Cryptic species and genetic connectivity among populations of the coral *Pocillopora damicornis* (Scleractinia) in the tropical southwestern Pacific

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Abstract :

Studying population genetic connectivity (i.e., identifying gene flow among populations and understanding their impacts on the genetic structure and diversity of populations) is first a matter of knowing what we work on, that is, accurately delimiting evolutionary units. Here, we focused on *Pocillopora damicornis* sensu stricto (or *Pocillopora* PSH04 sensu Glin et al. in Mol Phylogenet Evol 109:430–446. <http://dx.doi.org/10.1016/j.ympev.2017.01.018> PANIST, 2017). From 458 colonies sampled within the tropical southwestern Pacific [Chesterfield Islands and New Caledonia (Grande Terre and Loyalty Islands)], Bayesian assignments and network analyses were conducted with 11-microsatellite loci to first evaluate the genetic partitioning of the colonies in distinct Secondary Species Hypotheses (SSHs), then in distinct clusters. Population genetic connectivity was then assessed for each cluster separately. *Pocillopora* PSH04 was partitioned into two highly differentiated SSHs (SSH04a and SSH04b), regularly found in sympatry. Furthermore, SSH04a was subdivided into two clusters (SSH04a-1 and SSH04a-2). This pattern of genetic structuring seems not related to clonality, but rather to the establishment of reproductive barriers. Nevertheless, considering each cluster separately, the populations appeared highly differentiated, suggesting relatively weak gene flow. This low connectivity among populations, coupled with the existence of cryptic species, brings new insights to the connectivity pattern of this understudied Pacific region.

Introduction

Population connectivity (i.e. the process linking habitats and populations geographically separated) is a powerful force that maintains the genetic cohesion of a species over its distribution range, *via* the homogenisation of genetic variations among its populations (Mayr 1963). In marine environments, population connectivity occurs through exchanges of individuals or propagules (e.g. gametes, eggs or larvae), synonym of a transfer of alleles (effective dispersal; Cowen et al. 2003; Cowen and Sponaugle 2009). Population genetic connectivity therefore represents a key element of population dynamics, genetic structuring and diversification processes of marine organisms (Palumbi 1992; Paulay and Meyer 2002; Cowen et al. 2003; Bowen et al. 2013). Thus, understanding genetic connectivity among populations appears mandatory to define effective management and conservation units (Mills and Allendorf 1996; Mönkkönen and Reunanen 1999; Drechsler et al. 2003).

Studying genetic connectivity among populations of scleractinian corals is particularly crucial in the context of declining coral reefs (Wilkinson 2008). Indeed, most of the physical structure and the primary production of coral reef ecosystems are supplied directly or indirectly by scleractinian corals (e.g. Hatcher 1990). Thus, better understanding the processes that govern coral ecosystems, and those that promote the resilience and recovery of coral populations, such as connectivity (Hughes et al. 2011), is fundamental. However, scleractinians adopt several reproduction strategies (reviewed in Harrison 2011), influencing the dispersive capabilities of the propagules, and so the connectivity. In particular, they can reproduce asexually through different processes [e.g. by fragmentation (Highsmith 1982) or production of asexual larvae (Stoddart 1983)], leading to the production of genetically identical colonies. In the presence of clonal or partially clonal populations, traditional estimators of genetic structure and connectivity among populations might be biased (Balloux et al. 2003; Halkett et al. 2005), as the Hardy-Weinberg equilibrium tends to be modified. This renders more complex genetic connectivity studies, but must be taken into account to faithfully assess the genetic structure of populations.

Nevertheless, studying population genetic connectivity is first a matter of knowing what we work on, that is, accurately delimiting the evolutionary units. Indeed, incorrectly delimiting species and misidentifying these units of connectivity lead to biased estimation of connectivity among populations, as belonging to distinct species or regrouping individuals from distinct sympatric species. This seems trivial, however with the recent development and democratisation of genetic tools, discoveries of highly divergent clusters among populations reveal the possible presence of cryptic species, that the sole use of traditional taxonomic (often morphological) characters may have not highlighted (reviewed in e.g. Knowlton 1993; Bickford et al. 2007; Fišer et al. 2018). As an illustration, within scleractinian corals, the morphospecies *Stylophora pistillata*, previously

70 thought to be distributed in the whole Indo-Pacific and the Red Sea (Veron 2000), appears as a
71 complex of species with narrower distribution range (Keshavmurthy et al. 2013), as the coral
72 *Porites lobata* (Forsman et al. 2015). Two novel species of *Leptastrea*, formally considered as
73 *L. pruinosa*, were also recently delimited and described in the Indo-Pacific (Arrigoni et al. 2020).

74 The widespread Indo-Pacific coral genus *Pocillopora* particularly illustrates this issue, as
75 phenotypic plasticity encrypts the morphospecies boundaries and complicates the definition of valid
76 taxonomic units (see Todd 2008). Thus, in the last decade, several molecular approaches have
77 contributed to the investigation of *Pocillopora* species boundaries (summarized in Glin et al.
78 2017a). For example, the morphospecies *P. damicornis* (Linnaeus 1758; referred as *P. damicornis*
79 *sensu lato* hereafter to avoid any ambiguity) was disentangled in five genetic lineages:
80 *P. damicornis* types α , β , δ , γ and ε (Schmidt-Roach et al. 2012a), *a posteriori* defined as five
81 distinct species and named *P. damicornis* (Linnaeus 1758), *P. acuta* (Lamarck 1816), *P. aliciae*
82 (Schmidt-Roach, Miller and Andreakis 2013), *P. verrucosa* (Ellis and Solander 1786) and
83 *P. brevicornis* (Lamarck 1816), respectively (Schmidt-Roach et al. 2014). Besides, using species
84 delimitation methods based on genetic data, Glin et al. (2017a) defined within the *Pocillopora*
85 genus 16 Primary Species Hypotheses (PSHs *sensu* Pante et al. 2015), with some of them
86 partitioned into several Secondary Species Hypotheses (SSHs *sensu* Pante et al. 2015), themselves
87 partitioned into several divergent genetic clusters, often found in sympatry at the site scale. In this
88 latter study, lineages α (PSH04 therein), δ (PSH03) and ε (PSH10) appeared as unique entities with
89 no further genetic partitioning into SSH, but this needs to be confirmed by completing the sampling
90 and further genetic analyses. However lineage β (PSH05) was found to be subdivided in different
91 SSHs and clusters, revealing possible cryptic species in this lineage (Glin et al. 2017a, b, 2018b),
92 such as for lineage γ , whose ORF haplotypes were shared between PSH13 and PSH16 (Glin et al.
93 2017a) and which therefore needs to have its limits refined (Oury et al. submitted).

94 Here, we focused on *P. damicornis* type α *sensu* Schmidt-Roach et al. (2012a) or PSH04
95 *sensu* Glin et al. [2017a; also corresponding to *Pocillopora* type 4 *sensu* Pinzn et al. (2013) and
96 *Pocillopora* Clade Ib *sensu* Mart-Puig et al. (2014); referred as *P. damicornis sensu stricto*
97 hereafter to avoid confusing it with the morphospecies (i.e. *P. damicornis s.l.*)]. *Pocillopora*
98 *damicornis s.s.* is common and found in lagoons and shallow waters from the East and West coasts
99 of Australia (Pinzn et al. 2013; Torda et al. 2013a, b; Thomas et al. 2014; Schmidt-Roach et al.
100 2014), the northwestern subtropical and southwestern tropical regions of the Pacific Ocean (Pinzn
101 et al. 2013; Glin et al. 2017a). Colonies are also present, but rare, in the southwestern Indian Ocean
102 (two colonies over thousands sampled; Glin et al. 2017a) and in the central and northeastern
103 Pacific (Pinzn et al. 2013). It is a broadcast spawner (Schmidt-Roach et al. 2012b), and is also able
104 to propagate asexually (Torda et al. 2013a, b; Thomas et al. 2014) through fragmentation or release

105 of asexually produced larvae (Schmidt-Roach et al. 2012a). Previous studies (Richmond 1987; Harii
106 et al. 2002) reported a pelagic larval stage with zooxanthellae ranging from few hours to
107 ~ 100 days, suggesting high dispersal abilities. However, this must be taken cautiously, as inferred
108 from *P. damicornis* s.l. (probably *P. acuta*).

109 For now, few studies clearly investigated genetic connectivity in this redefined species as
110 previous studies dealt with *P. damicornis* s.l. and it was not always possible to identify *a posteriori*
111 the studied lineage(s). Besides, a relatively small part of its distribution range is covered. Thus, in
112 the Great Barrier Reef (GBR) region, strong genetic similarities at large spatial scales
113 (approximately 1,000 km) were observed among populations of *P. damicornis* s.s. However,
114 populations relatively close geographically were more differentiated (Torda et al. 2013b). On the
115 contrary, in western Australia (Ningaloo Reef and Muiron Islands), populations of
116 *P. damicornis* s.s. geographically close were poorly differentiated, while the differentiation among
117 populations increased with distance (Thomas et al. 2014). In both studies, clonality was important
118 [13.7% of the colonies shared their multi-locus genotype (MLG) with at least one other colony in
119 Torda et al. (2013b); 84 different MLGs were identified among 162 colonies in Thomas et al.
120 (2014)].

121 In front of such a lack of knowledge for *P. damicornis* s.s., and regarding the sampling
122 locations where we found it, we inferred the genetic connectivity among populations from an
123 ecoregion (*sensu* Spalding et al. 2007) located in the southern part of the distribution range of the
124 genus, which is largely understudied: New Caledonia. This ecoregion includes several archipelagos
125 comprising small islands (Chesterfield and Loyalty Islands) and one main island (Grande Terre).
126 Some are inhabited (Grande Terre and Loyalty Islands), with growing disturbances on marine
127 environment (e.g. coastal anthropisation, tourism, mining), while some others are uninhabited
128 (Chesterfield Islands), and thus relatively poorly influenced by human activities. Besides, this area
129 is protected by one of the largest Marine Protected Areas (MPAs): the Natural Park of the Coral Sea
130 (1.3×10^6 km²). This ecoregion thus represents an interesting patched framework to study
131 population connectivity in habitats differently impacted by human activities, but few studies
132 focused on this particular area (e.g. Planes et al. 1998; Postaire et al. 2017; Glin et al. 2018b),
133 especially in models with a life history similar to *Pocillopora*.

134 In this study, we first explored the genetic partitioning within *Pocillopora* PSH04, using
135 assignment and network analyses based on 11-microsatellite genotypes. Then, once all units of
136 connectivity (i.e. the clusters) were defined, the genetic diversity and the connectivity among
137 populations from New Caledonia ecoregion were assessed for each unit separately.

138

139 **Material and methods**

140 **Sampling design**

141 *Pocillopora* colonies were collected between March 2001 and October 2016 within three marine
142 provinces (*sensu* Spalding et al. 2007): the western Indian Ocean, the tropical southwestern Pacific
143 and the southeastern Polynesia, representing six ecoregions (*sensu* Spalding et al. 2007), 16
144 localities (Fig. 1) and over hundred sampling sites. Different habitats (reef slope, fringing reef, flat
145 reef or lagoon) were sampled, at various depths (from sea surface to 30 m depth), to maximise
146 colonies genetic diversity. On each site, colonies were haphazardly sampled (branch tip +
147 photograph) by snorkelling or scuba diving, without any *a priori* on morphology (a non-
148 discriminant character in this genus; Pinzón et al. 2013; Schmidt-Roach et al. 2014; Gélín et al.
149 2017a), except in southeastern Polynesia, where the sampling focused on colonies presenting
150 *P. verrucosa* macromorphology (but which could be *P. damicornis s.s.*). Samples were fixed in
151 90% ethanol at lab and stored at room temperature.

153 **DNA extraction, microsatellite genotyping and species identification**

154 From the sampled colonies, DNA was extracted using DNeasy Blood & Tissue kit (Qiagen™).
155 Samples were genotyped using 13 microsatellite loci, as in Gélín et al. (2017a; Online Resource 1).
156 Then, colonies belonging to *Pocillopora* PSH04 were identified *a posteriori* of sampling and *a*
157 *priori* of analyses using assignment tests performed with STRUCTURE 2.3.4 (Pritchard et al. 2000),
158 by compiling all the genotypes with the 975 ones from Gélín et al. (2017a), corresponding to
159 colonies from various PSHs already identified and whose ORF has been sequenced. Five iterations
160 of STRUCTURE were run at $K = 12$ (this value was found to retrieve the main PSHs in Gélín et al.
161 2017a), with the same parameters as in Gélín et al. (2017a). Colonies assigned to the cluster
162 corresponding to *Pocillopora* PSH04 (ORF07-17) with a mean probability over the five runs of at
163 least 0.75 (i.e. the mean assignment probability to include all colonies with PSH04 ORF haplotypes
164 but none with other haplotypes) were retained and constitute the dataset for this study (Online
165 Resource 2).

Fig. 1 Sampling localities of *Pocillopora* spp. colonies [from West to East and North to South: GLO: Glorioso Islands; MAY: Mayotte; JDN: Juan de Nova Island; BAS: Bassas da India; EUR: Europa Island; MAD: Madagascar; TRO: Tromelin Island; REU: Reunion Island; ROD: Rodrigues Island; CHE: Chesterfield Islands; NCA: New Caledonia (Grande Terre); LOY: Loyalty Islands; TON: Tonga; BOR: Bora-Bora; MOO: Moorea and TAH: Tahiti]. Localities for which colonies of *Pocillopora* PSH04 have been identified are in black (the number of colonies is indicated in parentheses). New Caledonia ecoregion is detailed below. Sites (detailed in Online Resource 4) are numerically identified from the locality code and the distribution of PSH04 clusters is represented [white and light grey represent the proportions of PSH04 colonies not assigned ($P < 0.75$) to a Secondary Species Hypothesis (SSH) or to a SSH04a cluster, respectively]. Arrows indicate the main currents (width proportional to speed; Vega et al. 2006)

Global diversity and clonality

For each locus, the number of alleles (N_a) and the percentage of missing data (%NA) were estimated. Then, the occurrence of identical multi-locus genotypes (MLGs) among the colonies was assessed with GENCLONE 2.0 (Arnaud-Haond and Belkhir 2007). The probability of obtaining the same MLG twice or more from distinct random reproductive events was further estimated using $P_{SEX}(F_{IS})$ (Arnaud-Haond et al. 2007). However, as GENCLONE considers missing data as different alleles (Arnaud-Haond and Belkhir 2007), the number of different MLGs in a population (N_{MLG}) could be overestimated. Thus, the genotypes of the colonies were also compared manually by considering missing data as potentially identical alleles. This latter method provides an

underestimation of N_{MLG} , but combined with GENCLONE method, both methods provide a range containing the true value of N_{MLG} . The clonal richness R (Dorken and Eckert 2001) was then calculated over all colonies and for each method, with the formula: $R = \frac{(N_{MLG}-1)}{(N-1)}$. Potential multi-locus lineages (MLLs) were identified using GENOTYPE (Meirmans and van Tienderen 2004), considering missing data as potentially identical alleles. Pairwise genetic distances based on mutational steps under both the Infinite Allele Model (IAM) and the Stepwise Mutational Model (SMM) were calculated for all pairs of MLGs, and a threshold in the genetic distance distribution was determined, under which distinct MLGs were considered to belong to the same MLL.

193

194 **Genetic partitioning exploration**

All further analyses were performed on both the entire dataset (i.e. keeping all colonies) and a truncated one (i.e. keeping one representative per potential MLG per population, considering missing data as potentially identical alleles), as suggested in Alberto et al. (2005). Indeed, while repeated MLGs can bias estimators which are not designed for clonal populations, colonies with the same genotype participate equally to sexual reproduction and gene flow, and should not be ignored. Therefore, analysing both datasets should take into account the effect of clonality.

First, null alleles and other potential technical biases were assessed with MICRO-CHECKER 2.2.3 (van Oosterhout et al. 2004), and genotypic linkage disequilibrium was tested with GENEPOP 4.7.0 (Raymond and Rousset 1995; Rousset 2008). Then, to infer the genetic partitioning within PSH04, we used and compared the results of assignment tests [STRUCTURE (Pritchard et al. 2000) and DAPC (Jombart et al. 2010)], Minimum Spanning Trees (MST; EDENETWORKS 2.18; Kivelä et al. 2015), allelic frequencies and F_{ST} (Weir and Cockerham 1984), as in Gélín et al. (2018a; see the Supplementary Method in Online Resource 3 for more details). We then defined the most likely number of genetically homogeneous groups (K) within the colonies as the highest K for which all previous methods were congruent for each dataset (i.e. the entire and the truncated). This level of differentiation should correspond to the SSH level.

In a hierarchical approach, and as a first level of structuration can hide a second one (see Gélín et al. 2018a), these analyses were repeated on each SSH separately. Once this second level of structuration has been tested, we defined the final number of genetic homogeneous groups (i.e. the clusters). Afterwards, we considered a population as all the colonies assigned to a given cluster with a probability of at least 0.75 (i.e. the minimum probability for which assignments in all datasets are strictly identical), sampled on the same site, at the same date (usually during a single dive and at the same depth). Colonies not assigned to a cluster with a probability ≥ 0.75 were considered admixed (i.e. assigned to more than one cluster due to hybridization, shared ancestry or bad assignment due to missing data). NEWHYBRIDS 1.1 (Anderson and Thompson 2002) was then run with 10^6

iterations after a burn-in period of 10^5 , to detect whether the admixed colonies could be considered as hybrids.

Genetic diversity and connectivity within each cluster

Allelic diversity

For each locus and each population, %NA, the percentage of missing data, N_a , the number of alleles and N_p , the number of population-private alleles, were estimated using FSTAT 2.9.3 (Goudet 2001). Then, for each population, mean indices (% NA_{pop} , $N_{a_{pop}}$ and $N_{p_{pop}}$, respectively) were calculated over all loci, as the percentage of polymorphic loci (P). The clonal richness R (Dorken and Eckert 2001) was also estimated for each population, as previously.

Afterwards, only the populations with $N \geq 10$ were considered. The observed heterozygosity (H_o), the expected heterozygosity at Hardy-Weinberg equilibrium (H_e , gene diversity) and the inbreeding coefficient (F_{IS} ; Wright 1931) were calculated with FSTAT 2.9.3 (Goudet 2001), for each locus and each population, and then for all loci within each population (noted $H_{o_{pop}}$, $H_{e_{pop}}$ and $F_{IS_{pop}}$, respectively).

Genetic connectivity

Two genetic differentiation indices were estimated among populations: F_{ST} (Weir and Cockerham 1984) and D_{est} (Jost 2008). F_{ST} were estimated using GENEPOP 4.7.0 (Raymond and Rousset 1995; Rousset 2008), while D_{est} with the package ‘*diveRsity*’ (Keenan et al. 2013) of the software R 3.3.1 (R Core Team 2016). Directional gene flow between populations were assessed by constructing a relative migration network with divMigrate (Sundqvist et al. 2016), implemented in the R package ‘*diveRsity*’ (Keenan et al. 2013). Finally, for each cluster, a population-based network was built using EDENetworks 2.18 (Kivelä et al. 2015) and the F_{ST} distance (Weir and Cockerham 1984). Populations with $N < 10$ were included. All networks were built at the same threshold [defined at the lowest percolation threshold (D_{pe}) found among clusters; i.e. the lowest F_{ST} threshold, below which the network is fragmented; Rozenfeld et al. 2007] to allow their comparison.

Results

Sampling and *Pocillopora* species identification

Over all localities, more than 9,000 colonies of *Pocillopora* were sampled, among which 462 colonies were assigned to PSH04 (Online Resource 2), all found in lagoons or upper reef slopes, between sea surface and 5 m depth (Online Resource 4). Among these 462 colonies, two were sampled in Rodrigues Island, in the southwestern Indian Ocean, and 460 in the tropical southwestern Pacific, within two ecoregions (*sensu* Spalding et al. 2007): New Caledonia ($N = 458$

colonies) and Tonga Islands ($N = 2$ colonies; Fig. 1). The colonies from New Caledonia ecoregion constitute the final dataset of this study. They were sampled on 30 sites within three localities: Chesterfield Islands (10 sites; CHE01-10; $N = 119$ colonies), Grande Terre (14 sites; NCA01-14; $N = 244$ colonies) and Loyalty Islands (6 sites; LOY01-06; $N = 95$ colonies; Fig. 1; Online Resource 4).

Global diversity and clonality

Among the 458 genotypes of the colonies retained, missing data represented 17.5%. Two loci (Poc40 and Pd3-009) showed very high levels of missing data (86.2% and 33.4%, respectively; Online Resource 1), and were not considered for further analyses, reducing the global proportion of missing data to 9.8%. An additional three loci (PV2, Pd3-005 and Pd3-EF65) showed relatively high levels of missing data ($15.3\% < \%NA < 19.7\%$) compared to the eight others ($3.2\% < \%NA < 8.6\%$; Online Resource 1). To deal with the high levels of missing data for these three loci without losing any crucial information, we decided to perform the analyses at 8 and 11 loci ($\%NA = 6.7\%$ and 9.8% , respectively; Table 1; Online Resource 1). All 11 loci were polymorphic, with a number of alleles per locus varying from 5 for Pd3-004 to 22 for Pd3-005 (Online Resource 1).

At 11 loci, 454 and 420 different MLGs over 458 colonies were detected, considering missing data as different or potentially identical alleles, respectively. Thus, the clonal richness R of the dataset was comprised between 0.99 and 0.92, respectively (Table 1). Considering missing data as different alleles (GENCLONE method), over the 454 MLGs found, one MLG was repeated four times in NCA01, and a second twice in LOY03. For both MLGs, $P_{SEX}(F_{IS})$ was very low ($< 10^{-12}$), indicating that the colonies came from a single sexual reproduction event and belonged to the same genet. However, only two colonies actually shared the same MLG at 13 loci. Considering missing data as potentially identical alleles, at least 27 MLGs were shared by a minimum of two colonies, but only three were shared between two colonies sampled in different sites, distant from 200 to 280 km. When reducing the number of loci to 8, 428 and 393 different MLGs over 458 colonies were detected considering missing data as different or potentially identical alleles, respectively ($0.86 < R < 0.93$; Table 1). According to GENCLONE (missing data as different alleles), 16 MLGs were repeated in two to seven colonies from the same site, except for one MLG shared between colonies from NCA01 and NCA05, distant from more than 400 km. However, $P_{SEX}(F_{IS})$ was comprised between 10^{-1} and 10^{-17} , suggesting that some colonies sharing the same MLG are probably not ramets from the same genet. With the other method (i.e. missing data as potentially identical alleles), at least 37 MLGs were found more than once, sometimes among very distant

colonies (> 750 km). Thus, keeping one representative per MLG and per population resulted in truncated datasets of 423 and 395 colonies at 11 and 8 loci, respectively (Table 1).

Both at 11 and 8 loci, no clear truncature was observed in the distribution of the pairwise genetic distances between MLGs under the IAM and the SMM (Online Resource 5), making difficult to define the threshold distinguishing MLGs from the same MLL. We thus considered that MLGs belong to the same MLL when they differed from one allele (IAM) or two mutational steps (SMM), as in a previous study focusing on *P. acuta* (PSH05; Glin et al. 2018b). Considering these thresholds, between 330 (IAM) and 389 (SMM) MLLs were detected at 11 loci, and between 161 (IAM) and 265 (SMM) at 8 loci.

Table 1 Summary of the different *Pocillopora* PSH04 datasets analysed. N_{loci} , N , and N_{MLG} : numbers of loci, colonies and multi-locus genotypes (MLGs), respectively; %NA: percentage of missing data; NA treatment: treatment of missing data (different of potentially identical alleles) for the identification of MLGs and R : clonal richness (Dorken and Eckert 2001)

N_{loci}	Dataset	N	%NA	NA treatment	N_{MLG}	R
11	Entire_11	458	9.8%	Different	454	0.99
				Identical	420	0.92
	Truncated_11	423	8.7%	-	420	0.99
8	Entire_8	458	6.7%	Different	428	0.93
				Identical	393	0.86
	Truncated_8	395	5.8%	-	393	0.99

Genetic partitioning exploration

Further analyses were performed on the four datasets summarised in Table 1 (i.e. an entire and a truncated one, both at 11 and 8 loci). No null allele nor other potential scoring error was detected with MICRO-CHECKER. Moreover, no genotypic linkage disequilibrium was found. Thus, all loci (11 or 8 depending on the datasets) were kept.

All results were very similar for the four datasets (Online Resource 6), so we presented here the results for the most complete one (Entire_11), specifying when differences were observed. For $K = 2$ and $K = 3$, the five runs of STRUCTURE were similar and congruent with DAPC (Fig. 2; Online Resources 7-9). From $K = 4$, the results of the two methods became incongruent, with more differences between datasets (Online Resources 6-7). The MST retrieved the genetic groups at $K = 2$ (Online Resource 8c), but not at $K = 3$ (Fig. 2c). Moreover, at $K = 2$, the allelic frequencies of each group were very different (Online Resource 8d), especially for loci Pd3-008, Pd11 and Pd13 for which F_{ST} estimates exceed 0.250*** (Online Resource 8e). A pairwise F_{ST} of 0.203*** was calculated. At $K = 3$, the allelic frequencies were less different (Online Resource 9d), and pairwise F_{ST} varied from 0.117*** to 0.269***. Thus, considering the congruency among the five methods (STRUCTURE, DAPC, MST, allelic frequencies and F_{ST} ; Online Resources 6-9) within the four datasets, the optimal K was defined at 2. The two groups were designated SSH04a and SSH04b, and

440 colonies (96.1%) were assigned to a unique SSH ($P \geq 0.75$; $N_{SSH04a} = 327$; $N_{SSH04b} = 113$; Fig. 1; Online Resource 4). SSH04a mainly regrouped colonies from Chesterfield Islands and western Grande Terre, while SSH04b was composed of colonies from eastern Grande Terre and Loyalty Islands (Fig. 2). However, the two SSHs were found in sympatry in eight sites (Fig. 1-2a). Moreover, 18 colonies (3.9%) were found admixed between the two SSHs: ten in Chesterfield Islands (CHE01-02-04-05-10), six in Grande Terre (NCA02-03-05-07) and two in Loyalty Islands (LOY02-03), but only four presented no missing data in their genotypes. Thus, these admixed colonies probably correspond to bad assignments. Additionally, NEWHYBRIDS detected only six hybrids among the 458 colonies (1.3%; all F2), and almost all colonies (~ 96%) assigned to a SSH were detected as pure lineages.

Then, assignment tests were performed using STRUCTURE and DAPC for each SSH separately (Online Resource 10). For SSH04a, both methods were congruent only at $K = 2$, and retrieved the two groups previously found for the overall dataset at $K = 3$ (Online Resource 10). As previously, the MST was not congruent with STRUCTURE and DAPC (Online Resource 11), and a pairwise F_{ST} of 0.117*** was calculated between the two groups. As these two groups were already found within the overall dataset, and as STRUCTURE and DAPC gave very similar results, we considered that SSH04a was partitioned into two clusters, named SSH04a-1 and SSH04a-2. The two clusters were found in sympatry in 11 sites, SSH04a-1 being the main cluster in Chesterfield Islands, while SSH04a-2 being the most abundant in western Grande Terre ($N_{SSH04a-1} = 136$; $N_{SSH04a-2} = 119$; Fig. 1-2; Online Resource 4). However, both clusters had only three populations with $N \geq 10$ over 23 and 13 for SSH04a-1 and SSH04a-2, respectively (Table 2; Online Resource 4). A high proportion of the colonies (22.0%) were found admixed between both clusters, within all localities (CHE: 16.5%; NCA: 23.5%; LOY: 42.9%), possibly due to bad assignments due to missing data. Nevertheless, 41.7% of these admixed colonies were detected as F2 hybrids.

For SSH04b, STRUCTURE and DAPC were incongruent from $K = 2$ (Online Resource 10). Thus, SSH04b was considered to be composed of a unique cluster, mostly found in eastern Grande Terre and Loyalty Islands. For this cluster, six populations over 11 had $N \geq 10$ (Table 2; Online Resource 4).

Fig. 2 *Pocillopora* PSH04 Secondary Species Hypotheses (SSHs) and clusters (Entire_11 dataset). (a) STRUCTURE plots at $K = 2$ and $K = 3$, (b) DAPC assignments for $K = 3$ and (c) Minimum Spanning Tree. Colonies are coloured according to the clusters identified by STRUCTURE at $K = 3$ (individual assignment probability > 0.75). Colonies with an assignment probability inferior to 0.75 for each cluster were coloured in grey

Genetic diversity and connectivity within each cluster

Allelic diversity

At 11 loci, among populations with $N \geq 10$, the percentage of polymorphic loci (P) varied from 73% for NCA02 SSH04a-1 to 100% for six populations. The percentage of missing data ($\%NA_{pop}$) ranged from 0.7% for NCA01 SSH04a-2 to 22.0% for LOY05 SSH04b, the mean number of alleles per locus (Na_{pop} ; $\pm$ SE) varied from 2.6 ± 0.3 for LOY05 SSH04b to 4.8 ± 0.8 for CHE05 SSH04a-1, and the mean number of population-private alleles (Np_{pop} ; $\pm$ SE) varied from 0.0 for five populations to 0.3 ± 0.1 for LOY04 SSH04b. Population clonal richnesses were high, varying from 0.88 to 1.00 when considering missing data as different alleles, or from 0.77 to 1.00 when considering missing data as potentially identical alleles (Table 2). Thus, the mean observed and expected heterozygosities (Ho_{pop} and He_{pop} , respectively; $\pm$ SE) and F_{IS} estimates were very similar between the entire and the truncated datasets. For the entire dataset (Entire_11), Ho_{pop} varied from 0.30 ± 0.09 for CHE01 SSH04a-1 to 0.61 ± 0.09 for LOY03 SSH04b and He_{pop} , from 0.42 ± 0.08 for LOY05 SSH04b to 0.58 ± 0.04 for LOY03 SSH04b. Almost all F_{IS} estimates (11/12) were not significantly different from zero (ranging from -0.10 ± 0.16^{NS} for LOY03 SSH04b to 0.22 ± 0.09^{NS} for NCA01 SSH04a-2), except in CHE01 SSH04a-1 ($F_{IS} = 0.40 \pm 0.14^{**}$; Table 2). All indices followed the same trends at 8 loci (Online Resource 12).

370 **Table 2** *Pocillopora* PSH04 population summary statistics at 11 loci. Only populations with at least 10 colonies were considered. Sites are detailed in Online Resource 4. *N*: number
371 of colonies; *N_{MLG}*: number of multi-locus genotypes (MLGs) for both treatments of missing data; *R*: clonal richness (Dorken and Eckert 2001); %*NA_{pop}*: percentage of missing data;
372 *P*: proportion of polymorphic loci; *Na_{pop}* and *Np_{pop}*: mean numbers ($\pm$ SE) of alleles and population-private alleles; *Ho_{pop}* and *He_{pop}*: mean ($\pm$ SE) observed and expected
373 heterozygosities and *F_{ISpop}*: mean ($\pm$ SE) inbreeding coefficient [Wright 1931; ^{NS}: non-significant ($P > 0.05$); **: $0.001 < P < 0.01$]

Population	<i>N</i>	<i>N</i> _{MLG}	<i>R</i>	% <i>NA</i> _{pop}	<i>P</i>	<i>Na</i> _{pop}	<i>Np</i> _{pop}	Entire_11			Truncated_11			
								<i>H</i> _{o pop}	<i>H</i> _{e pop}	<i>F</i> _{IS pop}	<i>H</i> _{o pop}	<i>H</i> _{e pop}	<i>F</i> _{IS pop}	
SSH04a-1														
CHE01	11	10-11	0.90-1.00	10.3%	91%	3.1±0.5	0.0±0.0	0.30±0.09	0.54±0.07	0.40±0.14**	0.30±0.08	0.56±0.07	0.40±0.14*	
CHE05	21	21	1.00	6.9%	100%	4.8±0.8	0.2±0.1	0.40±0.09	0.48±0.09	0.12±0.07 ^{NS}	0.40±0.09	0.48±0.09	0.12±0.07 ^{NS}	
NCA02	10	9-10	0.89-1.00	7.3%	73%	3.1±0.6	0.1±0.1	0.49±0.08	0.56±0.07	0.11±0.11 ^{NS}	0.45±0.07	0.56±0.07	0.15±0.11 ^{NS}	
Total	136	128-136	0.94-1.00	8.0%	100%	9.0±1.3	-	-	-	-	-	-	-	
SSH04a-2														
NCA01	25	22	0.88	0.7%	100%	4.3±0.5	0.2±0.1	0.36±0.07	0.45±0.07	0.22±0.09 ^{NS}	0.35±0.06	0.46±0.07	0.25±0.08**	
NCA05	42	39-42	0.93-1.00	9.2%	100%	3.9±0.5	0.0±0.0	0.38±0.08	0.45±0.07	0.10±0.12 ^{NS}	0.38±0.08	0.45±0.07	0.11±0.12 ^{NS}	
NCA06	31	24-31	0.77-1.00	11.3%	91%	3.5±0.5	0.1±0.1	0.41±0.10	0.46±0.07	0.11±0.13 ^{NS}	0.42±0.10	0.48±0.07	0.12±0.14 ^{NS}	
Total	119	106-116	0.89-0.97	8.3%	100%	5.2±0.8	-	-	-	-	-	-	-	
SSH04b														
NCA13	10	10	1.00	2.7%	100%	3.1±0.3	0.2±0.1	0.45±0.08	0.50±0.06	0.08±0.17 ^{NS}	0.45±0.08	0.50±0.06	0.08±0.17 ^{NS}	
NCA14	19	15-19	0.78-1.00	16.7%	91%	3.0±0.4	0.0±0.0	0.52±0.08	0.48±0.05	-0.09±0.14 ^{NS}	0.53±0.08	0.50±0.05	-0.09±0.14 ^{NS}	
LOY03	23	22	0.95	10.7%	100%	3.4±0.6	0.1±0.1	0.61±0.08	0.58±0.04	-0.10±0.16 ^{NS}	0.61±0.08	0.58±0.04	-0.10±0.15 ^{NS}	
LOY04	28	26-28	0.93-1.00	14.3%	100%	4.3±0.4	0.3±0.1	0.38±0.07	0.45±0.04	0.20±0.11 ^{NS}	0.39±0.07	0.48±0.05	0.22±0.10 ^{NS}	
LOY05	12	10-12	0.88-1.00	22.0%	82%	2.6±0.3	0.0±0.0	0.40±0.11	0.42±0.08	0.09±0.17 ^{NS}	0.40±0.10	0.45±0.08	0.11±0.15 ^{NS}	
LOY06	15	15	1.00	21.8%	91%	2.8±0.5	0.0±0.0	0.41±0.07	0.47±0.06	0.10±0.13 ^{NS}	0.40±0.07	0.45±0.06	0.09±0.12 ^{NS}	
Total	113	104-112	0.92-0.99	14.5%	100%	6.2±0.8	-	-	-	-	-	-	-	
Total PSH04	458	420-454	0.92-0.99	9.8%	100%	11.1±1.4	-	-	-	-	-	-	-	

374

375 *Genetic connectivity*

376 At 11 loci, for the entire dataset (Entire_11), F_{ST} estimates between intra-cluster pairs of
377 populations ranged from 0.025^{NS} for NCA13/LOY06 (SSH04b) to 0.230*** for NCA14/LOY05
378 (SSH04b; mean $\pm$ SE = 0.118 $\pm$ 0.137), and D_{est} estimates ranged from 0.009^{NS} to 0.166*** for the
379 same population pairs (mean $\pm$ SE = 0.065 $\pm$ 0.008; Online Resource 13a). Estimates were generally
380 lower for the truncated dataset (Truncated_11: 0.028^{NS} $< F_{ST} <$ 0.201***;
381 0.009^{NS} $< D_{est} <$ 0.163***), but followed the same trends. For both datasets, genetic differentiation
382 between populations from different clusters was higher, with F_{ST} ranging from 0.162*** to
383 0.407***, and D_{est} from 0.104*** to 0.448*** (Online Resource 13a). Again, at 8 loci, results were
384 very similar (Online Resource 13b).

385 The relative migration network retrieved the three clusters, but no particular pattern of
386 migration could be distinguished (Online Resource 14a), even when considering clusters separately
387 (Online Resource 14b), possibly due to the restricted size and number of populations.

388 Finally, population-based networks were built for each cluster independently. For SSH04a-1
389 and SSH04b, the D_{pe} was defined at 0.11, while it was higher for SSH04a-2 ($D_{pe} = 0.64$). Thus, all
390 networks were built at the F_{ST} threshold of 0.11 (Fig. 3). The populations from SSH04a-2 and
391 SSH04b, almost all in eastern New Caledonia and Loyalty Islands, appeared weakly connected,
392 while those from SSH04a-1, located in Chesterfield Islands and New Caledonia (East and West)
393 were more connected (Fig. 3).

394 **Fig. 3** Population-based networks for each cluster of *Pocillopora* PSH04 (Entire_11 dataset). (a) STRUCTURE plot at
395 $K = 3$, (b) population-based networks built with the F_{ST} distance (Weir and Cockerham 1984) thresholded at 0.11

Discussion

Our results evidenced that *Pocillopora* PSH04 colonies from the tropical southwestern Pacific belong to two SSHs (SSH04a and SSH04b), found in sympatry among several sites. Moreover, SSH04a split into two less differentiated clusters (SSH04a-1 and SSH04a-2), also sometimes sympatric. This partitioning seems unrelated to *corallum* macromorphology (Online Resource 15), nor clonality. Indeed, few repeated MLGs were detected among colonies, even when considering missing data as potentially identical alleles, and results were very similar whether keeping them or not. Finally, the studied populations appeared relatively differentiated (1) according to the relative abundance of the different SSHs and clusters (the connectivity units), and (2) among each connectivity unit, according to F_{ST} and D_{est} estimates.

A single or several species?

In this study, analysing the genetic partitioning within *Pocillopora* PSH04 using different assignment methods based on allelic frequencies or genetic distances estimated from microsatellite data, we found that colonies were divided into two divergent genetic groups (SSH04a and SSH04b), according to the congruence among the different methods used, and the different datasets analysed. These two groups were strongly differentiated ($F_{ST} = 0.203^{***}$), especially for some loci, and seem geographically separated (one SSH on each side of Grande Terre; Fig. 1). However, they were found in sympatry in some sites. No distinction between the two SSHs based on *corallum* macromorphology seems obvious (Online Resource 15). In addition, SSH04a was divided into two sympatric clusters (SSH04a-1 and SSH04a-2), which are themselves less, but still highly differentiated ($F_{ST} = 0.117^{***}$).

In a previous study (Gélin et al. 2017a), the species boundaries within the *Pocillopora* genus were redefined using species delimitation methods based on genetic information: 16 PSHs were defined within the genus, some of which splitting into several SSHs. For example, *Pocillopora* PSH05 (*sensu* Gélin et al. 2017a), corresponding to *P. acuta* (previously *P. damicornis* β), split into four SSHs (SSH05a, b, c and d), SSH05a and SSH05b being in sympatry in the Pacific Ocean, and SSH05c and SSH05d in the Indian Ocean (Gélin et al. 2018b). However, no genetic partitioning was previously identified within *Pocillopora* PSH04, as the former analyses were conducted on colonies belonging to the entire genus ($N = 975$ colonies of which 102 were assigned to *Pocillopora* PSH04, more precisely to SSH04a), and each locality was represented by only few colonies (Gélin et al. 2017a). In the present study, only colonies assigned to *Pocillopora* PSH04 were considered, representing a small proportion of the diversity of the genus, but a larger number of colonies per locality.

430 Discoveries of cryptic species are not rare within scleractinian corals. Indeed, many species
431 were defined on the sole use of traditional taxonomic (often morphological) characters (see Veron
432 2000), which are ambiguous due to phenotypic plasticity. Thus, many morphospecies previously
433 thought to be distributed in the whole Indo-Pacific, were in fact complexes of different species,
434 each restricted to the ocean basin [e.g. *P. damicornis* (Schmidt-Roach et al. 2014),
435 *P. eydouxi/meandrina* (Gélin et al. 2018a), *P. verrucosa* (Oury et al. submitted), *Stylophora*
436 *pistillata* (Keshavmurthy et al. 2013), *Leptastrea pruinosa* (Arrigoni et al. 2020)]. Sympatric
437 cryptic coral species are not unusual too. For example, four sympatric clusters were found within
438 *Seriatopora hystrix* colonies from Lizard and Palm Islands (GBR; Warner et al. 2015), three in the
439 Ryūkyū Archipelago (Japan; Nakajima et al. 2017). Misidentifying these cryptic species implies
440 many consequences, such as incorrect biodiversity and connectivity assessments, themselves
441 influencing the implementation of management and conservation plans.

442 In a previous study, Thomas et al. (2014) showed, using six microsatellite markers, that
443 *P. damicornis* s.s. colonies of Ningaloo Reef and Muiron Islands (western Australia) belong to two
444 distinct genetic clusters, one in the North of the sampling area, the other in the South, and in
445 sympatry only at intermediate latitude sites. This pattern of genetic structuring is similar to the one
446 observed by Gélin et al. (2017b), studying several populations of *Pocillopora* SSH05c in Reunion
447 Island (southwestern Indian Ocean). A geographic barrier or asynchronous spawning of the most
448 distant populations were mentioned to explain this pattern (Gélin et al. 2017b). A similar pattern
449 was also observed within colonies of *Acropora tenuis* from Nansei Islands (Japan), suggesting the
450 existence of two source populations at the geographic extremities of the sampling area, both mixing
451 within the intermediate populations (Zayasu et al. 2016). In the present study, if the two SSHs, or
452 the three clusters, constitute evolutionary units or distinct species, then reproductive barriers
453 probably established among them. Ecological gradients, such as depth, were already evoked to
454 explain the sympatry of *Seriatopora hystrix* clusters in the Ryūkyū Archipelago (Flot et al. 2008;
455 Bongaerts et al. 2010; van Oppen et al. 2011; Nakajima et al. 2017). The same would apply to
456 *Porites astreoides* (Lamarck, 1816) in Florida (southeastern USA; Serrano et al. 2016). However,
457 depth does not appear to be the reproductive barrier here, as colonies sampled on a same site were
458 usually at the same depth: all *P. damicornis* s.s. colonies were sampled in lagoons and upper reef
459 slopes, between sea surface and 5 m depth. However differential habitats on both sides of Grande
460 Terre could explain the SSHs. Indeed, in the GBR, differences in habitat specificity were found
461 among *Seriatopora hystrix* cryptic species, some being restricted to sheltered reefs, while others to
462 exposed reefs (Warner et al. 2015). A similar trend could be hypothesised here, with SSH04a being
463 mainly found in large and relatively sheltered lagoons (Chesterfield Islands and western Grande
464 Terre), while SSH04b in more exposed habitats (eastern Grande Terre and Loyalty Islands; Fig. 1).

Clonality or not clonality?

Among the 458 colonies studied, only two MLGs were found repeated within sympatric colonies ($R = 0.99$) when considering all 11 loci and missing data as different alleles. The clonality increased when considering missing data as potentially identical alleles, but remained weak (27 MLGs repeated over 458 colonies; $R = 0.92$; 330-389 MLLs). At 8 loci, clonal richness was lower (R between 0.93 and 0.86, considering missing data as different or potentially identical alleles, respectively; 161-265 MLLs), but colonies sharing the same MLG at 8 loci had distinct MLGs at 11 loci. Moreover, high $P_{SEX}(F_{IS})$ values and colonies sharing identical MLGs distant from more than 750 km suggest an underestimation of the clonal richness at 8 loci. This relatively low rate of clonality can be explained by a non-optimal sampling to detect clonality (unlike random sampling for example). Nevertheless, with the same sampling (except in Reunion Island), Glin et al. (2018b) found a high clonality rate in *Pocillopora* PSH05 [819 distinct MLGs (668-794 MLLs) among 1,418 colonies over 13 loci, including the 11 ones from the present study; $R = 0.577$]. Thus, although the sampling was not appropriate for the study of clonality, if asexual propagation was common such as in *Pocillopora* PSH05, then a higher clonality rate should have been observed.

In other genetic studies focusing on *P. damicornis* s.s., clonality rates were higher. Using six microsatellite loci, Thomas et al. (2014) obtained a global clonal richness of 0.52 ($N = 162$ colonies) but with a high spatial variability (R varying from 0.15 to 0.87 per site). Some MLGs were highly represented (up to 13 colonies sharing the same MLG) and others present in several sites (three MLGs present in two sites and one in three sites, distant from 6 to 240 km; Thomas et al. 2014). Same trends were found by Torda et al. (2013a, b) in the GBR region, using nine microsatellite loci. These differences in clonality rates could result from the lower number of loci used in previous studies (and from their low polymorphism and/or possible homoplasy). It could also be the result of a spatial variation in clonal propagation within *P. damicornis* s.s. (e.g. due to different hurricane frequencies favouring fragmentation), or the result of differences in clonal propagation between cryptic species. As an illustration, *Porites lobata* colonies from the eastern tropical Pacific were disentangled in two species: *Porites lobata*, which reproduces mainly sexually, and *Porites evermanni*, which propagates through fragmentation by triggerfishes (Boulay et al. 2014). Different clonality rates were also found between western and eastern Caribbean *Acropora palmata* populations, possibly related to habitat characteristics (Baums et al. 2006). Whatever the cause of these differences, clonal propagation in *P. damicornis* s.s. populations from New Caledonia appears relatively occasional and/or accidental.

Weak connectivity in New Caledonia

500 Considering the clusters as connectivity units, some populations, sometimes relatively distant (e.g.
501 NCA13 and LOY06 within SSH04b, ~ 340 km apart), were genetically undifferentiated, while
502 some populations belonging to the same locality, or even neighbours (i.e. a few tens kilometres
503 apart), were highly differentiated. Such pattern could be a consequence of the restricted size and
504 number of populations within each cluster (due to cryptic species), or suggests that population
505 differentiation is not entirely related to geographic distance (isolation by distance hypothesis could
506 not be tested). Currents could also be involved, as water exchanges between Grande Terre lagoons
507 and the open ocean are weak and regional currents are dominated by a flow from East to West,
508 resulting from the southeastern trade winds (Fig. 1; Vega et al. 2006). This suggests the existence of
509 two reef systems hydrologically isolated on both sides of Grande Terre. Accordingly, populations of
510 eastern Grande Terre (sinks) would be connected to Loyalty Islands populations (sources) by a
511 unidirectional gene flow from East to West, following currents. Grande Terre would act as a
512 geographical barrier for this flow, explaining why SSH04a-2 and SSH04b are almost restricted to
513 the East of the ecoregion. However, it is conceivable that gene flow from eastern Grande Terre or
514 Loyalty Islands will persist and reach Chesterfield Islands either directly through surface currents
515 bypassing Grande Terre from the North, or indirectly through intermediate population(s) (stepping
516 stone colonization). Unfortunately, we were unable to confirm this pattern of migration from the
517 relative migration networks, again possibly due to the size and number of populations.

518 A high genetic differentiation was also observed between four *Pocillopora* PSH05
519 (*P. acuta*) populations from Grande Terre (corresponding to NCA01, NCA03, NCA05-06 and
520 NCA11 herein; Glin et al. 2018b). In addition, Postaire et al. (2017) showed a strong genetic
521 differentiation between populations of the hydrozoan *Macrorhynchia phoenicea* α (*sensu* Postaire et
522 al. 2016) in Chesterfield Islands, Grande Terre and Loyalty Islands (many sites in common with this
523 study), explained by the ecology of this species, often found attached at the base of *Pocillopora*
524 colonies, although presenting a medusoid phase. Similar results were obtained from three new
525 caledonian populations (close from NCA02, NCA05-06 and NCA10 herein) of two reef fishes:
526 *Acanthurus triostegus* (larval stage duration: 60 d) and *Stegastes nigricans* (24 d; Planes et al.
527 1998). In contrast, the same three populations of another reef fish, *Epinephelus merra* (39 d), were
528 found weakly differentiated in the same study (Planes et al. 1998). This difference was explained by
529 (1) a limited sampling and (2) the high migratory capabilities of *E. merra* adults during spawning.
530 Nevertheless, although several studies have revealed a weak connectivity in this ecoregion, the
531 pattern seems not generalizable to all species. Indeed, using the mitochondrial COI, a high
532 connectivity was found within populations of four squat lobster-like and a gastropod species from
533 Isle of Pines and Norfolk seamounts (southern of Grande Terre; Samadi et al. 2006). It is thus

necessary to multiply genetic connectivity investigations in this under-studied Pacific region to achieve accurate multi-specific models.

Conclusion

Our results provide insights on the genetic diversity, structure, and connectivity of populations of *Pocillopora damicornis* s.s., a recently delimited *Pocillopora* species that is thus largely understudied. In addition, this study focused on a marine province located in the South of the distribution range of this species: the tropical southwestern Pacific, largely understudied as well. Thus, several evolutionary units, perhaps even several species, are distinguished under the name of *Pocillopora damicornis* s.s. Nevertheless, focusing on each evolutionary unit, their populations from the tropical southwestern Pacific appeared differentiated, probably due to restricted gene flow, limited by currents, habitat specificities and/or geographical distances among populations. This low connectivity between populations, coupled with the existence of cryptic species, brings new insights to the connectivity pattern of New Caledonia ecoregion. Such results must be considered for setting up appropriate management plans for the Natural Park of the Coral Sea.

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571 **Conflict of interest/Competing interests** The authors declare that they have no conflict of interest.

572 **Ethics approval** All applicable international, national and/or institutional guidelines for sampling,
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577 **Consent for publication** Not applicable.

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580 **Author's contributions** HM collected samples. NO, PG and HM did lab steps and analysed the
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583

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799 **Electronic supplementary material**

800 **Online Resource 1** Loci used in this study

801 **Online Resource 2** *Pocillopora* PSH04 genetic identification

802 **Online Resource 3** Supplementary method

803 **Online Resource 4** Sampled sites in New Caledonia ecoregion and *Pocillopora* PSH04 cluster
804 distribution

805 **Online Resource 5** Distributions of the pairwise genetic distances between multi-locus genotypes

806 **Online Resource 6** Comparison of the genetic assignment analysis for the four datasets

807 **Online Resource 7** Genetic assignment analysis of the *Pocillopora* PSH04 colonies

808 **Online Resource 8** *Pocillopora* PSH04 Secondary Species Hypotheses

- 809 **Online Resource 9** *Pocillopora* PSH04 clusters
- 810 **Online Resource 10** Genetic assignment analysis of the *Pocillopora* PSH04 colonies, for each
811 Secondary Species Hypothesis separately
- 812 **Online Resource 11** *Pocillopora* SSH04a clusters
- 813 **Online Resource 12** *Pocillopora* PSH04 population summary statistics at 8 loci
- 814 **Online Resource 13** Genetic differentiation among populations
- 815 **Online Resource 14** Relative migration networks
- 816 **Online Resource 15** *Pocillopora* PSH04 *corallum* macromorphology diversity

Cryptic species and genetic connectivity among populations of the coral *Pocillopora damicornis* (Scleractinia) in the tropical southwestern Pacific – *Marine Biology Original Paper* –
 Nicolas Oury, Pauline Glin, Hlne Magalon

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Online Resource 1 Loci used in this study, regrouped in panels. Size ranges (in base pairs) are given for this study. %NA: percentage of missing data; Na: number of alleles

Panel	Locus name	Repeat motif	Dye	Size (bp)	%NA	Na	Reference
1	Pd3-004	(ATG) ₈	6-FAM	178-190	8.0%	5	[4]
	Poc40	(CAA) _X	6-FAM	308-341	86.2%	-	[3]
	Pd3-005	(TGA) ₉	NED	206-272	19.4%	22	[4]
	PV2	(GA) ₂₀	VIC	147-181	15.3%	6	[2]
	PV7	(GT) ₅ (CT) ₂ GT (CT) ₃	VIC	242-260	3.2%	9	[2]
2	Pd2-001	(CA) ₁₁	VIC	212-216	6.3%	8	[4]
	Pd2-006	(CA) ₈	NED	205-237	8.3%	13	[4]
	Pd3-008	(CTG) ₇	6-FAM	176-197	3.9%	8	[4]
	Pd3-009	(CAA) ₇ (GAG) ₆	6-FAM	333-372	33.4%	-	[4]
3	Pd3-EF65	(GTT) ₅ (TGC) ₁₁	PET	197-242	19.7%	15	[1]
	Pd4	(AAAC) ₅	6-FAM	144-164	7.5%	11	[5]
	Pd11	(CA) ₇ T (AC) ₁₃	VIC	142-172	8.6%	13	[5]
	Pd13	(TCTT) ₅	NED	160-200	7.4%	12	[5]
				Total_{13 loci}	17.5%	-	
				Total_{11 loci}	9.8%	11.1 ± 1.4	
				Total_{8 loci}	6.7%	9.9 ± 0.9	

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– Marine Biology Original Paper –

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Online Resource 2 *Pocillopora* PSH04 genetic identification. Mean STRUCTURE assignments over the five iterations at $K = 12$ for (a) all colonies, Q-sorted, and (b) only colonies with their Open Reading Frame (ORF) haplotype identified ($N = 943$), Q-sorted per haplotype. Primary Species Hypotheses (PSHs; *sensu* Gélén et al. 2017) are indicated above each chart and ORF haplotypes (*sensu* Gélén et al. 2017) are indicated below chart (b). Horizontal dashed lines represent a PSH04 assignment probability (fuchsia bars) of 0.75 and vertical dashed lines in (a) delimit the colonies identified as PSH04 in this study (i.e. with a PSH04 assignment probability ≥ 0.75 ; $N = 462$).

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Online Resource 3 Supplementary method for the genetic partitioning exploration

To infer the genetic partitioning within PSH04, a Bayesian analysis was performed with STRUCTURE 2.3.4 (Pritchard et al. 2000). The admixture model with default settings for inferring alpha was used, assuming correlated allele frequencies. Five iterations of 10^6 MCMC generations after an initial burn-in of 10^5 generations were run for each K , varying from $K = 1$ to $K = 10$. The five iterations of each K were then combined by averaging the assignment probabilities of each genetic group using STRUCTURE HARVESTER 0.6.94 (Earl 2012). Results were combined with CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007) and visualised with DISTRUCT 1.1 (Rosenberg 2004). The web program CLUMPAK (Kopelman et al. 2015) was also used. In addition to direct examination of graphical results from STRUCTURE, the mean likelihood over several iterations of the same K [$\Pr(X | K)$; Pritchard et al. 2000] and the Evanno's ΔK (Evanno et al. 2005) were estimated with STRUCTURE HARVESTER to help defining K . However, as STRUCTURE analyses are based on strong hypotheses on populations (Hardy-Weinberg equilibrium and no linkage disequilibrium), a discriminant analysis of principal components (DAPC; Jombart et al. 2010) was also performed with the package 'adegenet' (Jombart 2008) from the software R 3.1.1 (R Core Team 2016). Results from DAPC were represented like STRUCTURE plots to ease the comparison of both methods. Then, for each value of K , a Minimum Spanning Tree (MST) based on the shared allele distance between colonies was built with EDENETWORKS 2.18 (Kivel et al. 2015). The nodes were coloured according to the genetic groups previously assigned in STRUCTURE with an average probability over the five iterations of at least 0.75 (i.e. the minimum probability for which assignments in all datasets are strictly identical). Moreover, for each group, the allele frequencies of each locus were calculated and compared between groups. F_{ST} (Weir and Cockerham 1984) between each pair of groups were estimated for each locus and for all loci using GENEPOP 4.7.0 (Raymond and Rousset 1995; Rousset 2008). We then defined the most likely number of genetically homogeneous groups (K) within the colonies as the highest K for which all previous methods (STRUCTURE, DAPC, MST, allelic frequencies and F_{ST}) were congruent for each dataset. This level of differentiation should correspond to the Secondary Species Hypothesis (SSH) level.

In a hierarchical approach, and as a first level of structuration can hide a second one (see Glin et al. 2018a), these analyses were repeated on each SSH separately. Once this second level of structuration has been tested, we defined the final number of genetic homogeneous groups (i.e. the clusters).

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Online Resource 4 Sampled sites in New Caledonia ecoregion and *Pocillopora* PSH04 cluster distribution.

N: number of colonies

Island/Region	Site	Site Name	Latitude	Longitude	Depth	Date	<i>N</i> _{total}	<i>N</i> _{PSH04}	<i>N</i> _{SSH04a-1}	<i>N</i> _{SSH04a-2}	<i>N</i> _{SSH04b}
Bampton reefs	CHE01	Bampton Nord	-19.11743	158.60130	1-3 m	11/2015	104	13	11		
	CHE02	Ilot Avon	-19.48388	158.25730	1-3 m		74	18	9	2	
	CHE09	Caye Skeleton	-19.43758	158.91200	1-2 m		60	6	6		
	CHE10	Ilot Reynard	-19.21313	158.94680	1-3 m		110	11	9		
Chesterfield reefs	CHE03	Ilot du Passage	-19.91032	158.36190	1-2 m	11/2015	121	9	8		
	CHE08	Ilots du Mouillage	-19.81050	158.44270	4-5 m		100	5	4		
Bellona reefs	CHE04	Bellona Nord-Ouest	-20.81102	158.45370	1-2 m	11/2015	110	8	3		
	CHE05	R��cif du Milieu	-21.45978	159.03160	1-2 m		145	30	21	1	
	CHE06	Bellona Sud	-21.85195	159.47450	1-2 m		94	12	9	1	
	CHE07	R��cif Olry	-21.39863	159.56270	1-2 m		110	7	7		
Total Chersterfield Islands							1028	119	87	4	0
Western Grande Terre	NCA01	B��lep	-19.66400	163.62230	1-2 m	11/2013	74	27		25	
	NCA02	Poum	-20.30878	163.88750	4-5 m		148	15	10		1
	NCA03	Voh	-21.03538	164.62190	1-2 m		192	18	6	3	1
	NCA04	Bourail	-21.70310	165.47570	2-5 m	04/2014	150	17	5	2	
	NCA05	Noum��a (Senez)	-22.32252	166.36798	2-5 m		60	56	6	42	
	NCA06	Noum��a (U��r��)	-22.31276	166.47162	2-5 m		59	31		31	
	NCA07	Noum��a (Slope)	-22.34067	166.23050	2-5 m		145	25	9	3	
Eastern Grande Terre	NCA08	Goro	-22.33710	167.02200	2-5 m	03/2014	120	2	1		
	NCA09	Kuaku��	-21.79187	166.63520	2-5 m		150	4	1	1	2
	NCA10	Port Bouquet	-21.59297	166.42030	2-5 m		150	4	2	1	1
	NCA11	Poindimi�� (Ilot Tibarama)	-20.92092	165.36950	2-5 m		39	2	1	1	
	NCA12	Poindimi�� (Ile au Sable)	-20.83467	165.41250	2-5 m		150	6	2		
	NCA13	Hiengh��ne	-20.56117	165.00860	2-5 m		154	16	4		10
	NCA14	Pou��bo	-20.17618	164.44320	2-5 m		150	21			19
Total Grande Terre							1741	244	47	109	34
Loyalty Islands	LOY01	Astrolabe (R��cif Ouest)	-19.86990	165.55630	2-5 m	02/2014	49	1			
	LOY02	Ouv��a (Ile Hue)	-20.41447	166.13850	2-5 m		111	1			1
	LOY03	Ouv��a (Mouly)	-20.72440	166.39650	2-5 m		150	23			23
	LOY04	Lifou (Pointe Chateaubriand)	-20.85547	167.28610	2-5 m		152	39	1	6	28
	LOY05	Mar�� (Cap Machan)	-21.41612	167.81920	2-5 m		126	12			12
	LOY06	Mar�� (Cap Coster)	-21.48673	168.11940	2-5 m		170	19	1		15
Total Loyalty Islands							758	95	2	6	79
Total							3527	458	136	119	113

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Online Resource 5 Distributions of the pairwise genetic distances between multi-locus genotypes (MLGs) under the Infinite Allele Model (IAM) and the Stepwise Mutational Model (SMM), at (a) 11 and (b) 8 loci.

(a) 11 loci (89,253 comparisons)

(b) 8 loci (77,815 comparisons)

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Online Resource 6 Comparison of the genetic assignment analysis [STRUCTURE (S.) and DAPC (D.) plots from $K = 2$ to $K = 5$] for the four *Pocillopora* PSH04 datasets: (a) Entire_11, (b) Truncated_11, (c) Entire_8 and (d) Truncated_8.

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Online Resource 7 Genetic assignment analysis of the *Pocillopora* PSH04 colonies (Entire_11 dataset). (a) mean likelihood over the five iterations of the same K , (b) Evanno's ΔK distribution, (c) BIC distribution and (d) plots from $K = 2$ to $K = 10$ for STRUCTURE (S.) and DAPC (D.)

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Online Resource 8 *Pocillopora* PSH04 Secondary Species Hypotheses (SSHs; Entire_11 dataset). (a) STRUCTURE plot at $K = 2$, (b) DAPC assignments, (c) Minimum Spanning Tree, (d) allelic frequencies for each locus and each SSH and (e) Weir and Cockerham (1984) F_{ST} estimated per locus. Colonies are coloured according to the genetic groups identified by STRUCTURE (individual assignment probability ≥ 0.75). Colonies with an assignment probability inferior to 0.75 for each group were coloured in grey

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Online Resource 9 *Pocillopora* PSH04 clusters (Entire_11 dataset). (a) STRUCTURE plot at $K = 3$, (b) DAPC assignments, (c) Minimum Spanning Tree, (d) allelic frequencies for each locus and each cluster and (e) Weir and Cockerham (1984) F_{ST} estimated per locus for each pair of clusters. Colonies are coloured according to the clusters identified by STRUCTURE (individual assignment probability ≥ 0.75). Colonies with an assignment probability inferior to 0.75 for each cluster were coloured in grey

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Online Resource 10 Genetic assignment analysis of the *Pocillopora* PSH04 colonies, for each Secondary Species Hypothesis (SSH) separately (Entire_11 dataset). (a) STRUCTURE (S.) and DAPC (D.) plots at $K = 2$ for all colonies and (b) plots from $K = 1$ to $K = 5$ for each SSH separately

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Online Resource 11 *Pocillopora* SSH04a clusters (Entire_11 dataset). (a) STRUCTURE plot at $K = 2$, (b) DAPC assignments, (c) Minimum Spanning Tree, (d) allelic frequencies for each locus and each cluster and (e) Weir and Cockerham (1984) F_{ST} estimated per locus. Colonies are coloured according to the clusters identified by STRUCTURE (individual assignment probability ≥ 0.75). Colonies with an assignment probability inferior to 0.75 for each cluster were coloured in grey

Population	N	N_{MLG}	R	$\%NA_{pop}$	P	Na_{pop}	Np_{pop}	Entire_8			Truncated_8		
								Ho_{pop}	He_{pop}	FIS_{pop}	Ho_{pop}	He_{pop}	FIS_{pop}
SSH04a-1													
CHE01	11	10-11	0.90-1.00	10.2%	100%	2.8±0.4	0.0±0.0	0.24±0.07	0.51±0.08	0.42±0.16*	0.25±0.06	0.52±0.08	0.41±0.15*
CHE05	21	20-21	0.95-1.00	6.5%	100%	4.0±0.6	0.1±0.1	0.39±0.08	0.47±0.10	0.12±0.05 ^{NS}	0.39±0.08	0.48±0.10	0.14±0.06*
NCA02	10	9	0.89	5.0%	75%	2.5±0.4	0.1±0.1	0.46±0.07	0.49±0.06	0.05±0.13 ^{NS}	0.43±0.07	0.49±0.06	0.08±0.12 ^{NS}
<i>Total</i>	136	128-132	0.94-0.97	6.3%	100%	7.9±1.0	-	-	-	-	-	-	-
SSH04a-2													
NCA01	25	22	0.88	1.0%	100%	3.6±0.4	0.0±0.0	0.36±0.09	0.41±0.08	0.15±0.10 ^{NS}	0.35±0.07	0.44±0.07	0.19±0.09 ^{NS}
NCA05	42	33-38	0.78-0.90	7.3%	88%	2.9±0.4	0.0±0.0	0.37±0.10	0.42±0.06	0.15±0.16 ^{NS}	0.34±0.06	0.43±0.08	0.13±0.09 ^{NS}
NCA06	31	16-24	-0.77	3.1%	100%	3.6±0.5	0.0±0.0	0.34±0.06	0.42±0.08	0.14±0.09 ^{NS}	0.37±0.11	0.47±0.06	0.21±0.18 ^{NS}
<i>Total</i>	119	85-104	0.71-0.87	5.3%	100%	4.3±0.4	-	-	-	-	-	-	-
SSH04b													
NCA13	10	10	1.00	2.5%	100%	3.0±0.3	0.1±0.1	0.56±0.06	0.49±0.05	-0.19±0.12 ^{NS}	0.56±0.06	0.49±0.05	-0.19±0.12 ^{NS}
NCA14	19	14-16	0.72-0.83	6.6%	100%	3.4±0.4	0.0±0.0	0.56±0.10	0.49±0.06	-0.15±0.17 ^{NS}	0.58±0.09	0.52±0.06	-0.15±0.16 ^{NS}
LOY03	23	22	0.95	9.8%	100%	2.8±0.4	0.1±0.1	0.63±0.08	0.54±0.02	-0.19±0.18 ^{NS}	0.64±0.08	0.54±0.02	-0.20±0.17 ^{NS}
LOY04	28	25-28	0.89-1.00	10.3%	100%	4.3±0.5	0.4±0.2	0.44±0.09	0.48±0.05	0.10±0.12 ^{NS}	0.46±0.08	0.50±0.05	0.11±0.12 ^{NS}
LOY05	12	9-11	0.73-0.91	12.5%	88%	2.5±0.3	0.0±0.0	0.38±0.09	0.42±0.09	0.04±0.14 ^{NS}	0.42±0.07	0.49±0.10	0.06±0.11 ^{NS}
LOY06	15	15	1.00	14.2%	100%	2.8±0.5	0.0±0.0	0.42±0.06	0.44±0.06	0.00±0.11 ^{NS}	0.42±0.06	0.44±0.06	0.00±0.11 ^{NS}
<i>Total</i>	113	99-109	0.88-0.96	9.5%	100%	5.6±0.7	-	-	-	-	-	-	-
Total PSH04	458	393-428	0.86-0.93	6.7%	100%	9.9±1.0	-	-	-	-	-	-	-

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Online Resource 13 Genetic differentiation among populations of *Pocillopora* PSH04 [F_{ST} (Weir and Cockerham 1984) in bottom left and D_{est} (Jost 2008) in top right; truncated dataset in parentheses]. Only populations with at least 10 colonies were considered. (a) 11 loci and (b) 8 loci. Values in bold are significant ($P < 0.001$)

(a) 11 loci

		SSH04a-1			SSH04a-2			SSH04b					
		CHE01	CHE05	NCA02	NCA01	NCA05	NCA06	NCA13	NCA14	LOY03	LOY04	LOY05	LOY06
SSH04a-1	CHE01 (11) (10)	-	0.082 (0.072)	0.049 (0.026)	0.167 (0.135)	0.129 (0.113)	0.164 (0.141)	0.257 (0.260)	0.249 (0.249)	0.178 (0.167)	0.182 (0.170)	0.243 (0.259)	0.189 (0.200)
	CHE05 (21)	0.103 (0.094)	-	0.070 (0.071)	0.131 (0.134)	0.120 (0.122)	0.168 (0.166)	0.156 (0.151)	0.218 (0.203)	0.178 (0.170)	0.137 (0.125)	0.193 (0.173)	0.208 (0.204)
	NCA02 (10) (9)	0.084 (0.055)	0.144 (0.144)	-	0.135 (0.129)	0.125 (0.104)	0.153 (0.126)	0.258 (0.243)	0.225 (0.237)	0.208 (0.198)	0.213 (0.191)	0.333 (0.312)	0.192 (0.199)
SSH04a-2	NCA01 (25) (22)	0.208 (0.170)	0.164 (0.162)	0.255 (0.234)	-	0.060 (0.053)	0.064 (0.047)	0.372 (0.373)	0.441 (0.448)	0.266 (0.259)	0.260 (0.247)	0.374 (0.361)	0.372 (0.377)
	NCA05 (42) (39)	0.200 (0.179)	0.193 (0.196)	0.230 (0.206)	0.102 (0.087)	-	0.030 (0.020)	0.289 (0.287)	0.411 (0.402)	0.173 (0.169)	0.188 (0.176)	0.304 (0.287)	0.316 (0.315)
	NCA06 (31) (24)	0.221 (0.188)	0.217 (0.206)	0.261 (0.231)	0.120 (0.098)	0.055 (0.046)	-	0.303 (0.304)	0.403 (0.396)	0.273 (0.281)	0.240 (0.227)	0.355 (0.338)	0.374 (0.376)
SSH04b	NCA13 (10)	0.258 (0.252)	0.233 (0.232)	0.310 (0.307)	0.371 (0.358)	0.337 (0.335)	0.360 (0.347)	-	0.031 (0.032)	0.048 (0.046)	0.053 (0.054)	0.065 (0.048)	0.009 (0.009)
	NCA14 (19) (15)	0.291 (0.273)	0.267 (0.254)	0.316 (0.309)	0.396 (0.380)	0.396 (0.385)	0.407 (0.385)	0.058 (0.055)	-	0.099 (0.097)	0.095 (0.096)	0.166 (0.163)	0.041 (0.044)
	LOY03 (23) (22)	0.195 (0.186)	0.205 (0.204)	0.246 (0.244)	0.279 (0.268)	0.262 (0.261)	0.283 (0.275)	0.100 (0.099)	0.148 (0.142)	-	0.060 (0.054)	0.138 (0.111)	0.048 (0.034)
	LOY04 (28) (26)	0.248 (0.215)	0.229 (0.207)	0.310 (0.277)	0.338 (0.303)	0.301 (0.273)	0.309 (0.274)	0.122 (0.110)	0.185 (0.166)	0.115 (0.099)	-	0.067 (0.053)	0.028 (0.027)
	LOY05 (12) (10)	0.277 (0.257)	0.272 (0.256)	0.388 (0.365)	0.389 (0.368)	0.367 (0.353)	0.392 (0.364)	0.142 (0.108)	0.230 (0.201)	0.175 (0.155)	0.115 (0.083)	-	0.064 (0.064)
	LOY06 (15)	0.269 (0.266)	0.263 (0.261)	0.321 (0.317)	0.391 (0.379)	0.361 (0.358)	0.390 (0.379)	0.025 (0.028)	0.099 (0.100)	0.093 (0.078)	0.106 (0.093)	0.168 (0.146)	-

Online Resource 13 (Continued)

(b) 8 loci

		SSH04a-1			SSH04a-2			SSH04b					
		CHE01	CHE05	NCA02	NCA01	NCA05	NCA06	NCA13	NCA14	LOY03	LOY04	LOY05	LOY06
SSH04a-1	CHE01 (11) (10)	-	0.086 (0.072)	0.069 (0.036)	0.131 (0.083)	0.082 (0.053)	0.125 (0.084)	0.243 (0.255)	0.222 (0.212)	0.115 (0.106)	0.123 (0.120)	0.162 (0.183)	0.147 (0.154)
	CHE05 (21) (20)	0.117 (0.097)	-	0.108 (0.095)	0.100 (0.092)	0.078 (0.056)	0.132 (0.104)	0.176 (0.167)	0.262 (0.210)	0.141 (0.129)	0.097 (0.090)	0.194 (0.172)	0.188 (0.175)
	NCA02 (10) (9)	0.115 (0.078)	0.192 (0.171)	-	0.093 (0.077)	0.072 (0.044)	0.115 (0.069)	0.321 (0.305)	0.244 (0.239)	0.152 (0.139)	0.159 (0.142)	0.305 (0.290)	0.162 (0.159)
SSH04a-2	NCA01 (25) (20)	0.202 (0.146)	0.153 (0.134)	0.281 (0.250)	-	0.047 (0.024)	0.046 (0.024)	0.432 (0.408)	0.473 (0.446)	0.265 (0.249)	0.212 (0.190)	0.294 (0.287)	0.402 (0.385)
	NCA05 (42) (31)	0.172 (0.124)	0.176 (0.152)	0.227 (0.180)	0.105 (0.063)	-	0.026 (0.004)	0.361 (0.332)	0.474 (0.418)	0.193 (0.174)	0.167 (0.148)	0.250 (0.228)	0.347 (0.324)
	NCA06 (31) (14)	0.241 (0.141)	0.242 (0.177)	0.315 (0.223)	0.127 (0.091)	0.065 (0.024)	-	0.449 (0.400)	0.523 (0.455)	0.343 (0.283)	0.220 (0.175)	0.294 (0.251)	0.424 (0.367)
SSH04b	NCA13 (10)	0.271 (0.273)	0.262 (0.255)	0.370 (0.37)	0.424 (0.398)	0.402 (0.390)	0.453 (0.395)	-	0.039 (0.028)	0.029 (0.026)	0.048 (0.047)	0.047 (0.013)	0.001 (0.001)
	NCA14 (19) (13)	0.275 (0.250)	0.287 (0.253)	0.349 (0.332)	0.426 (0.387)	0.420 (0.384)	0.461 (0.381)	0.076 (0.059)	-	0.077 (0.063)	0.067 (0.059)	0.181 (0.140)	0.025 (0.036)
	LOY03 (23) (22)	0.188 (0.187)	0.217 (0.209)	0.276 (0.275)	0.329 (0.307)	0.313 (0.302)	0.351 (0.305)	0.110 (0.108)	0.137 (0.125)	-	0.038 (0.037)	0.103 (0.065)	0.019 (0.016)
	LOY04 (28) (25)	0.189 (0.176)	0.194 (0.178)	0.287 (0.274)	0.327 (0.292)	0.300 (0.279)	0.319 (0.260)	0.090 (0.082)	0.133 (0.109)	0.109 (0.098)	-	0.068 (0.043)	0.035 (0.033)
	LOY05 (12) (8)	0.234 (0.212)	0.275 (0.237)	0.406 (0.376)	0.397 (0.357)	0.379 (0.352)	0.429 (0.351)	0.147 (0.069)	0.241 (0.156)	0.184 (0.155)	0.118 (0.060)	-	0.051 (0.035)
	LOY06 (15)	0.250 (0.255)	0.261 (0.252)	0.334 (0.337)	0.434 (0.411)	0.406 (0.394)	0.458 (0.401)	0.013 (0.013)	0.063 (0.061)	0.083 (0.080)	0.072 (0.066)	0.179 (0.109)	-

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Online Resource 14 Relative migration networks for (a) all *Pocillopora* PSH04 colonies and (b) each cluster separately (Entire_11 dataset). Nodes represent populations and arrows represent migrations

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Online Resource 15 *Pocillopora* PSH04. Miscellany pictures for each Secondary Species Hypothesis (SSH) and each cluster, representing *corallum* macromorphology diversity (scale $\approx$ 5 cm)

SSH04a-1

SSH04a-2

SSH04b