $np(1-p)$, where n = number of samples, p = proportion). Values in bold denote significant differences among depths at a given site for a given species. n indicates the number of samples of that species at each depth.

Figure 4: Ordination biplot of the first two axes of the distance-based Redundancy Analysis (db-RDA) using the environmental variables as the constraining variables. Sampling locations are labelled by their site number in black. In a) species scores are plotted in blue, indicating the relative contribution of each species in causing differences in the community composition among sampling locations. Polygons group sites according to their depth. In b) arrows indicate biplot scores for the environmental variables (constraining variables). Axis dbRDA1 explained 81.53%, and axis dbRDA2 explained 5.62%, of the variation in the Bray-Curtis dissimilarity matrix. All environmental data are for summer-time temperature (December to May) and light (December to February) regimes, unless otherwise indicated.

Figure



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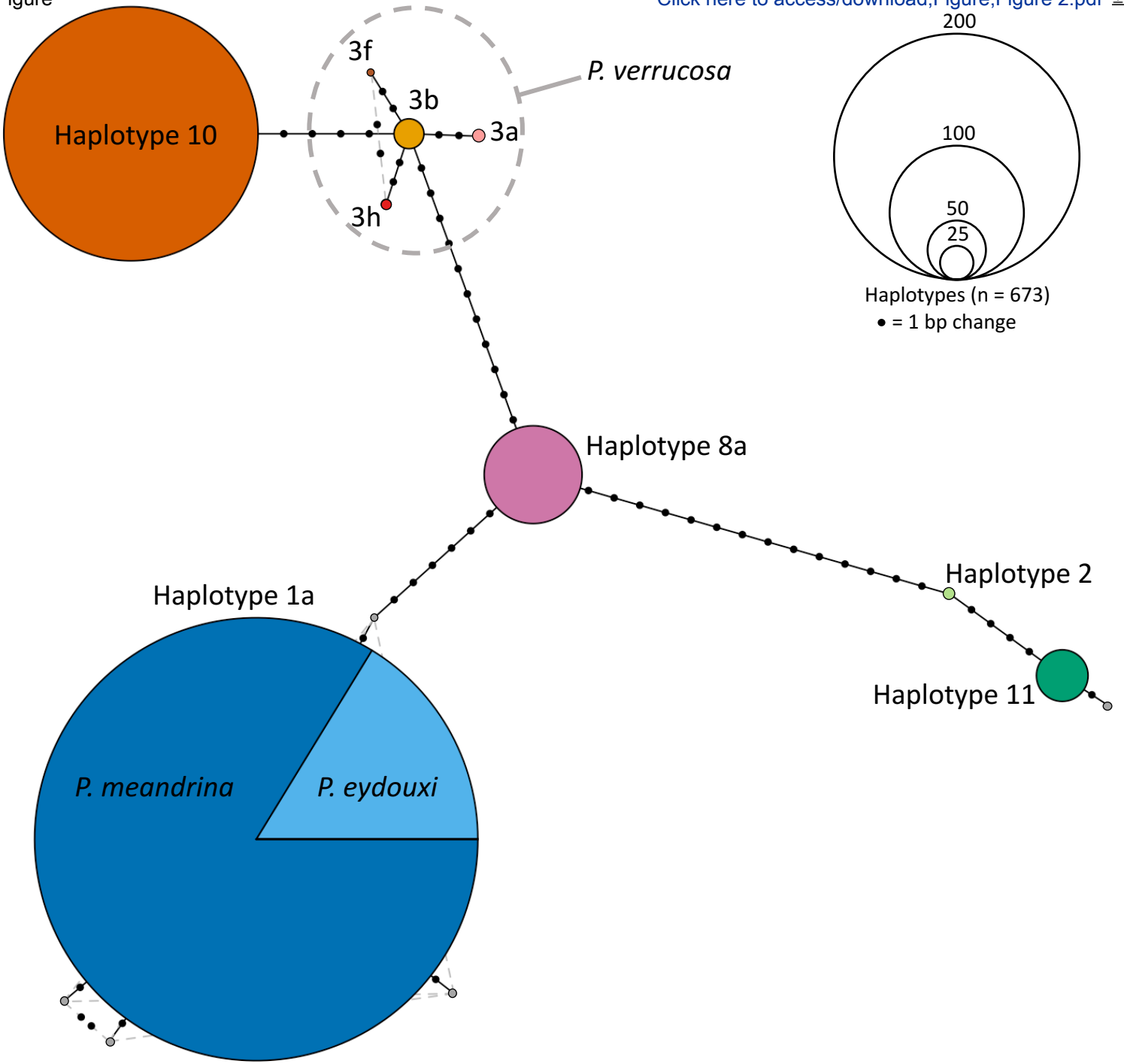

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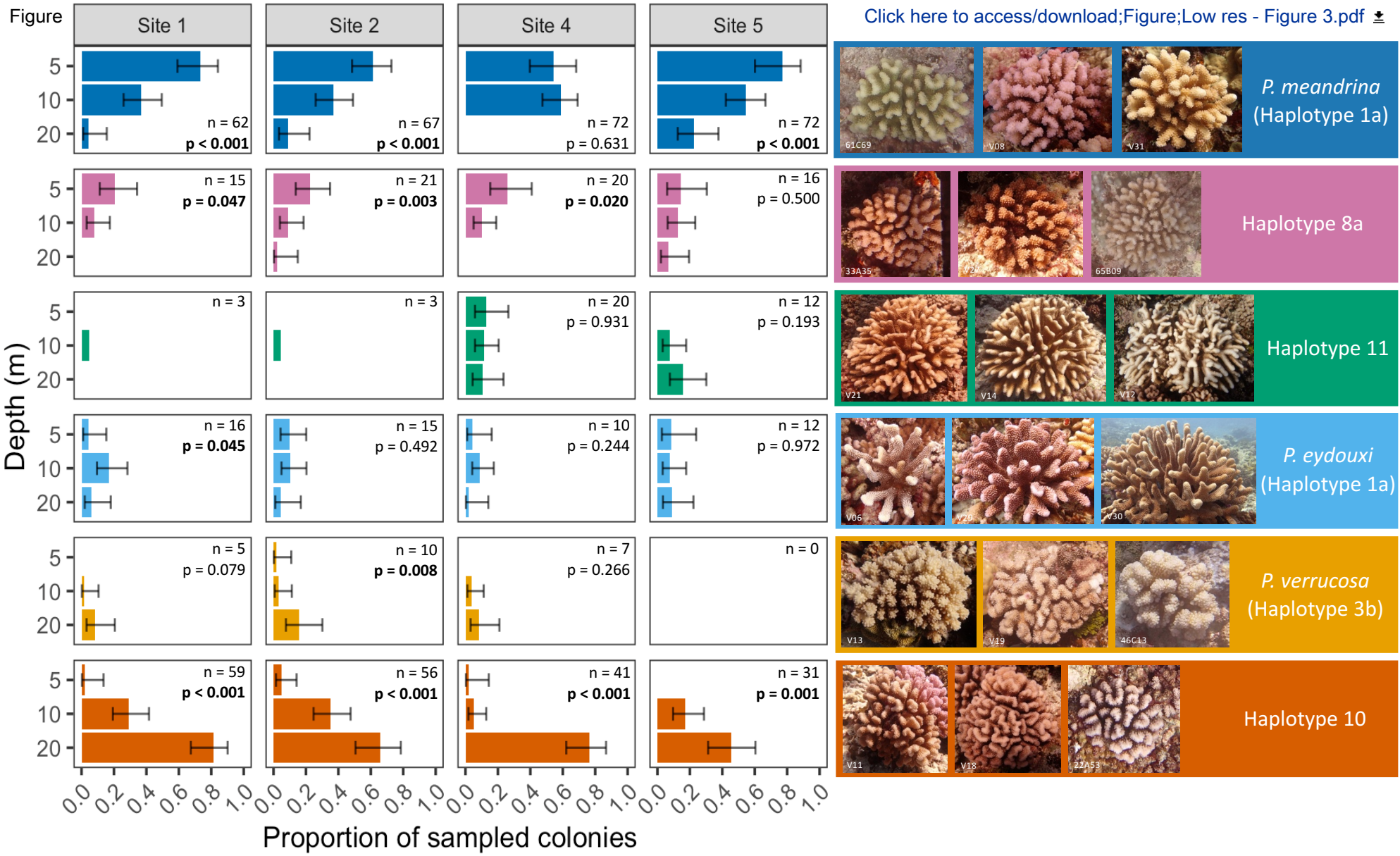

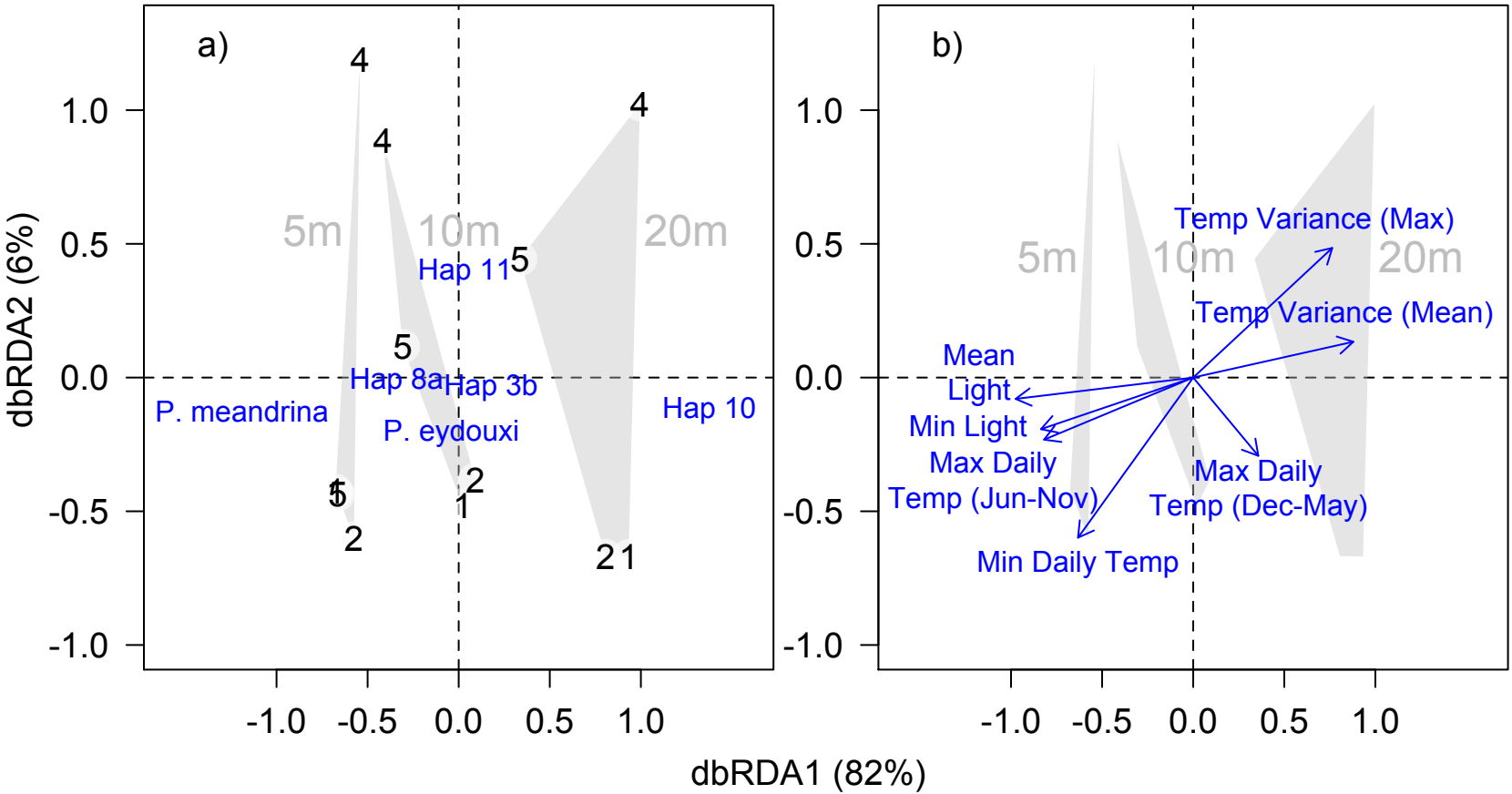

Table 1: Number of *Pocillopora* samples collected from each site at 5, 10, and 20 m depths.

Site	5 m depth	10 m depth	20 m depth
1	50	65	48
2	62	69	46
4	51	83	48
5	37	68	46

Table 2: ANOVA permutation test of the effect of depth (5, 10, and 20 m) and site (1, 2, 4, and 5), based on a distance-based Redundancy Analysis (db-RDA) using the environmental variables as the constraining variables. Tests of each factor are conditional on the presence of the other factor in the model (i.e., marginal tests). p-values are based on 9999 permutations.

	df	Sums of Squares	F-value	p-value
Depth	2	1.302	28.161	<0.01
Site	3	0.198	2.861	0.092
Residual	6	0.139		