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Same places, same stories? Genomics reveals similar structuring and demographic patterns for four *Pocillopora* coral species in the southwestern Indian Ocean

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Abstract :

Aim

Efficiently protecting species requires knowing their ecological, life-history and reproductive traits. This is particularly decisive for scleractinian corals, key components of coral reefs, which are experiencing critical declines. Yet their connectivity remains insufficiently documented. Here, we focused on four distinct species of the coral genus Pocillopora found in diverse habitats of the southwestern Indian Ocean and presenting various reproductive strategies. We aimed to understand whether these traits affect species connectivity.

Location

Archipelagos and islands of the southwestern Indian Ocean.

Taxon

Pocillopora spp.

Methods

We used target capture to collect single-nucleotide polymorphisms (SNPs) from over a thousand colonies sampled across nine localities. From the ca. 1400 SNPs retained per species, Bayesian clustering methods, networks and demographic inferences were applied to first infer the population genetic structure and connectivity of each species, then the demographic history of each population.

Results

All four Pocillopora species exhibited almost the same genetic structuring pattern, reflecting the sampled ecoregions (Madagascar and surrounding islands vs. Mascarene Islands). However, the genetic differentiation was stronger (FST about 10 times higher) for P. acuta, the species inhabiting more enclosed habitats, such as lagoons and shallow waters, and reproducing mainly asexually. Similarly, all populations, except those from P. acuta, showed a signature of population expansion ca. 100,000 years ago, following the penultimate glacial period.

Main Conclusions

These results indicate reduced gene flow between Madagascar and the Mascarene Islands, probably linked to currents, suggesting distinct connectivity networks that should be considered independently when setting up conservation plans. In addition, shared demographic histories reflect that populations from these species have probably met the same environmental constraints and reacted similarly, something that should be considered in light of the ongoing rapid climate change.

Keywords : Bayesian assignment, demographic inference, genetic connectivity, Indian Ocean, scleractinian, single-nucleotide polymorphism, target capture, ultraconserved element

SIGNIFICANCE STATEMENT

Pocillopora corals are widely distributed through the Indo-Pacific and play crucial roles in reef ecosystems' functioning. Yet, some species remain understudied both in terms of genetic connectivity and evolution, mainly due to species delimitation issues within the genus. Here, based on a panel of genome-wide SNPs, we assessed the population connectivity of four species abundantly found in the southwestern Indian Ocean and inferred their demographic histories. We revealed similar genetic structuring patterns and demographic histories among species, reflecting weak connectivity between Madagascar and the Mascarene Islands, partly due to currents.

INTRODUCTION

Efficiently protecting species requires knowing their ecological, life history and reproductive traits (Clark, 1993). When organisms are difficult to access or when some key processes (e.g., mating, gene flow) are cryptic, such as for marine benthic species, population genetics appears useful to infer population structure and connectivity, but also evolutionary histories (e.g., Maggioni et al., 2020; Padovan et al., 2020). Gathering such data appears crucial to assess evolutionary potential and long-term conservation of species under ongoing changing environments (Gray, 1997).

Scleractinian corals, the cornerstone of coral reefs, have experienced critical declines since the 1980s (Eddy, Cheung, & Bruno, 2018), making them one of the top science and conservation priorities globally. Yet, the connectivity among their populations, and even more so their evolutionary history, remain insufficiently documented.

One of the scleractinian genera whose connectivity is relatively well-documented is the genus *Pocillopora* (e.g., De Palmas, Soto, Ho, Denis, & Chen, 2021; Gélin, Fauvelot, et al., 2017; Gélin, Pirog, Fauvelot, & Magalon, 2018; Magalon, Adjeroud, & Veuille, 2005; Oury, Gélin, & Magalon, 2020, 2021; Ridgway, Riginos, Davis, & Hoegh-Guldberg, 2008; Robitzch, Banguera-Hinestroza, Sawall, Al-Sofyani, & Voolstra, 2015; Souter, Henriksson, Olsson, & Grahn, 2009; Torres, Forsman, & Ravago-Gotanco, 2020). Its colonies, abundantly distributed throughout the Indo-Pacific and the Red Sea, are the main bioconstructors in some reefs (e.g., Benzoni, Bianchi, & Morri, 2003). Previous literature assumed that several species (e.g., *P. damicornis*, *P. meandrina*, *P. verrucosa*) were widely distributed throughout the range of the genus (Veron, 2000). However, recent investigations suggested a deep lack of connectivity between both sides of the Indo-Pacific (Gélin, Fauvelot, Bigot, Baly, & Magalon, 2018; Gélin, Pirog, et al., 2018; Oury et al., 2021), to the point that different species could be considered (Gélin, Postaire, Fauvelot, & Magalon, 2017; Oury, Noël, Mona, Aurelle, & Magalon, 2023). The last decades were characterised by a growing number of studies multiplying the methods and lines of evidence to explore species limits within the genus *Pocillopora* (e.g., Gélin, Postaire, et al., 2017; Johnston et al., 2017; Oury et al., 2023; Pinzón et al., 2013; Schmidt-Roach, Miller, Lundgren, & Andreakis, 2014), and move towards an integrative taxonomic revision.

Using species delimitation methods based on sequence data from colonies sampled in three marine provinces (western Indian Ocean, tropical southwestern Pacific and south-east Polynesia), Gélin, Postaire, et al. (2017) defined 16 primary species hypotheses (PSHs *sensu* Pante et al., 2015) within the genus *Pocillopora*. Species boundaries were then refined using 13 microsatellite markers and genetic assignment tests, leading to the definition of secondary species hypotheses (SSHs *sensu* Pante et al., 2015) and clusters (Gélin, Postaire, et al., 2017; Gélin, Fauvelot, et al., 2017, 2018; Gélin, Pirog, et al., 2018; Oury et al., 2020, 2021; Oury, Gélin, Rajaonarivelo, & Magalon, 2022). Then, from a subset of individuals representative of each PSH, SSH and cluster, 21 genomic species hypotheses (GSHs) were defined based on genome-wide single-nucleotide polymorphisms (SNPs) (Oury et al., 2023). These GSHs were compared to other lines of evidence in an integrative approach, leading to the definition of 13 strongly supported species, three of which potentially represent species complexes. Most of the colonies from the southwestern Indian Ocean (SWIO) studied therein were attributed to GSH05c-1, GSH05c-2 and GSH05d (all three corresponding to *P. acuta* species

complex), GSH09a (*Pocillopora* aff. *P. meandrina*, called *P. eydouxi* in the region but morphologically and genetically closer to *P. meandrina*; see Oury et al., 2023), GSH13a (*Pocillopora* aff. *P. verrucosa*) and GSH13b (*P. villosa nomen nudum*). Hereafter, to lighten the writing, these four species will be referred to as *P. acuta*, *P.* aff. *meandrina*, *P.* aff. *verrucosa* and *P. villosa*, respectively.

Although accurate knowledge of these species ecology is still lacking, they present different reproductive strategies (with or without clonal propagation; Gélin, Fauvelot, et al., 2017; Oury, Gélin, Massé, & Magalon, 2019; Schmidt-Roach, Lundgren, et al., 2012) and colonise different, more or less open, and/or shallow habitats (e.g., lagoons vs. outer reef slopes; Oury et al., 2023; Schmidt-Roach et al., 2014; Veron, 2000). All four species are sexual broadcast spawners (Schmidt-Roach, Miller, Woolsey, Gerlach, & Baird, 2012), with different timings depending on locality (e.g., Bouwmeester, Coker, Sinclair-Taylor, & Berumen, 2021; Buck-Wiese et al., 2018; Kruger & Schleyer, 1998), but only *P. acuta* has been reported as an asexual brooder with no doubt (Oury et al., 2019). This latter species seems also more proponent of fragmentation due to its finer branches, and is mostly found in shallow (< 5 m depth) and relatively enclosed habitats compared to other species (Veron, 2000).

Different patterns of genetic connectivity might thus be expected for these species, since previous studies have shown more restricted connectivity in brooding corals compared to broadcast spawners (e.g., Thomas et al., 2020; van der Ven, Heynderickx, & Kochzius, 2021), related to, amongst other things, differential planktonic larval durations and behaviours (Coelho & Lasker, 2016). As such, genetic connectivity has already been studied among populations of these four species in the SWIO using allozymes (Ridgway, Hoegh-Guldberg, & Ayre, 2001) or microsatellites (Gélin, Fauvelot, et al., 2018, 2017; Gélin, Pirog, et al., 2018; Oury et al., 2021; Ridgway et al., 2008; Souter et al., 2009). Different structuring patterns were found depending on the species and the genetic markers (see Appendix S1, Table S1.1 in Supporting Information for a summary and the correspondences with previous studies): while a general high connectivity was reported for *P.* aff. *verrucosa* and *P. villosa* using 13 microsatellites (Oury et al., 2021), a strong genetic differentiation was found within *P. acuta* with the same 13 microsatellites, which may be related to its different reproductive strategy (Gélin, Pirog, et al., 2018). However, for *P.* aff. *meandrina*, the same 13 microsatellites highlighted the presence of three sympatric clusters found in relatively similar proportions in all sampled sites, and the connectivity was high within each cluster (Gélin, Fauvelot, et al., 2018; Oury et al., 2021). This diversity of patterns found within the same region and within congeneric species, some of which adopt the same reproductive strategy, seems surprising and questions the origin of such differences.

Here, to confirm or refute previous genetic structuring patterns found in these four *Pocillopora* species from the SWIO, we used target-capture of ultraconserved elements (UCEs) and exon loci, from over a thousand colonies, to collect a panel of genome-wide SNPs. Bayesian clustering methods, networks and demographic inferences were applied to infer the population genetic structure and connectivity of each species, but also the demographic history of each population. Through a multi-species approach, these results provide insights for a better understanding of the evolutionary history

of these species, as well as the connectivity pattern in the SWIO. Ultimately, this will allow the implementation of effective conservation measures in a context of coral decline.

MATERIALS AND METHODS

Sampling

The sampling was the same as in our previous studies (e.g., Oury et al., 2022), but focusing only on colonies from the southwestern Indian Ocean (SWIO). It represents ca. 5,000 *Pocillopora* colonies sampled within more than 40 sites from 11 localities. All colonies were previously genotyped with 13 microsatellites and a subset (ca. 10%) was also amplified for the mitochondrial open reading frame marker (mtORF). Based on these genetic data, each colony was assigned beforehand to a primary and a secondary species hypothesis (PSH and SSH, respectively; *sensu* Gélin, Postaire, et al., 2017), and a cluster when appropriate. Here, to further study the genetic structure of the four targeted species (i.e., *P. acuta*, *P.* aff. *meandrina*, *P.* aff. *verrucosa* and *P. villosa*), we sequenced, when possible, a subset of at least 20 colonies per locality and per genetic cluster. Accordingly, 1,023 *Pocillopora* colonies from 35 sites and nine localities were considered (Table 1; Fig. 1; see Appendix S2, Table S2.2).

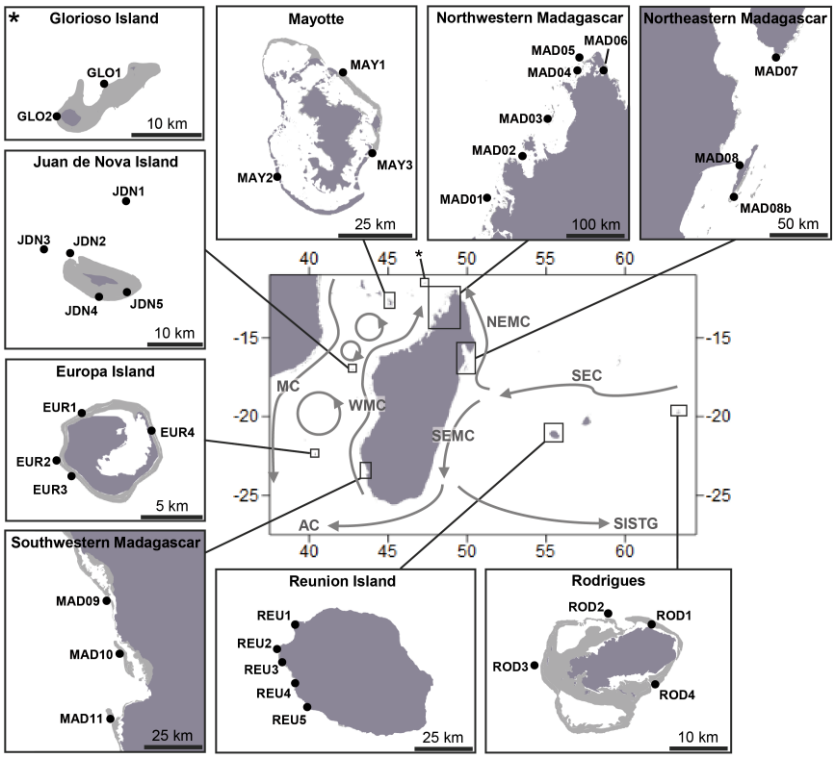
Table 1 Sampling localities of *Pocillopora* colonies (see Appendix S2, Table S2.2 in Supporting Information for details per site). N_{sites}: number of sites sampled; N, N_L, N_{acuta}, N_{meand}, N_{verru} and N_{villo}: total numbers of sampled colonies, of clonal lineages and of colonies assigned to *P. acuta*, *Pocillopora* aff. *P. meandrina*, *Pocillopora* aff. *P. verrucosa* and *P. villosa nomen nudum*, respectively; R: clonal richness (Dorken & Eckert, 2001). Two *P. acuta* colonies from northwestern Madagascar (MADnw) were removed due to missing data and are not counted here.

Ecoregion	Island/Region	Code	Latitude	Longitude	N_{sites}	N	N_{acuta}	N_{meand}	N_{verru}	N_{villo}
Western and Northern Madagascar	Mayotte	MAY	-12.83131	45.16044	3	153	30	85	20	18
	Glorioso Island	GLO	-11.56377	47.29394	2	10	0	6	2	2
	Juan de Nova Island	JDN	-17.04855	42.72176	5	148	48	77	21	2
	Europa	EUR	-22.36783	40.37185	4	81	0	46	20	15
	Northwestern Madagascar	MADnw	-16.18321	49.94950	6	118	43	48	23	4
	Northeastern Madagascar	MADne	-13.46366	48.25272	3	60	4	6	35	15
	Southwestern Madagascar	MADse	-23.47539	43.66148	3	141	24	76	21	20
Mascarene Islands	Reunion Island	REU	-21.16115	55.57841	5	176	65	72	20	19
	Rodrigues	ROD	-19.69775	63.44172	4	134	27	80	20	7
				N	35	1021	241	496	182	102
				N_L	-	850	95	490	179	86
				R	-	0.83	0.39	0.99	0.98	0.84

Laboratory and preliminary bioinformatics steps

Total genomic DNA was extracted using the DNeasy® Blood & Tissue kit (QIAGEN GmbH, Hilden, Germany), according to manufacturer protocol. Samples were then PE150 sequenced with an Illumina NovaSeq 6000 (Illumina, San Diego, CA) at the platform iGenSeq (ICM, Paris, France), following a capture protocol targeting 1,248 ultraconserved elements (UCEs) and 1,385 exon loci (Cowman et al., 2020), as in Oury et al. (2023). Seven haphazardly chosen samples were independently prepared and sequenced twice (sequencing replicates) to estimate the sequencing error rate, and the variant calling and filtering accuracy. After sequencing, reads were processed as in Oury

et al. (2023) and mapped to the 2,068 reference sequences constructed *de novo* therein (available at https://doi.org/10.5281/zenodo.7885458).



[2/3rd column] **Figure 1** Sampling localities of *Pocillopora* colonies (dark and light greys indicate lands and coral reefs, respectively). Sites are numerically identified from the island code: GLO: Glorioso Islands, MAY: Mayotte, MAD: Madagascar, JDN: Juan de Nova Island, EUR: Europa Island, REU: Reunion Island and ROD: Rodrigues. Major oceanic currents are indicated schematically: MC: Mozambique current, WMC: west Madagascar current, AC: Agulhas current, NEMC: north-east Madagascar current, SEMC: south-east Madagascar current, SEC: south equatorial current and SISTG: south Indian subtropical gyre (Hancke, Roberts, & Ternon, 2014; Lutjeharms & Bornman, 2010; Schott & McCreary Jr, 2001).

Species identification of the colonies

To verify the identification of the colonies in the light of recent genomic investigations (Oury et al., 2023), a first dataset was constructed by calling the genotypes of each sample for the 1,559 SNPs that were used for species delimitation in Oury et al. (2023; see Appendix S3 for more details). A single representative of each sequencing replicate (the one with the least missing data) was kept.

Assignment tests were then performed with sNMF (Frichot, Mathieu, Trouillon, Bouchard, & François, 2014), implemented in the R v4.0.4 (R Core Team, 2021) library '*LEA*' (Frichot & François, 2015). Besides, 167 of the 1,023 colonies considered in this study (16%) were previously used in the genomic species delimitation analyses from Oury et al. (2023), and their corresponding genomic species hypotheses (GSHs) are thus known. sNMF was first run with these 167 colonies only, to retrieve the GSHs, then including all 1,023 colonies. Five repetitions per *K* were run, with *K* varying from 2 to 10. Results were visualised with CLUMPAK (Kopelman, Mayzel, Jakobsson, Rosenberg, & Mayrose, 2015), and used to identify colonies to the species level (see Results). A principal component analysis (PCA) including all 1,023 colonies was also performed with the R library '*adegenet*' (Jombart, 2008).

Population structure and connectivity

Datasets construction

Once species were identified, four separate datasets (one for each species) were distinguished, from which SNPs were recalled from the individual bam files to get a more accurate genotyping (see Appendix S3 for more details). Tri- and tetra-allelic sites, as well as sites presenting more than 20% of missing data and sites with a minor allele frequency (MAF) inferior to 0.05 were discarded. Two *P. acuta* individuals presenting high proportions of missing data (> 75%) were removed. Then, one SNP was randomly chosen per locus to reduce the effect of linkage disequilibrium, resulting in the four datasets that were used for subsequent analyses.

Clonal lineages identification

Clonal lineages (i.e., groups of genetically related individuals resulting from asexual reproduction) were identified by computing the genetic distance [number of different alleles estimated with the *diss.dist* function from the R library '*poppr*' (Kamvar, Tabima, & Grünwald, 2013) over number of sites genotyped for both individuals] between all pairs of individuals within each dataset. The distribution of these genetic distances among individuals was then plotted and the first antimode was defined as the threshold separating individuals belonging to the same clonal lineage (smaller distances between individuals) from those belonging to different clonal lineages (larger distances between individuals). Sequencing replicates were used to help position the threshold. Clonal lineages were then visualised in R with a hierarchical clustering of the individuals based on genetic distances. The clonal richness (*R*; Dorken & Eckert, 2001) of each dataset was then calculated as $\frac{N_L-1}{N-1}$, with *N* and N_L, the total numbers of colonies and clonal lineages in the dataset, respectively.

Structure analyses

All further analyses were performed keeping one representative of each clonal lineage per population, as closely related individuals can bias estimators which are not designed for clonal populations. However, for *P. acuta*, as a significant number of colonies was removed (61%; see Results), and since all colonies theoretically participate equally in sexual reproduction and gene flow, analyses were performed on both a truncated (i.e., keeping one representative of each clonal lineage per population) and an entire (i.e., keeping all individuals) datasets.

First, assignment tests were performed with sNMF (Frichot et al., 2014), STRUCTURE v2.3.4 (Pritchard, Stephens, & Donnelly, 2000) and discriminant analyses of principal components (DAPC; Jombart, Devillard, & Balloux, 2010). STRUCTURE was run with the admixture model, assuming correlated allele frequencies. Three iterations of 5×10^5 MCMC generations after an initial burn-in of 5×10^4 generations were run for each *K*, varying from $K = 2$ to $K = 10$. sNMF and DAPC were performed with the R libraries *'LEA'* (Frichot & François, 2015) and '*adegenet'* (Jombart, 2008), respectively. Five repetitions per *K*, with *K* varying from 2 to 10, were run for sNMF, with a maximum of 500 iterations before reaching stationarity. Results were STRUCTURE-like plotted for all three assignment methods (i.e., STRUCTURE, sNMF and DAPC) with CLUMPAK (Kopelman et al., 2015), to allow their comparison. Additionally, a principal component analysis (PCA) was performed with the

R library '*adegenet*' (Jombart, 2008). Nei (1972) individual genetic distances were estimated with the R library '*StAMPP*' (Pembleton, Cogan, & Forster, 2013), and were used to build a minimum spanning tree (MST) and an unrooted equal-angle split network, with EDENETWORKS v2.18 (Kivelä, Arnaud-Haond, & Saramäki, 2015) and SplitsTree v4.15.1 (Huson & Bryant, 2006), respectively.

Finally, once the number of clusters defined for each species, a population was considered as all colonies sampled in the same site and assigned to the same cluster according to the three assignment methods (i.e., sNMF, STRUCTURE and DAPC). Populations with less than 10 individuals were not retained for further analyses, but some sites were pooled together as a single population to achieve larger population sizes (Fig. 2; see Appendix S2, Table S2.2). Since this pooling of populations may affect the results of some analyses, the distance between pooled sites was limited to a few tens of kilometres and results were interpreted carefully. F_{ST} (Weir & Cockerham, 1984) were computed with the R library '*StAMPP*' (Pembleton et al., 2013) for each pair of conspecific populations.

Direction and barrier to gene flow

Directional gene flow among populations was assessed by constructing a relative migration network with *divMigrate* (Sundqvist, Keenan, Zackrisson, Prodöhl, & Kleinhans, 2016), implemented in the R library *'diveRsity'* (Keenan, McGinnity, Cross, Crozier, & Prodöhl, 2013). Analyses were run for all populations within each species using the G_{ST} (Nei, 1973) and 1,000 bootstraps, and by incrementing the filter threshold (t) by 0.05 until the network becomes fragmented.

Then, geographic areas with pronounced genetic discontinuity between populations were identified with the Barrier v2.2 program (Manni, Guérard, & Heyer, 2004). The geographical coordinates and genetic distances (Nei, 1972) were thus connected by Delauney triangulation such that each connection had an associated distance, and barriers were identified using a Monmonier (1973) maximum distance algorithm. Barrier support was assessed through 1,000 distance matrices bootstrapped over loci.

Isolation by distance × environment

To explore the effect of distance and environment on the population structure among all four species, a factorial analysis of mixed data (FAMD) was performed using the R library *'FactoMineR'* (Lê, Josse, & Husson, 2008). Within-species pairwise population F_{ST} and shortest distances at sea (computed with QGIS v2.18.28; http://www.qgis.org) were used as measures of population structure and geographic distance, respectively. Environmental layers (present mean surface temperature, salinity, current velocity and chlorophyll concentration) were downloaded from Bio-ORACLE v2.2 (Assis et al., 2018) and queried with the population site coordinates using the R libraries *'sdmpredictors'* (Bosch & Fernandez, 2023) and *'raster'* (Hijmans, 2023). From the data extracted for each environmental layer, two statistics were then calculated per population pair: the mean and the difference, resulting in eight environmental variables. Finally, to account for species intrinsic differences (e.g., reproduction strategy), a qualitative variable "species" was included in the analysis.

Mantel (1967) tests were also performed in R to evaluate the correlation between F_{ST} and shortest distances at sea among populations for each species and each cluster separately.

Past effective population sizes

For each population, to infer population demographic histories, site allele frequency likelihoods were generated with ANGSD v0.935 (Korneliussen, Albrechtsen, & Nielsen, 2014), directly from the individual bam files. Genotype likelihoods were computed using the samtools method (-GL 1; Li et al., 2009), requiring a mapping quality (minMapQ) and a base quality (minQ) of at least 30 and 20, respectively, and considering only sites with no missing data (see Appendix S3, Table S3.3). From that, the folded site frequency spectrum (SFS) was estimated using REALSFS (Nielsen, Korneliussen, Albrechtsen, Li, & Wang, 2012). Past variations in effective population sizes (*Ne*) were reconstructed using Stairway Plot v2.1 (Liu & Fu, 2020) from the folded SFS, both keeping or discarding singletons. Generation time was assumed to be five years for each species, as in *Acropora* (Mao, Economo, & Satoh, 2018; Matz, Treml, Aglyamova, & Bay, 2018), regarding their relatively similar life history traits (e.g., fast growth and maturity). Likewise, the mutation rate per site and per generation was set to 3×10^{-8} (Mao et al., 2018).

RESULTS

A total of 1,023 *Pocillopora* colonies were sequenced (plus seven sequencing replicates), leading to 4.0×10^9 reads (6.1×10^{11} bp), with between 1.7×10^6 and 6.8×10^6 reads per individual [mean ± s.e. = $(3.9 \pm 0.0) \times 10^6$ reads]. Quality controls and adapter trims then led to the removal of 2.6% of the bases. Between 12.1% and 85.4% trimmed reads per individual were successfully mapped on the reference sequences (mean ± s.e. = 76.8 ± 0.2%; only two individuals had less than 50% of their reads mapped and were removed *a posteriori*), with a mean coverage depth (± s.e.) of 48.6× (± 0.1).

Species identification

Genotype calling for the 1,559 SNPs used in the species delimitation analyses in Oury et al. (2023) led to a dataset of 1,023 individuals × 1,559 SNPs, with 4.5% missing data (see Appendix S3, Table S3.4) and a mean SNP coverage depth (± s.e.) of 72.4× (± 1.5). Individual proportions of missing data ranged from 0.3% to 35.5%, except for two individuals (> 75%; removed *a posteriori*).

sNMF assignments at $K = 4$ grouped all 167 colonies already identified in Oury et al. (2023) to a cluster corresponding to their respective species (i.e., *P. acuta*, *P.* aff. *meandrina*, *P.* aff. *verrucosa* or *P. villosa*), with few admixture [mean (± s.e.) colonies assignment probability to the cluster corresponding to the species = 0.96 ± 0.00], while at $K = 6$, clusters corresponded to the genomic species hypotheses (GSHs), but admixture blurred some clusters boundaries [mean (± s.e.) colonies assignment probability to the cluster corresponding to the GSH = 0.89 ± 0.01; see Appendix S4, Fig. S4.1]. Accordingly, the PCA with all 1,023 colonies distinguished four groups corresponding to the four species (see Appendix S4, Fig. S4.2). Thus, the remaining colonies were identified to the species level and were considered to belong to a species when they were assigned to the corresponding

specific cluster with a probability ≥ 0.9 at $K = 4$. Accordingly, all colonies were identified, with 243 colonies assigned to *P. acuta*, 496 to *P.* aff. *meandrina*, 182 to *P.* aff. *verrucosa* and 102 to *P. villosa* (Table 1; see Appendix S2, Table S2.2).

Population structure and connectivity

SNP calling and filtering for each species separately led to four distinct datasets: *P. acuta* [244 individuals (including three replicates) × 1,493 SNPs; *%NA* = 3.9%], *P.* aff. *meandrina* [497 individuals (including one replicate) × 1,412 SNPs; *%NA* = 4.2%], *P.* aff. *verrucosa* [185 individuals (including three replicates) × 1,446 SNPs; *%NA* = 4.1%] and *P. villosa* [102 individuals (no replicate) × 1,351 SNPs; *%NA* = 4.6%] (see Appendix S3, Table S3.4).

Clonal lineages identification

Over all datasets, sequencing replicates differed by less than 0.5% (see Appendix S5, Fig. S5.3). The histograms of the pairwise distances showed a clear antimode for three species: *P.* aff. *meandrina*, *P.* aff. *verrucosa* and *P. villosa*, with no comparison falling between 0.5% and 18-20%. Thus, for these three species, colonies were considered to belong to the same clonal lineage when they differed from less than 1%. Accordingly, one lineage was represented by 11 sympatric colonies in *P. villosa*, and 12 others were represented by two or three sympatric colonies (six in *P.* aff. *meandrina*, two in *P.* aff. *verrucosa* and four in *P. villosa*), resulting in clonal richnesses (R) of 0.99, 0.98 and 0.84 for *P.* aff. *meandrina*, *P.* aff. *verrucosa* and *P. villosa*, respectively (Table 1; see Appendix S2, Table S2.2). For *P. acuta*, only one comparison fell between 1.3% and 4.9% (see Appendix S5, Fig. S5.3). The threshold was thus defined at 3% so that the colonies diverging from 2.4% belong to the same clonal lineage. Accordingly, a total of 95 different *P. acuta* clonal lineages were detected among the 241 colonies ($R = 0.39$; Table 1; see Appendix S2, Table S2.2), with 51 lineages represented by two to 18 colonies. Five lineages were found at different sampling sites: one in MAD05/MAD06 (distant from 38 km), three in REU3/REU5 (22 km) and one in REU4/REU5 (11 km).

Structure analyses

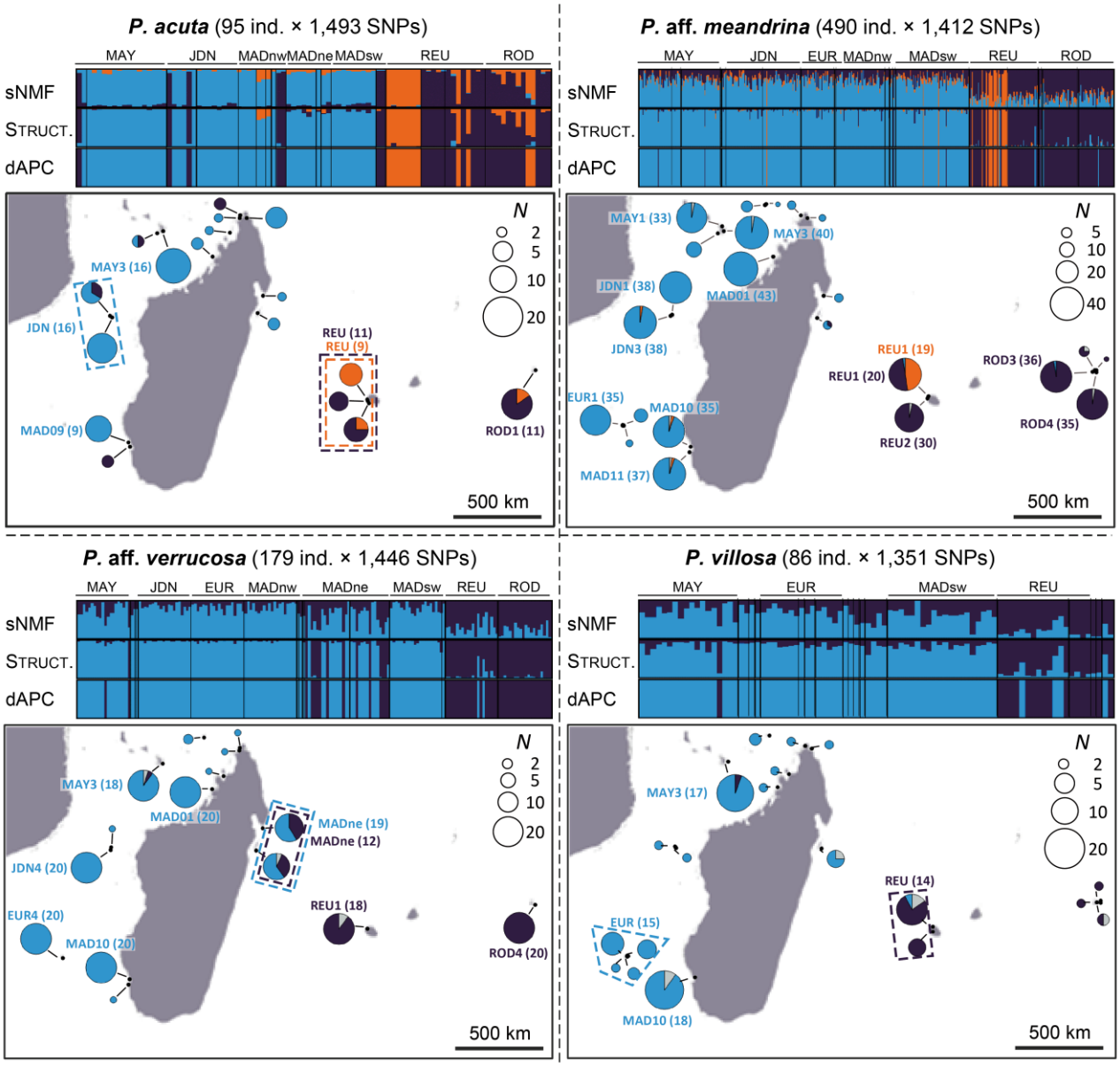
Results from the three assignment methods (i.e., sNMF, STRUCTURE and DAPC) were very consistent across each of the four species, at least for the first K values (Fig. 2; see Appendix S6). However, their respective decision criteria [i.e., the cross-entropy for sNMF, the estimated posterior probability LnP(D) for STRUCTURE and the Bayesian information criteria (BIC) for DAPC] supported different most likely K values. Representing mathematical estimates and not always the biological truth, we retained for each species the maximum K for which all methods were congruent, rather than the value suggested by the criteria (which was not always the same).

For *P. acuta*, both for the entire and the truncated datasets (see Appendix S6, Fig. S6.4 and S6.5), the three assignment methods were congruent at $K = 2$ and $K = 3$ and retrieved the three GSHs from Oury et al. (2023; i.e., GSH05c-1, GSH05c-2 and GSH05d, corresponding to the orange, purple and blue clusters herein, respectively). From $K = 4$, assignments became incongruent between

datasets, but also between methods for the entire dataset, suggesting three clusters for *P. acuta*. The PCA, the MST and the network also retrieved these three clusters (see Appendix S6, Fig. S6.4 and S6.4). All colonies were assigned to one of the three clusters [N_{blue} = 141 (55 clonal lineages; R_{blue} = 0.39); N_{purple} = 45 (29 clonal lineages; R_{purple} = 0.64); N_{orange} = 55 (11 clonal lineages; R_{orange} = 0.19); see Appendix S2, Table S2.2], with a clear ecoregion pattern [95% of the colonies sampled in Madagascar and surrounding islands belong to the blue cluster, while 100% of the colonies sampled in the Mascarene Islands (Reunion and Rodrigues) belong to the purple and orange clusters; Fig. 2; see Appendix S6, Fig. S6.6]. However, this partitioning induced small population sizes, especially for the truncated dataset. F_{ST} between populations were all significantly high ($P < 0.001$), ranging from 0.032*** to 0.332*** for the entire dataset, and from 0.045*** to 0.273*** for the truncated one, but intra-cluster F_{ST} (mean ± s.e. = 0.129 ± 0.013 and 0.059 ± 0.010 for the entire and truncated datasets, respectively) were generally smaller than inter-cluster ones (0.261 ± 0.007 and 0.212 ± 0.009, respectively; see Appendix S6, Table S6.5a-b and Fig. S6.7). In particular, the highest F_{ST} were found for inter-cluster population pairs involving a population belonging to the purple cluster.

For *P.* aff. *meandrina* (see Appendix S6, Fig. S6.8), three clusters were found by the three assignment methods and the PCA, but the MST and the network only distinguished the orange cluster (Fig. 2; see Appendix S6, Fig. S6.8). All but seven colonies (1%) were assigned to one of the three clusters (N_{blue} = 335, N_{purple} = 126, N_{orange} = 22; see Appendix S2, Table S2.2), with the same geographic pattern as identified for *P. acuta* (99% to the blue cluster in Madagascar vs. 99% to the purple and orange clusters in the Mascarenes; Fig. 2). Thirteen populations were retained for subsequent analyses (Fig. 2). Considering only the blue and purple clusters, F_{ST} ranged from -0.001^{NS} to 0.010***, with significant and higher F_{ST} for inter-cluster comparisons [mean intra-cluster F_{ST} (± s.e.) = 0.000 ± 0.000; mean inter-cluster F_{ST} (± s.e.) = 0.008 ± 0.000]. However, inter-cluster F_{ST} involving the population from the orange cluster were almost 10 times higher (mean ± s.e. = 0.066 ± 0.001; see Appendix S6, Table S6.5c and Fig. S6.7).

Finally, for *P.* aff. *verrucosa* and *P. villosa* (see Appendix S6, Fig. S6.9 and S6.10, respectively), results were very similar and suggested two clusters for each species (Fig. 2). Indeed, all three assignment methods were congruent for $K = 2$, while incongruent for $K \geq 3$. The PCA retrieved each cluster, but the MST and the network did not (see Appendix S6, Fig. S6.9 and S6.10). All colonies, except four (2%) for *P.* aff. *verrucosa* and six (7%) for *P. villosa*, were assigned to one of the two clusters (*P.* aff. *verrucosa*: N_{blue} = 124, N_{purple} = 51; *P. villosa*: N_{blue} = 62, N_{purple} = 18; see Appendix S2, Table S2.2), again according to their ecoregion (*P.* aff. *verrucosa*: 91% to the blue cluster in Madagascar vs. 100% to the purple cluster in the Mascarenes; *P. villosa*: 98% to the blue cluster in Madagascar vs. 94% to the purple cluster in the Mascarenes; Fig. 2). Nine and four populations were retained for subsequent analyses, for *P.* aff. *verrucosa* and *P. villosa*, respectively (Fig. 2). F_{ST} were of the same order of magnitude for both species (*P.* aff. *verrucosa*: $-0.002^{NS} < F_{ST} < 0.014$***; *P. villosa*: $-0.003^{NS} < F_{ST} < 0.016$***) and were significantly positive, with inter-cluster F_{ST} being higher [both species: mean intra-cluster F_{ST} (± s.e.) = 0.000 ± 0.000; mean inter-cluster F_{ST} (± s.e.) = 0.011 ± 0.000; see Appendix S6, Table S6.4d-e and Fig. S6.7].

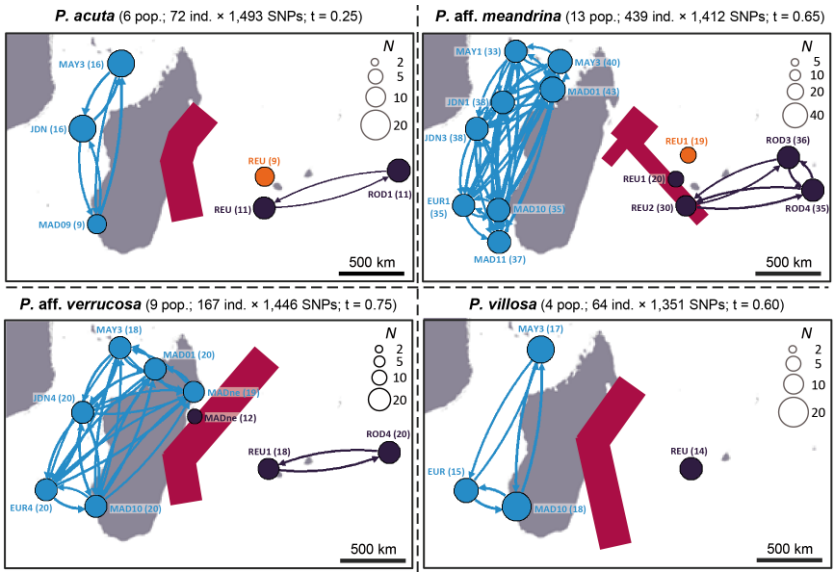


[double column] **Figure 2** Population structure of each *Pocillopora* species (i.e., *P. acuta*, *Pocillopora* aff. *P. meandrina*, *Pocillopora* aff. *P. verrucosa* and *P. villosa nomen nudum*). For each species (numbers of individuals and SNPs of the corresponding dataset in parentheses), results from the three assignment methods (sNMF, STRUCTURE and DAPC) at the retained *K* (*K* = 2 for *P.* aff. *verrucosa* and *P. villosa*; *K* = 3 for *P. acuta* and *P.* aff. *meandrina*) are indicated above, as well as the corresponding cluster repartition below (grey portions represent individuals not assigned to the same cluster by all methods). Populations retained for further analyses are labelled (colour refers to the cluster; population size in parentheses). Dashed polygons represent pooled populations. *N*: number of colonies; MAY: Mayotte, JDN: Juan de Nova Island, EUR: Europa Island, MAD: Madagascar (nw: northwestern, ne: northeastern, sw: southwestern), REU: Reunion Island, ROD: Rodrigues.

Direction and barrier to gene flow

The networks of relative migration direction among populations and barrier analyses gave similar results among species and highlighted reduced gene flow between Madagascar and the Mascarene Islands, in concordance with the clusters previously delimited. Thus, gene flow among populations from the same cluster was higher compared to that among populations from different clusters, but showed no dominant direction (Fig. 3; see Appendix S7, Fig. S7.11). All species but *P. acuta* had a

similar filter threshold beyond which the network becomes fragmented (0.65 ≤ t ≤ 0.75 vs. 0.25 for *P. acuta*; Fig. 3).

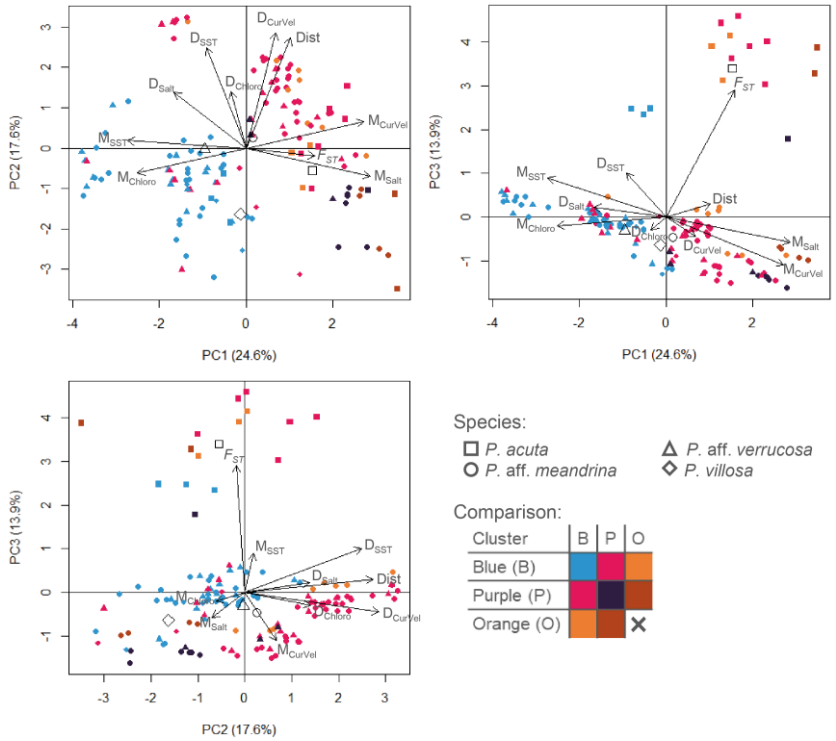


[2/3rd column] **Figure 3** Direction and barrier to gene flow for each *Pocillopora* species (i.e., *P. acuta*, *Pocillopora* aff. *P. meandrina*, *Pocillopora* aff. *P. verrucosa* and *P. villosa nomen nudum*). Populations are coloured according to clusters. Arrows indicate gene flow above the filter threshold for which the network becomes fragmented (t; indicated above, along with the numbers of populations, individuals and SNPs retained). Note that no arrows do not indicate the absence of gene flow. Red lines symbolise barriers (width proportional to support over 1,000 bootstrap replicates).

Isolation by distance × environment

The first three principal components (PC1-3) of the FAMD explained 56.1% of the variability (Fig. 4). PC1 and PC2 separated population pairs of Madagascar (i.e., comparisons within the blue cluster for each species) from other pairs, in relation with environmental variables, while PC3 separated population pairs based on species (*P. acuta* being more distant), due to F_{ST}. Thus, no correlation was found between F_{ST} and environmental variables, nor with distances, but rather with the species variable (accounting for species intrinsic differences; Fig. 4).

Mantel tests revealed a significant, but weak, correlation between F_{ST} and shortest distances at sea for *P.* aff. *verrucosa* (N = 36; R^2 = 0.291; P < 0.001***) and its blue cluster (N = 15; R^2 = 0.267; P < 0.048*). All other correlations were not significant ($P > 0.05^{NS}$; see Appendix S8, Fig. S8.12).



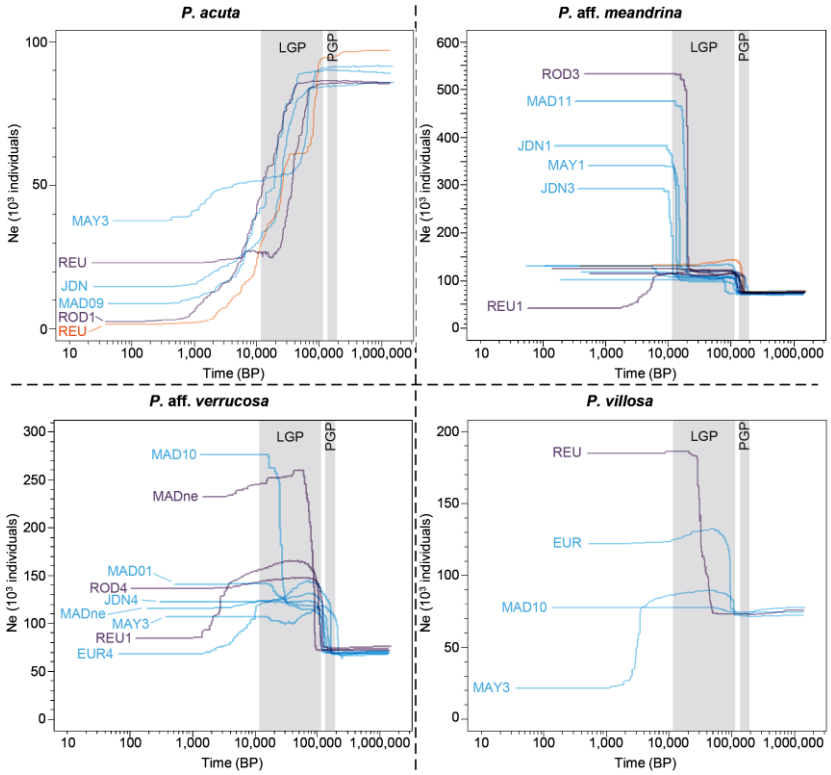
[2/3rd column] **Figure 4** Isolation by distance × environment in *Pocillopora* species from the southwestern Indian Ocean (i.e., *P. acuta*, *Pocillopora* aff. *P. meandrina*, *Pocillopora* aff. *P. verrucosa* and *P. villosa nomen nudum*; indicated by a different symbol). First three principal components (PC1-3; percentages of variation explained in parentheses) of the factorial analysis of mixed data (FAMD) with within-species pairwise population F_{ST}, shortest distances at sea (Dist) and eight environmental variables: mean (M) and difference (D) in present mean surface temperature (SST), salinity (Salt), current velocity (CurVel) and chlorophyll concentration (Chloro). The correlation circle of these 10 quantitative variables is projected on the individual plot. Individuals (i.e., population pairs) are coloured differently depending on cluster assignments, as indicated by the table in the legend (e.g., comparisons between two populations belonging to a blue cluster are shown in blue). Non-coloured symbols indicate the qualitative variable "species".

Past effective population sizes

Past effective population size variations were very similar whether singletons were included or not. Therefore, here, we only present results without singletons, as they show fewer variations on small time scales and instead allow focusing on variation trends.

Except for *P. acuta*, similar ancestral variations of *Ne* through time were reconstructed among species. All populations from *P.* aff. *meandrina*, *P.* aff. *verrucosa* and *P. villosa* (it was less obvious for this latter species, probably due to smaller population sample sizes) thus showed an ancestral signature of population expansion between ca. 100,000 and 200,000 years ago, which coincides with the end of the penultimate glacial period (PGP; ca. 135,000-194,000 years ago; Colleoni, Wekerle, Näslund, Brandefelt, & Masina, 2016). This expansion brought the ancestral *Ne* from ca. 75,000 to 125,000 individuals (Fig. 5; see Appendix S9, Fig. S9.13). However, recent variations were different among species and among populations within species. Some populations of *P.* aff. *meandrina* thus showed a second signature of population expansion between ca. 10,000 and 20,000 years ago, which coincides with the end of the last glacial period (LGP; ca. 11,700-115,000 years ago; Adams, Maslin, & Thomas, 1999), while other populations showed no variation or a decline between ca. 2,000 and 5,000 years ago. Finally, for *P. acuta*, all populations showed a bottleneck between ca. 2,000 and

100,000 years ago, bringing *Ne* from ca. 90,000 to less than 40,000 individuals depending on the population (Fig. 5; see Appendix S9, Fig. S9.13).



[2/3rd column] **Figure 5** Past effective population sizes (*Ne*) for each population (see Fig. 2 for the codes; colour refers to the cluster) of the four *Pocillopora* species from the southwestern Indian Ocean (i.e., *P. acuta*, *Pocillopora* aff. *P. meandrina*, *Pocillopora* aff. *P. verrucosa* and *P. villosa nomen nudum*). Only populations with divergent variations are labelled for *P.* aff. *meandrina* to lighten the figure. Grey areas indicate glacial periods (LGP: last glacial period: ca. 11,700-115,000 years ago; PGP: penultimate glacial period: ca. 135,000-194,000 years ago).

DISCUSSION

Focusing on *Pocillopora* species from the southwestern Indian Ocean (SWIO), this study assesses the genetic structure of four species presenting different reproductive strategies and colonising various habitats using genome-wide SNPs. Our results highlighted a similar structuring pattern within each species suggesting weak connectivity between Madagascar and the Mascarene Islands ecoregions. Moreover, similar demographic histories were inferred among populations (except for *P. acuta*), potentially indicating that populations from these different species have met the same environmental constraints and reacted similarly. This should be considered in light of ongoing rapid climate change. Altogether, through a multi-species genomic approach, these results offer new insights to better understand the connectivity pattern in the SWIO and to implement effective conservation measures in a context of coral decline.

Weak connectivity between Madagascar and the Mascarene Islands

In this study, whichever the species considered, more than 90% of the colonies sampled in the Madagascar ecoregion were assigned to a single genetic cluster, while more than 90% of the colonies sampled in the Mascarene Islands were assigned to one or two distinct clusters restricted almost

exclusively to this ecoregion. This, together with other analyses (networks, F_{ST}), supports a clear genetic structuring pattern, related to geography, in all four investigated *Pocillopora* species.

This difference among genetic structuring patterns was previously found using microsatellites in a larger number of colonies (including colonies from this study; see Appendix S1, Table S1.1): while high connectivity was reported for *P.* aff. *meandrina, P.* aff. *verrucosa* and *P. villosa* (SSH09a, SSH13a and SSH13b in Oury et al., 2021, respectively), strong genetic differentiation was found within *P. acuta* (PSH05; Gélin, Pirog, et al., 2018), so as in this study. Noteworthy, for *P.* aff. *meandrina*, the three sympatric clusters previously found in relatively similar proportions in all sampled sites from the SWIO (SSH09a-1, SSH09a-2 and SSH09a-3 *sensu* Gélin, Fauvelot, et al., 2018) were not retrieved: this over-partitioning was caused by a single microsatellite locus (PV7). At the level of SSH09a (i.e., *P.* aff. *meandrina*), general high connectivity among populations was found at the scale of the SWIO, as for *P.* aff. *verrucosa* and *P. villosa*. The microsatellites used thus appear not enough informative to detect subtle structuring patterns such as those found between the blue and purple clusters in *P.* aff. *meandrina*, *P.* aff. *verrucosa* and *P. villosa* using genomic data, while remaining efficient when patterns are more pronounced, such as in *P. acuta*. Genomic data thus allows finer resolution of connectivity patterns, as previously suggested (e.g., Coscia et al., 2020; Lal, Southgate, Jerry, & Zenger, 2016).

Weak connectivity was already reported between Madagascar and the Mascarenes for several other taxa, including hydrozoans (Postaire, Gélin, Bruggemann, & Magalon, 2017; Postaire, Gélin, Bruggemann, Pratlong, & Magalon, 2017), giant clams (Fauvelot et al., 2020), holoturians (Pirog et al., 2019), brittle stars (Hoareau, Boissin, Paulay, & Bruggemann, 2013) and fishes (Muths, Tessier, & Bourjea, 2015). Geographic distances (although no significant isolation by distance was found), coupled with currents, likely explain this weak gene flow between both ecoregions. The SWIO oceanic circulation is strongly influenced by the south equatorial current (SEC). The latter, going from east to west, transports propagules from the Mascarenes to Madagascar. However, Madagascar acts as a land barrier, deflecting currents (and propagules) to the south (= south-east Madagascar current; SEMC;), and then to the east due to the Coriolis force, generating the south Indian subtropical gyre (SISTG; Hancke, Roberts, & Ternon, 2014; Lutjeharms & Bornman, 2010; Schott & McCreary Jr, 2001; Fig. 1), congruent with larval dispersal models (Crochelet et al., 2020; Gamoyo, Obura, & Reason, 2019). Accordingly, asymmetric migration from the Mascarenes to the east coast of Madagascar, a locality little sampled in our study, is expected to occur, something that could then be tested using coalescent-based demographic simulations. Further studies, including samples from eastern Madagascar, are thus needed to clarify the connectivity of the whole SWIO region.

Habitats and reproductive strategies influence connectivity

Although similar structuring patterns were found among SWIO populations for the four *Pocillopora* species, the genetic differentiation was stronger (F_{ST} about 10 times higher) for *P. acuta*. This seems related to intrinsic differences among species, and particularly to preferred habitats and reproductive strategies.

Pocillopora acuta is mainly found in shallow (< 5 m depth) habitats, such as lagoons or flat reefs (Veron, 2000), which are relatively enclosed. Conversely, the other species are found on outer reef slopes in contact with the open ocean (Veron, 2000). Populations from *P. acuta* would therefore be more prone to self-recruitment (see e.g., Pinsky, Palumbi, Andréfouët, & Purkis, 2012), leading to the higher genetic differentiation found among them. Additionally, this species reproduces both through sexual and asexual strategies (Gélin, Fauvelot, et al., 2017), with a high prevalence of clonal propagation (e.g., Gélin, Fauvelot, et al., 2017; Gorospe & Karl, 2013; Torda, Lundgren, Willis, & van Oppen, 2013a, 2013b), as found here. Although our sampling was not designed to study clonality, several colonies of *P. acuta* belonged to the same clonal lineage (clonal richness, $R = 0.39$), compared to other species ($R \geq 0.84$). Most colonies from the same clonal lineage were found in the same site, and only few were found in different sites less than 40 km apart, confirming previous observations (Gélin, Fauvelot, et al., 2017; Souter et al., 2009). Dispersal over hundreds or thousands of kilometres of asexually produced larvae (Oury et al., 2019), and even more so of fragments, therefore appears limited. Accordingly, genetic differentiation among *P. acuta* populations should be higher than in other species for which clonal propagation is rarer.

Other species-specific differences could be responsible for the observed differences. For instance, larval biology represents a key element of dispersal abilities. Differences in settlement behaviour and competency periods among species could induce dispersal at greater or lesser scales. In *P. damicornis*, planulae competent over 100 days were reported (Richmond, 1987), but this duration remains unknown for other species.

The Mascarenes as stepping stones for long-distance gene flow?

For two species (*P. acuta* and *P.* aff. *meandrina*), colonies sampled in the Mascarenes were assigned to two distinct and sympatric clusters (the purple and orange ones) strongly differentiated. These clusters may represent distinct cryptic species or lineages that diverged recently and are found in apparent sympatry but with depth or microhabitat differential distributions (as in *Seriatopora hystrix*; van Oppen, Bongaerts, Underwood, Peplow, & Cooper, 2011). However, although not having precise depth and habitat data for each sample, samples from the same site and assigned to the two clusters were collected during the same dive and mixed in sampling order, suggesting no depth nor habitat-dependent distribution.

The purple cluster found in *P. acuta* was previously detected in a study exploring species limits within the genus using genomics (Oury et al., 2023; corresponding to GSH05c-2 therein). Surprisingly, it was found genetically closer to *P. acuta* colonies from New Caledonia ecoregion than to colonies of the SWIO. This may suggest an eastern origin of these colonies (central or eastern Indo-Pacific), but the geographic distances involved appear too large, even through stepping-stones (Wood, Paris, Ridgwell, & Hendy, 2014), for conventional gene flow (the distance between the Mascarenes and western Australia is over 5,000 km). Indeed, weak connectivity was previously reported between populations of *Pocillopora* corals from the Indian and Pacific Oceans (e.g., Gélin, Pirog, et al., 2018; Oury et al., 2021), but also in hydrozoans (Postaire, Gélin, Bruggemann, & Magalon, 2017; Postaire, Gélin, Bruggemann, Pratlong, et al., 2017), holothurians (Pirog et al., 2019) or starfishes (Otwoma &

Kochzius, 2016). Gene flow through passive oceanic rafting (Nikula, Spencer, & Waters, 2013) or human movements (e.g., ballast waters, hull fouling; Gollasch, 2007) may be involved.

For *P.* aff. *meandrina*, the most genetically distant cluster was the orange one, restricted to REU1, close to the main international seaport of Reunion Island. As no colonies were found admixed between the orange and purple clusters, although being sympatric and supposedly belonging to the same species (i.e., being interfertile), a recent colonisation (inducing limited reproduction events between both clusters), through maritime transport, can be hypothesised. However, in this case, a recent bottleneck effect should have been detected, whereas *Ne* variations of this population appear similar to the others, whether singletons are considered or not. It is therefore unclear whether the Mascarenes could represent stepping-stones for long-distance gene flow and complementary larger-scale studies, including colonies from the northern and eastern Indian Ocean, are needed to confirm the origin of these clusters. Noteworthy, should they represent distinct species, results and interpretations of this study remain the same since analyses were performed on each cluster separately.

Shared demographic histories and constraints

As genetic structuring patterns among *Pocillopora* species in the SWIO, ancestral demographic histories were very similar, except for *P. acuta*. They suggested an expansion of all SWIO populations from *P.* aff. *meandrina*, *P.* aff. *verrucosa* and *P. villosa* ca. 100,000 years ago, following the penultimate glacial period (Colleoni et al., 2016), as previously found in *Acropora tenuis* (Cooke et al., 2020; Mao et al., 2018). This period was characterised by a global warming of ocean temperatures (Herbert, Peterson, Lawrence, & Liu, 2010), a sea level rise associated with the melting of glaciers (Rohling et al., 1998, 2014), as well as an intensification of currents and a change in their direction (Colleoni et al., 2016). Altogether, these changes probably induced the colonisation of new habitats, and therefore demographic expansions.

More recently, demographic reconstructions diverged among populations, some showing an expansion between ca. 10,000 and 20,000 years ago, following the last glacial maximum, while others remained stable or showed a bottleneck over the same period. On one hand, these differences could result from differential environmental constraints depending on the populations. For example, changes in currents might both favour gene flow among some populations but increase the isolation of others. However, demographic inferences differed between sympatric populations from different species, questioning this hypothesis. On the other hand, differences could result from methodological artefacts, as the number of SNPs used (see Appendix S9, Fig. S9.13) might be insufficient for accurate demographic inferences (Excoffier, Dupanloup, Huerta-Sánchez, Sousa, & Foll, 2013; Marchi, Schlichta, & Excoffier, 2021; Terhorst & Song, 2015).

Finally, concerning *P. acuta*, all populations showed a constant demographic decline for about 80,000 years which is probably related to the strong genetic structuring among populations (Heller, Chikhi, & Siegismund, 2013; Lesturgie, Planes, & Mona, 2022). Inferred sizes of *P. acuta* populations must nevertheless be interpreted cautiously, as representing the effective and not the real population sizes. Consequently, a clonal lineage is considered as a single individual, whereas it could

be represented by dozens of colonies that are all able to reproduce sexually. Populations sizes of this species are thus certainly underestimated, especially since the models on which demographic inferences are based were not designed for clonal populations.

Thus, except for *P. acuta*, all *Pocillopora* populations from the SWIO showed similar demographic signals, suggesting that they met the same environmental constraints and reacted in the same way. This similar sensitivity to environmental changes among species should be taken into account when implementing conservation measures, especially with ongoing climate change.

In conclusion, this study assesses for the first time the connectivity and demographic history of four *Pocillopora* species from the SWIO using genome-wide SNPs. Genomic data refined the genetic structuring patterns previously inferred using microsatellites and detected a weak connectivity between Madagascar and the Mascarene Islands ecoregions. Moreover, this multi-species approach highlighted different genetic structures likely linked to species-specific characteristics, such as habitats and reproductive strategies. Similarly, demographic reconstructions highlighted shared demographic histories (except for *P. acuta*), probably as populations from the different species shared the same environmental constraints and reacted similarly. Altogether, these results suggest that the four species of *Pocillopora* studied, especially *P.* aff. *meandrina*, *P.* aff. *verrucosa* and *P. villosa*, show the same sensitivity to environmental changes. Their conservation must therefore be done as a whole, with appropriate measures for each management unit (i.e., distinguishing Madagascar and the Mascarene Islands ecoregions).

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CONFLICT OF INTEREST

The authors state that there is no conflict of interest.

DATA ACCESSIBILITY

Raw sequencing reads were deposited on the NCBI (BioProject PRJNA909966). All other data underlying this article (metadata, VCF files, etc.) are available online (https://doi.org/10.5061/dryad.pnvx0k6vw).

REFERENCES

Adams, J., Maslin, M., & Thomas, E. (1999). Sudden climate transitions during the Quaternary. *Progress in Physical Geography*, *23*(1), 1-36. https://doi.org/10.1177/030913339902300101

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., & De Clerck, O. (2018). Bio-ORACLE v2.0 : Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, *27*(3), 277-284. https://doi.org/10.1111/geb.12693

Benzoni, F., Bianchi, C. N., & Morri, C. (2003). Coral communities of the northwestern Gulf of Aden (Yemen) : Variation in framework building related to environmental factors and biotic conditions. *Coral Reefs*, *22*(4), 475-484. https://doi.org/10.1007/s00338-003-0342-1

Bosch, S., & Fernandez, S. (2023). *sdmpredictors : Species distribution modelling predictor datasets* [R]. https://CRAN.R-project.org/package=sdmpredictors

Bouwmeester, J., Coker, D. J., Sinclair-Taylor, T. H., & Berumen, M. L. (2021). Broadcast spawning of *Pocillopora verrucosa* across the eastern and western coast of the central Red Sea. *Ecosphere*, *12*(1), 03340. https://doi.org/10.1002/ecs2.3340

Buck-Wiese, H., Burgués, I., Medrano, A., Navarrete-Fernandez, T., Garcia, M., & Wieters, E. A. (2018). Patterns in sexual reproduction of the dominant scleractinian corals at Rapa Nui (Easter Island) : *Pocillopora verrucosa* and *Porites lobata*. *Aquatic Biology*, *27*, 1-11. https://doi.org/10.3354/ab00691

Clark, T. W. (1993). Creating and using knowledge for species and ecosystem conservation : Science, organizations, and policy. *Perspectives in Biology and Medicine*, *36*(3), 497-525. https://doi.org/10.1353/pbm.1993.0013

Coelho, M. A. G., & Lasker, H. R. (2016). Larval dispersal and population connectivity in Anthozoans. In S. Goffredo & Z. Dubinsky (Éds.), *The Cnidaria, Past, Present and Future* (p. 291-315). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-31305-4_19

Colleoni, F., Wekerle, C., Näslund, J.-O., Brandefelt, J., & Masina, S. (2016). Constraint on the penultimate glacial maximum Northern Hemisphere ice topography (≈140 kyrs BP). *Quaternary Science Reviews*, *137*, 97-112. https://doi.org/10.1016/j.quascirev.2016.01.024

Cooke, I., Ying, H., Forêt, S., Bongaerts, P., Strugnell, J. M., Simakov, O., … Miller, D. J. (2020). Genomic signatures in the coral holobiont reveal host adaptations driven by Holocene climate change and reef specific symbionts. *Science Advances*, *6*(48), abc6318. https://doi.org/10.1126/sciadv.abc6318

Coscia, I., Wilmes, S. B., Ironside, J. E., Goward-Brown, A., O’Dea, E., Malham, S. K., … Robins, P. E. (2020). Fine-scale seascape genomics of an exploited marine species, the common cockle *Cerastoderma edule*, using a multimodelling approach. *Evolutionary Applications*, *13*(8), 1854-1867. https://doi.org/10.1111/eva.12932

Cowman, P. F., Quattrini, A. M., Bridge, T. C. L., Watkins-Colwell, G. J., Fadli, N., Grinblat, M., … Baird, A. H. (2020). An enhanced target-enrichment bait set for Hexacorallia provides phylogenomic resolution of the staghorn corals (Acroporidae) and close relatives. *Molecular Phylogenetics and Evolution*, *153*, 106944. https://doi.org/10.1016/j.ympev.2020.106944

Crochelet, E., Barrier, N., Andrello, M., Marsac, F., Spadone, A., & Lett, C. (2020). Connectivity between seamounts and coastal ecosystems in the Southwestern Indian Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, *176*, 104774. https://doi.org/10.1016/j.dsr2.2020.104774

De Palmas, S., Soto, D., Ho, M.-J., Denis, V., & Chen, C. A. (2021). Strong horizontal and vertical connectivity in the coral *Pocillopora verrucosa* from Ludao, Taiwan, a small oceanic island. *PLoS ONE*, *16*(10), 0258181. https://doi.org/10.1371/journal.pone.0258181

Dorken, M. E., & Eckert, C. G. (2001). Severely reduced sexual reproduction in northern populations of a clonal plant, *Decodon verticillatus* (Lythraceae). *Journal of Ecology*, *89*(3), 339-350. https://doi.org/10.1046/j.1365-2745.2001.00558.x

Eddy, T. D., Cheung, W. W., & Bruno, J. F. (2018). Historical baselines of coral cover on tropical reefs as estimated by expert. *PeerJ*, *6*, 4308. https://doi.org/10.7717/peerj.4308

Excoffier, L., Dupanloup, I., Huerta-Sánchez, E., Sousa, V. C., & Foll, M. (2013). Robust demographic inference from genomic and SNPdata. *PLoS Genetics*, *9*(10), 1003905. https://doi.org/10.1371/journal.pgen.1003905

Fauvelot, C., Zuccon, D., Borsa, P., Grulois, D., Magalon, H., Riquet, F., … Bouchet, P. (2020). Phylogeographical patterns and a cryptic species provide new insights into Western Indian Ocean giant clams phylogenetic relationships and colonization history. *Journal of Biogeography*, *47*(5), 1086-1105. https://doi.org/10.1111/jbi.13797

Frichot, E., & François, O. (2015). LEA : An R package for landscape and ecological association studies. *Methods in Ecology and Evolution*, *6*(8), 925-929. https://doi.org/10.1111/2041-210X.12382

Frichot, E., Mathieu, F., Trouillon, T., Bouchard, G., & François, O. (2014). Fast and efficient estimation of individual ancestry coefficients. *Genetics*, *196*(4), 973-983. https://doi.org/10.1534/genetics.113.160572

Gamoyo, M., Obura, D., & Reason, C. J. C. (2019). Estimating connectivity through larval dispersal in the western Indian Ocean. *Journal of Geophysical Research: Biogeosciences*, *124*(8), 2446-2459. https://doi.org/10.1029/2019JG005128

Gélin, P., Fauvelot, C., Bigot, L., Baly, J., & Magalon, H. (2018). From population connectivity to the art of striping Russian dolls : The lessons from *Pocillopora* corals. *Ecology and Evolution*, *8*(2), 1411-1426. https://doi.org/10.1002/ece3.3747

Gélin, P., Fauvelot, C., Mehn, V., Bureau, S., Rouzé, H., & Magalon, H. (2017). Superclone expansion, long-distance clonal dispersal and local genetic structuring in the coral *Pocillopora damicornis* type *β* in Reunion Island, South Western Indian Ocean. *PLoS ONE*, *12*(1), 0169692. https://doi.org/10.1371/journal.pone.0169692

Gélin, P., Pirog, A., Fauvelot, C., & Magalon, H. (2018). High genetic differentiation and low connectivity in the coral *Pocillopora damicornis* type *β* at different spatial scales in the Southwestern Indian Ocean and the Tropical Southwestern Pacific. *Marine Biology*, *165*, 167. https://doi.org/10.1007/s00227-018-3428-6

Gélin, P., Postaire, B., Fauvelot, C., & Magalon, H. (2017). Reevaluating species number, distribution and endemism of the coral genus *Pocillopora* Lamarck, 1816 using species delimitation methods and microsatellites. *Molecular Phylogenetics and Evolution*, *109*, 430-446. https://doi.org/10.1016/j.ympev.2017.01.018

Gollasch, S. (2007). Is ballast water a major dispersal mechanism for marine organisms? In W. Nentwig (Éd.), *Biological Invasions* (p. 49-57). Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-540-36920-2_4

Gorospe, K. D., & Karl, S. A. (2013). Genetic relatedness does not retain spatial pattern across multiple spatial scales : Dispersal and colonization in the coral, *Pocillopora damicornis*. *Molecular Ecology*, *22*(14), 3721-3736. https://doi.org/10.1111/mec.12335

Gray, J. S. (1997). Marine biodiversity : Patterns, threats and conservation needs. *Biodiversity and Conservation*, *6*, 153-175. https://doi.org/10.1023/a:1018335901847

Hancke, L., Roberts, M. J., & Ternon, J.-F. (2014). Surface drifter trajectories highlight flow pathways in the Mozambique Channel. *Deep Sea Research Part II: Topical Studies in Oceanography*, *100*, 27-37. https://doi.org/10.1016/j.dsr2.2013.10.014

Heller, R., Chikhi, L., & Siegismund, H. R. (2013). The confounding effect of population structure on Bayesian skyline plot inferences of demographic history. *PLoS ONE*, *8*(5), 62992. https://doi.org/10.1371/journal.pone.0062992

Herbert, T. D., Peterson, L. C., Lawrence, K. T., & Liu, Z. (2010). Tropical ocean temperatures over the past 3.5 million years. *Science*, *328*(5985), 1530-1534. https://doi.org/10.1126/science.1185435

Hijmans, R. J. (2023). *raster : Geographic data analysis and modeling* [R]. https://CRAN.R-project.org/package=raster

Hoareau, T. B., Boissin, E., Paulay, G., & Bruggemann, J. H. (2013). The Southwestern Indian Ocean as a potential marine evolutionary hotspot : Perspectives from comparative phylogeography of reef brittle-stars. *Journal of Biogeography*, *40*(11), 2167-2179. https://doi.org/10.1111/jbi.12155

Huson, D. H., & Bryant, D. (2006). Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution*, *23*(2), 254-267. https://doi.org/10.1093/molbev/msj030

Johnston, E. C., Forsman, Z. H., Flot, J.-F., Schmidt-Roach, S., Pinzón, J. H., Knapp, I. S. S., & Toonen, R. J. (2017). A genomic glance through the fog of plasticity and diversification in *Pocillopora*. *Scientific Reports*, *7*(1), 5991. https://doi.org/10.1038/s41598-017-06085-3

Jombart, T. (2008). adegenet : A R package for the multivariate analysis of genetic markers. *Bioinformatics*, *24*(11), 1403-1405.

Jombart, T., Devillard, S., & Balloux, F. (2010). Discriminant analysis of principal components : A new method for the analysis of genetically structured populations. *BMC Genetics*, *11*(1), 94. https://doi.org/10.1186/1471-2156-11-94

Kamvar, Z. N., Tabima, J. F., & Grünwald, N. J. (2013). Poppr : An R package for genetic analysis of populations with clonal or partially clonal reproduction. *PeerJ*, *4*, 281. https://doi.org/10.7287/peerj.preprints.161v1

Keenan, K., McGinnity, P., Cross, T. F., Crozier, W. W., & Prodöhl, P. A. (2013). diveRsity : An R package for the estimation and exploration of population genetics parameters and their associated errors. *Methods in Ecology and Evolution*, *4*(8), 782-788. https://doi.org/10.1111/2041-210X.12067

Kivelä, M., Arnaud-Haond, S., & Saramäki, J. (2015). EDENetworks : A user-friendly software to build and analyse networks in biogeography, ecology and population genetics. *Molecular Ecology Resources*, *15*(1), 117-122. https://doi.org/10.1111/1755-0998.12290

Kopelman, N. M., Mayzel, J., Jakobsson, M., Rosenberg, N. A., & Mayrose, I. (2015). CLUMPAK : A program for identifying clustering modes and packaging population structure inferences across *K*. *Molecular Ecology Resources*, *15*(5), 1179-1191. https://doi.org/10.1111/1755-0998.12387

Korneliussen, T. S., Albrechtsen, A., & Nielsen, R. (2014). ANGSD : Analysis of Next Generation Sequencing Data. *BMC Bioinformatics*, *15*(1), 356. https://doi.org/10.1186/s12859-014-0356-4

Kruger, A., & Schleyer, M. H. (1998). Sexual reproduction in the coral *Pocillopora verrucosa* (Cnidaria : Scleractinia) in KwaZulu-Natal, South Africa. *Marine Biology*, *132*(4), 703-710. https://doi.org/10.1007/s002270050434

Lal, M. M., Southgate, P. C., Jerry, D. R., & Zenger, K. R. (2016). Fishing for divergence in a sea of connectivity : The utility of ddRADseq genotyping in a marine invertebrate, the black-lip pearl oyster Pinctada margaritifera. *Marine Genomics*, *25*, 57-68. https://doi.org/10.1016/j.margen.2015.10.010

Lê, S., Josse, J., & Husson, F. (2008). FactoMineR : an R package for multivariate analysis. *Journal of Statistical Software*, *25*(1). https://doi.org/10.18637/jss.v025.i01

Lesturgie, P., Planes, S., & Mona, S. (2022). Coalescence times, life history traits and conservation concerns : An example from four coastal shark species from the Indo-Pacific. *Molecular Ecology Resources*, *22*(2), 554-566. https://doi.org/10.1111/1755-0998.13487

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., … 1000 Genome Project Data Processing Subgroup. (2009). The Sequence Alignment/Map format and SAMtools. *Bioinformatics*, *25*(16), 2078-2079. https://doi.org/10.1093/bioinformatics/btp352

Liu, X., & Fu, Y.-X. (2020). Stairway Plot 2 : Demographic history inference with folded SNP frequency spectra. *Genome Biology*, *21*(1), 280. https://doi.org/10.1186/s13059-020-02196-9

Lutjeharms, J. R., & Bornman, T. G. (2010). The importance of the greater Agulhas Current is increasingly being recognised. *South African Journal of Science*, *106*(3-4), 1-4.

Magalon, H., Adjeroud, M., & Veuille, M. (2005). Patterns of genetic variation do not correlate with geographical distance in the reef-building coral *Pocillopora meandrina* in the South Pacific. *Molecular Ecology*, *14*(7), 1861-1868. https://doi.org/10.1111/j.1365-294X.2005.02430.x

Maggioni, D., Arrigoni, R., Seveso, D., Galli, P., Berumen, M. L., Denis, V., … Montano, S. (2020). Evolution and biogeography of the *Zanclea*-Scleractinia symbiosis. *Coral Reefs*. https://doi.org/10.1007/s00338-020-02010-9

Manni, F., Guérard, E., & Heyer, E. (2004). Geographic patterns of (genetic, morphologic, linguistic) variation : How barriers can be detected by using Monmonier's algorithm. *Human Biology*, *76*(2), 173-190. https://doi.org/10.1353/hub.2004.0034

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, *27*, 209-220.

Mao, Y., Economo, E. P., & Satoh, N. (2018). The roles of introgression and climate change in the rise to dominance of *Acropora* corals. *Current Biology*, *28*(21), 3373-3382.e5. https://doi.org/10.1016/j.cub.2018.08.061

Marchi, N., Schlichta, F., & Excoffier, L. (2021). Demographic inference. *Current Biology*, *31*(6), R276-R279. https://doi.org/10.1016/j.cub.2021.01.053

Matz, M. V., Treml, E. A., Aglyamova, G. V., & Bay, L. K. (2018). Potential and limits for rapid genetic adaptation to warming in a Great Barrier Reef coral. *PLoS Genetics*, *14*(4), e1007220. https://doi.org/10.1371/journal.pgen.1007220

Monmonier, M. S. (1973). Maximum-difference barriers : An alternative numerical regionalization method. *Geographical Analysis*, *5*(3), 245-261.

Muths, D., Tessier, E., & Bourjea, J. (2015). Genetic structure of the reef grouper *Epinephelus merra* in the West Indian Ocean appears congruent with biogeographic and oceanographic boundaries. *Marine Ecology*, *36*(3), 447-461. https://doi.org/10.1111/maec.12153

Nei, M. (1972). Genetic distance between populations. *The American Naturalist*, *106*(949), 283-292. https://doi.org/10.1086/282771

Nei, M. (1973). Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences*, *70*(12), 3321-3323. https://doi.org/10.1073/pnas.70.12.3321

Nielsen, R., Korneliussen, T., Albrechtsen, A., Li, Y., & Wang, J. (2012). SNP calling, genotype calling, and sample allele frequency estimation from new-generation sequencing data. *PLoS ONE*, *7*(7), 37558. https://doi.org/10.1371/journal.pone.0037558

Nikula, R., Spencer, H. G., & Waters, J. M. (2013). Passive rafting is a powerful driver of transoceanic gene flow. *Biology Letters*, *9*(1), 20120821. https://doi.org/10.1098/rsbl.2012.0821

Otwoma, L. M., & Kochzius, M. (2016). Genetic population structure of the coral reef sea star *Linckia laevigata* in the western Indian Ocean and Indo-West Pacific. *PLoS ONE*, *11*(10), 0165552. https://doi.org/10.1371/journal.pone.0165552

Oury, N., Gélin, P., & Magalon, H. (2020). Cryptic species and genetic connectivity among populations of the coral *Pocillopora damicornis* (Scleractinia) in the tropical southwestern Pacific. *Marine Biology*, *167*, 142. https://doi.org/10.1007/s00227-020-03757-z

Oury, N., Gélin, P., & Magalon, H. (2021). High connectivity within restricted distribution range in *Pocillopora* corals. *Journal of Biogeography*, *48*(7), 1679-1692. https://doi.org/10.1111/jbi.14104

Oury, N., Gélin, P., Massé, L., & Magalon, H. (2019). First study of asexual planulae in the coral *Pocillopora damicornis* type *β* SSH05c from the southwestern Indian Ocean. *Coral Reefs*, *38*(3), 499-503. https://doi.org/10.1007/s00338-019-01800-0

Oury, N., Gélin, P., Rajaonarivelo, M., & Magalon, H. (2022). Exploring the *Pocillopora* cryptic diversity : A new genetic lineage in the Western Indian Ocean or remnants from an ancient one? *Marine Biodiversity*, *52*, 5. https://doi.org/10.1007/s12526-021-01246-0

Oury, N., Noël, C., Mona, S., Aurelle, D., & Magalon, H. (2023). From genomics to integrative species delimitation? The case study of the Indo-Pacific *Pocillopora* corals. *Molecular Phylogenetics and Evolution*, *184*, 107803. https://doi.org/10.1016/j.ympev.2023.107803

Padovan, A., Chick, R. C., Cole, V. J., Dutoit, L., Hutchings, P. A., Jack, C., … Fraser, C. I. (2020). Genomic analyses suggest strong population connectivity over large spatial scales of the commercially important baitworm, *Australonuphis teres* (Onuphidae). *Marine and Freshwater Research*, *71*(11), 1549-1556. https://doi.org/10.1071/MF20044

Pante, E., Puillandre, N., Viricel, A., Arnaud-Haond, S., Aurelle, D., Castelin, M., … Samadi, S. (2015). Species are hypotheses : Avoid connectivity assessments based on pillars of sand. *Molecular Ecology*, *24*(3), 525-544. https://doi.org/10.1111/mec.13048

Pembleton, L. W., Cogan, N. O. I., & Forster, J. W. (2013). StAMPP : An R package for calculation of genetic differentiation and structure of mixed-ploidy level populations. *Molecular Ecology Resources*, *13*(5), 946-952. https://doi.org/10.1111/1755-0998.12129

Pinsky, M. L., Palumbi, S. R., Andréfouët, S., & Purkis, S. J. (2012). Open and closed seascapes : Where does habitat patchiness create populations with high fractions of self-recruitment? *Ecological Applications*, *22*(4), 1257-1267. https://doi.org/10.1890/11-1240.1

Pinzón, J. H., Sampayo, E., Cox, E., Chauka, L. J., Chen, C. A., Voolstra, C. R., & LaJeunesse, T. C. (2013). Blind to morphology : Genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). *Journal of Biogeography*, *40*, 1595-1608. https://doi.org/10.1111/jbi.12110

Pirog, A., Latreille, A. C., Madelaine, C., Gélin, P., Frouin, P., & Magalon, H. (2019). High clonal propagation and low population connectivity in the holothurian *Stichopus chloronotus* from the Indo-Pacific. *Marine Biology*, *166*(5), 63. https://doi.org/10.1007/s00227-019-3512-6

Postaire, B., Gélin, P., Bruggemann, J. H., & Magalon, H. (2017). One species for one island? Unexpected diversity and weak connectivity in a widely distributed tropical hydrozoan. *Heredity*, *118*(4), 385-394. https://doi.org/10.1038/hdy.2016.126

Postaire, B., Gélin, P., Bruggemann, J. H., Pratlong, M., & Magalon, H. (2017). Population differentiation or species formation across the Indian and the Pacific Oceans? An example from the brooding marine hydrozoan *Macrorhynchia phoenicea*. *Ecology and Evolution*, *7*(20), 8170-8186. https://doi.org/10.1002/ece3.3236

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*(2), 945-959.

R Core Team. (2021). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

Richmond, R. H. (1987). Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. *Marine Biology*, *93*(4), 527-533. https://doi.org/10.1007/BF00392790

Ridgway, T., Hoegh-Guldberg, O., & Ayre, D. (2001). Panmixia in *Pocillopora verrucosa* from South Africa. *Marine Biology*, *139*(1), 175-181. https://doi.org/10.1007/s002270100573

Ridgway, T., Riginos, C., Davis, J., & Hoegh-Guldberg, O. (2008). Genetic connectivity patterns of *Pocillopora verrucosa* in southern African Marine Protected Areas. *Marine Ecology Progress Series*, *354*, 161-168. https://doi.org/10.3354/meps07245

Robitzch, V., Banguera-Hinestroza, E., Sawall, Y., Al-Sofyani, A., & Voolstra, C. R. (2015). Absence of genetic differentiation in the coral *Pocillopora verrucosa* along environmental gradients of the Saudi Arabian Red Sea. *Frontiers in Marine Science*, *2*, 5. https://doi.org/10.3389/fmars.2015.00005

Rohling, E. J., Fenton, M., Jorissen, F. J., Bertrand, P., Ganssen, G., & Caulet, J. P. (1998). Magnitudes of sea-level lowstands of the past 500,000 years. *Nature*, *394*(6689), 162-165. https://doi.org/10.1038/28134

Rohling, E. J., Foster, G. L., Grant, K. M., Marino, G., Roberts, A. P., Tamisiea, M. E., & Williams, F. (2014). Sea-level and deep-sea-temperature variability over the past 5.3 million years. *Nature*, *508*(7497), 477-482. https://doi.org/10.1038/nature13230

Schmidt-Roach, S., Lundgren, P., Miller, K. J., Gerlach, G., Noreen, A. M. E., & Andreakis, N. (2012). Assessing hidden species diversity in the coral *Pocillopora damicornis* from Eastern Australia. *Coral Reefs*, *32*(1), 161-172. https://doi.org/10.1007/s00338-012-0959-z

Schmidt-Roach, S., Miller, K. J., Lundgren, P., & Andreakis, N. (2014). With eyes wide open : A revision of species within and closely related to the *Pocillopora damicornis* species complex (Scleractinia; Pocilloporidae) using morphology and genetics. *Zoological Journal of the Linnean Society*, *170*(1), 1-33. https://doi.org/10.1111/zoj.12092

Schmidt-Roach, S., Miller, K. J., Woolsey, E., Gerlach, G., & Baird, A. H. (2012). Broadcast spawning by *Pocillopora* species on the Great Barrier Reef. *PLoS ONE*, *7*(12), 50847. https://doi.org/10.1371/journal.pone.0050847

Schott, F. A., & McCreary Jr, J. P. (2001). The monsoon circulation of the Indian Ocean. *Progress in Oceanography*, *51*(1), 1-123. https://doi.org/10.1016/S0079-6611(01)00083-0

Souter, P., Henriksson, O., Olsson, N., & Grahn, M. (2009). Patterns of genetic structuring in the coral *Pocillopora damicornis* on reefs in East Africa. *BMC Ecology*, *9*, 19. https://doi.org/10.1186/1472-6785-9-19

Sundqvist, L., Keenan, K., Zackrisson, M., Prodöhl, P., & Kleinhans, D. (2016). Directional genetic differentiation and relative migration. *Ecology and Evolution*, *6*(11), 3461-3475. https://doi.org/10.1002/ece3.2096

Terhorst, J., & Song, Y. S. (2015). Fundamental limits on the accuracy of demographic inference based on the sample frequency spectrum. *Proceedings of the National Academy of Sciences*, *112*(25), 7677-7682. https://doi.org/10.1073/pnas.1503717112

Thomas, L., Underwood, J. N., Adam, A. A. S., Richards, Z. T., Dugal, L., Miller, K. J., & Gilmour, J. P. (2020). Contrasting patterns of genetic connectivity in brooding and spawning corals across a remote atoll system in northwest Australia. *Coral Reefs*, *39*(1), 55-60. https://doi.org/10.1007/s00338-019-01884-8

Torda, G., Lundgren, P., Willis, B. L., & van Oppen, M. J. H. (2013a). Genetic assignment of recruits reveals short-and long-distance larval dispersal in *Pocillopora damicornis* on the Great Barrier Reef. *Molecular Ecology*, *22*(23), 5821-5834. https://doi.org/10.1111/mec.12539

Torda, G., Lundgren, P., Willis, B. L., & van Oppen, M. J. H. (2013b). Revisiting the connectivity puzzle of the common coral *Pocillopora damicornis*. *Molecular Ecology*, *22*(23), 5805-5820. https://doi.org/10.1111/mec.12540

Torres, A. F., Forsman, Z. H., & Ravago-Gotanco, R. (2020). Shifts in coral clonality along a gradient of disturbance : Insights on reproduction and dispersal of *Pocillopora acuta*. *Marine Biology*, *167*(11), 161. https://doi.org/10.1007/s00227-020-03777-9

van der Ven, R. M., Heynderickx, H., & Kochzius, M. (2021). Differences in genetic diversity and divergence between brooding and broadcast spawning corals across two spatial scales in the Coral Triangle region. *Marine Biology*, *168*(2), 17. https://doi.org/10.1007/s00227-020-03813-8

van Oppen, M. J. H., Bongaerts, P., Underwood, J. N., Peplow, L. M., & Cooper, T. F. (2011). The role of deep reefs in shallow reef recovery : An assessment of vertical connectivity in a brooding coral from west and east Australia. *Molecular Ecology*, *20*(8), 1647-1660. https://doi.org/10.1111/j.1365-294X.2011.05050.x

Veron, J. E. N. (2000). *Corals of the world*. Australia: Australian Institute of Marine Science.

Weir, B. S., & Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution*, *38*(6), 1358-1370. https://doi.org/10.1111/j.1558-5646.1984.tb05657.x

Wood, S., Paris, C. B., Ridgwell, A., & Hendy, E. J. (2014). Modelling dispersal and connectivity of broadcast spawning corals at the global scale. *Global Ecology and Biogeography*, *23*(1), 1-11. https://doi.org/10.1111/geb.12101

SUPPORTING INFORMATION

Appendix S1 Correspondences with previous studies.

Appendix S2 Detailed sampling and colonies distribution among clusters.

Appendix S3 Datasets construction.

Appendix S4 Species identification.

Appendix S5 Clonal lineages identification.

Appendix S6 Genetic structure analyses.

Appendix S7 Direction and barrier to gene flow.

Appendix S8 Isolation by distance.

Appendix S9 Population demographic histories.

BIOSKETCHES

Nicolas Oury is PhD student interested in the evolutionary history, biogeography and population connectivity of marine species, notably the scleractinian genus *Pocillopora*. This work emerged from his PhD, supervised by **Hélène Magalon**, assistant professor at Reunion Island University. **Stefano Mona** is assistant professor at the EPHE in Paris and a specialist in demographic inferences. All authors are interested in biogeography, population demography and connectivity in marine environments.

Author contributions: NO and HM designed the study; HM collected samples; NO and HM did lab steps; NO analysed the results with helpful guidance from SM; NO wrote the original draft and all authors reviewed and edited the manuscript.

FIGURE LEGENDS

Figure 1 Sampling localities of *Pocillopora* colonies (dark and light greys indicate lands and coral reefs, respectively). Sites are numerically identified from the island code: GLO: Glorioso Islands, MAY: Mayotte, MAD: Madagascar, JDN: Juan de Nova Island, EUR: Europa Island, REU: Reunion Island and ROD: Rodrigues. Major oceanic currents are indicated schematically: MC: Mozambique current, WMC: west Madagascar current, AC: Agulhas current, NEMC: north-east Madagascar current, SEMC: south-east Madagascar current, SEC: south equatorial current and SISTG: south Indian subtropical gyre (Hancke, Roberts, & Ternon, 2014; Lutjeharms & Bornman, 2010; Schott & McCreary Jr, 2001).

Figure 2 Population structure of each *Pocillopora* species (i.e., *P. acuta*, *Pocillopora* aff. *P. meandrina*, *Pocillopora* aff. *P. verrucosa* and *P. villosa nomen nudum*). For each species (numbers of individuals and SNPs of the corresponding dataset in parentheses), results from the three assignment methods (sNMF, STRUCTURE and DAPC) at the retained K ($K = 2$ for *P.* aff. *verrucosa* and *P. villosa*; $K = 3$ for *P. acuta* and *P.* aff. *meandrina*) are indicated above, as well as the corresponding cluster repartition below (grey portions represent individuals not assigned to the same cluster by all methods). Populations retained for further analyses are labelled (colour refers to the cluster; population size in parentheses). Dashed polygons represent pooled populations. *N*: number of colonies; MAY: Mayotte, JDN: Juan de Nova Island, EUR: Europa Island, MAD: Madagascar (nw: northwestern, ne: northeastern, sw: southwestern), REU: Reunion Island, ROD: Rodrigues.

Figure 3 Direction and barrier to gene flow for each *Pocillopora* species (i.e., *P. acuta*, *Pocillopora* aff. *P. meandrina*, *Pocillopora* aff. *P. verrucosa* and *P. villosa nomen nudum*). Populations are coloured according to clusters. Arrows indicate gene flow above the filter threshold for which the network becomes fragmented (t; indicated above, along with the numbers of populations, individuals and SNPs retained). Note that no arrows do not indicate the absence of gene flow. Red lines symbolise barriers (width proportional to support over 1,000 bootstrap replicates).

Figure 4 Isolation by distance × environment in *Pocillopora* species from the southwestern Indian Ocean (i.e., *P. acuta*, *Pocillopora* aff. *P. meandrina*, *Pocillopora* aff. *P. verrucosa* and *P. villosa nomen nudum*; indicated by a different symbol). First three principal components (PC1-3; percentages of variation explained in parentheses) of the factorial analysis of mixed data (FAMD) with within-species pairwise population F_{ST}, shortest distances at sea (Dist) and eight environmental variables: mean (M) and difference (D) in present mean surface temperature (SST), salinity (Salt), current velocity (CurVel) and chlorophyll concentration (Chloro). The correlation circle of these 10 quantitative variables is projected on the individual plot. Individuals (i.e., population pairs) are coloured differently depending on cluster assignments, as indicated by the table in the legend (e.g., comparisons between two populations belonging to a blue cluster are shown in blue). Non-coloured symbols indicate the qualitative variable "species".

Figure 5 Past effective population sizes (*Ne*) for each population (see Fig. 2 for the codes; colour refers to the cluster) of the four *Pocillopora* species from the southwestern Indian Ocean (i.e., *P. acuta*, *Pocillopora* aff. *P. meandrina*, *Pocillopora* aff. *P. verrucosa* and *P. villosa nomen nudum*). Only populations with divergent variations are labelled for *P.* aff. *meandrina* to lighten the figure. Grey areas indicate glacial periods (LGP: last glacial period: ca. 11,700-115,000 years ago; PGP: penultimate glacial period: ca. 135,000-194,000 years ago).