



Distinct lineages and population genomic structure of the coral *Pachyseris speciosa* in the small equatorial reef system of Singapore

Bar Feldman¹ · Lutfi Afiq-Rosli^{2,3} · Noa Simon-Blecher¹ · Elena Bollati² · Benjamin John Wainwright^{2,4} · Pim Bongaerts⁵ · Danwei Huang^{2,3,6} · Oren Levy¹

Received: 13 January 2021 / Accepted: 13 July 2021 / Published online: 4 August 2021
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract Genetic population patterns in coral reefs are important for understanding biodiversity and forecasting recovery following disturbance. Studying gene flow between small and disrupted marine ecosystems, such as the reefs along the Singapore Strait, is especially crucial due to their fragile nature. Here we sampled the ubiquitous coral species complex *Pachyseris speciosa* from seven sites in Singapore and applied genotyping-by-sequencing (nextRAD) for a fine-scale population genomic assessment. Our results confirm the existence of two clearly distinct, possibly cryptic, lineages that occur sympatrically at each of the seven sampling sites and are related to the “blue” and “green” lineages found in other parts of the Indo-Pacific. The closely related lineages show contrasting patterns

characterised by panmixia and substantial (but unexplained) substructuring, respectively. Analysis of barriers and corridors to gene flow reveals limited connectivity between the two largest clusters of reefs at the eastern and western sectors of Singapore’s southern coastal waters. Our results extend the geographic range of the two recently uncovered *P. speciosa* species, further confirming their status as distinct and widespread species. More broadly, our findings highlight how conservation and management strategies may maximise connectivity among Singapore’s urbanised reef ecosystems.

Keywords Connectivity · Coral reef · Genetic structure · Genotyping-by-sequencing · Population genetics · Scleractinia

B. Feldman and L. Afiq-Rosli have equally contributed.

Topic Editor: Francesca Benzoni

✉ Bar Feldman
barbarfel24@gmail.com

Lutfi Afiq-Rosli
lutfiqiqrosli@u.nus.edu

Noa Simon-Blecher
blechn@gmail.com

Elena Bollati
e.bollati@nus.edu.sg

Benjamin John Wainwright
ben.wainwright@yale-nus.edu.sg

Pim Bongaerts
pbongaerts@calacademy.org

Danwei Huang
huangdanwei@nus.edu.sg

Oren Levy
Oren.levy@biu.ac.il

¹ Faculty of Life Sciences, The Mina and Everard Goodman, Bar-Ilan University, 5290002 Ramat-Gan, Israel

² Department of Biological Sciences, National University of Singapore, 16 Science Drive 4, Singapore 117558, Singapore

³ Tropical Marine Science Institute, National University of Singapore, 18 Kent Ridge Road, Singapore 119227, Singapore

⁴ Yale-NUS College, 16 College Avenue West, #01-220, Singapore 138527, Singapore

⁵ California Academy of Sciences, San Francisco, CA, USA

⁶ Centre for Nature-based Climate Solutions, National University of Singapore, 16 Science Drive 4, Singapore 117558, Singapore

Introduction

Describing all the species on Earth is a task that may never be completed (Scheffers et al. 2012). Yet, estimation of species diversity has been and continues to be of great interest, motivated mainly by the need to provide a reference point for current and future losses of biodiversity (Mora et al. 2011). Assessments on the number of marine species range widely, between 226,000 species at the conservative end (Appeltans et al. 2012) and up to 10 million and more (Frederick Grassle and Maciolek 1992; Costello et al. 2012). A significant factor for this broad range is the presence of taxonomically cryptic species (Bickford et al. 2007; Pfenninger and Schwenk 2007; Nygren 2014), and methods for delimiting them are one of the most pertinent issues in biological science (Sites and Marshall 2003). Taxonomically cryptic species are broadly defined as two or more genetically distinct taxa that are erroneously classified as a single species (Richards et al. 2016; Sheets et al. 2018; Bongaerts et al. 2021). This problem could be due to morphological resemblance despite the genetic divergence (Pfenninger and Schwenk 2007; Fišer et al. 2018). Studies on cryptic species have increased exponentially over the past three decades since genetic techniques started to be applied (Bickford et al. 2007; Nygren 2014). They are evenly distributed among biogeographical regions (Pfenninger and Schwenk 2007) and could be found in many major metazoan and plant groups (Grundt et al. 2006; Pfenninger and Schwenk 2007). In particular, marine environments are known to host numerous such cryptic species groups likely due to their species-rich habitats (Willig et al. 2003). Identification of cryptic species is crucial for biodiversity conservation, management and understanding the evolutionary processes which drive speciation (Chadè et al. 2008; Baird et al. 2011; Andrews et al. 2014). Given that most species remain undescribed, efforts to catalogue and explain biodiversity need to be prioritised (Bickford et al. 2007).

Scleractinian corals (Cnidaria: Anthozoa: Scleractinia) are difficult to classify due to their morphological plasticity (Todd 2008; Paz-García et al. 2015) and pervasive convergent evolution (e.g. Fukami et al. 2004, 2008; Huang et al. 2009). Taxonomically cryptic diversity has been documented in several coral genera, for example, in *Acropora* Oken, 1815 (Ladner and Palumbi 2012; Richards et al. 2016), *Stylophora* Schweigger, 1820 (Stefani et al. 2011), *Pocillopora* Lamarck, 1816 (Souter 2010; Schmidt-Roach et al. 2013; Gélin et al. 2017), and *Seriatopora* Lamarck, 1816 (Bongaerts et al. 2010; Warner et al. 2015). For centuries, morphology was the sole means to delimit one species from another (e.g. Lamarck 1815; Wells 1956; Chevalier 1975; Lang 1984; Veron 2002). However,

integrative studies that rely on combining morphological and multi-locus molecular approaches for phylogenetic reconstruction have proved to be furthermost accurate (Benzoni et al. 2007, 2011, 2014; Kitahara et al. 2012, 2013; Huang et al. 2014; Arrigoni et al. 2014, 2015). For example, Arrigoni et al. (2019) recently described a new cryptic genus and species *Paraechinophyllia variabilis*, Arrigoni, Benzoni and Stolarski, 2019, which could not be distinguished from other lobophylliids based on morphological characters alone, and delimited it from other species from the family using six molecular markers (COI, 12S, ATP6-NAD4, NAD3-NAD5, histone H3 and ITS). Notably, species boundaries within the genus *Leptastrea* Milne-Edwards & Haime, 1849, have been evaluated by applying restriction site-associated DNA sequencing (RADseq) to sample single nucleotide polymorphisms (SNPs) across the genome, complementing detailed morphological diagnoses (Arrigoni et al. 2020). Such reduced-representation genomic approaches provide high coverage of homologous portions of the genome from multiple individuals for comparatively low cost and effort by sequencing only certain regions of DNA adjacent to restriction endonuclease sites (Toonen et al. 2013).

The zooxanthellate genus *Pachyseris* Milne-Edwards & Haime, 1849, is widely distributed throughout the Indo-Pacific and can be found in all reef habitats but most commonly on lower reef slopes (Veron 1980, 2000; Scheer and Pillai 1983; Sheppard and Sheppard 1991). In particular, *Pachyseris speciosa* Dana, 1846, the most widespread nominal species in the genus, is found in the Indo-Pacific from the Red Sea to the Philippines and Tahiti (Veron 2000; Hughes et al. 2013). There are currently six valid species in the genus (Hoeksema and Cairns 2020), which has been well represented in systematic and phylogenetic studies (Fukami et al. 2008; Kitahara et al. 2010; Terraneo et al. 2014). However, the relationships among *Pachyseris* species and within even the most widespread *P. speciosa* are unclear. Terraneo et al. (2014) reconstructed *Pachyseris* phylogeny inferred from Bayesian inference analysis of mitochondrial intergenic spacer between COI and 16S-rRNA. Three lineages were analysed: *P. rugosa* and *P. speciosa* were recovered as sister species and both were sister to *P. inattesa*. Despite the ecological prominence of *P. speciosa* on Indo-Pacific reefs, much of its evolution and population genetic structure remain obscure. Recently, Bongaerts et al. (2021) used reduced-representation sequencing to show that *P. speciosa* actually represents a species complex, with three sister species occurring sympatrically throughout Australasia. The genomic differentiation was accompanied by ecological, physiological and reproductive differences, yet there was a lack of morphological characters distinguishing the three lineages.

Members of the *P. speciosa* species complex are characterised as gonochores with a broadcasting reproductive mode (Kerr et al. 2011; Bongaerts et al. 2021). Their ecologically opportunistic nature is reflected in it being one of the most common species throughout Singapore's reefs (Guest et al. 2016; Wong et al. 2018) and across depths (Chow et al. 2019). Ship movement rousing the shallow seafloor of the Singapore Strait (Browne et al. 2014, 2015) and the extensive urban coastal development projects are the main causes for the turbid water in the reefs here (Dikou and van Woesik 2006; Sin et al. 2016). Due to this high turbidity and the consequent high light attenuation (i.e. < 1% of surface PAR at ~ 9 m depth; Todd et al. 2004), foliose corals with large areal extents for light capture, such as *P. speciosa*, are most common at 3–8 m depth (Dikou and van Woesik, 2006; Guest et al. 2016; Chow et al. 2019).

In this study, we used a genotyping-by-sequencing approach to characterise the *P. speciosa* species complex and population genomic variation across seven sites on Singapore reefs (~ 2–15 km apart) situated along the Singapore Strait. We confirm the presence of two distinct and possibly cryptic species with further genetic sub-structuring uncovered that cannot be related to the studied geographic locations.

Materials and methods

Sample collection and DNA extraction

We focused on the highly urbanised reef system in Singapore where we targeted seven sampling sites—Raffles, Semakau, Hantu, TPT, Kusu, St. John and Sisters Islands (Fig. 1). Sites were chosen depending on the abundance and availability of *Pachyseris speciosa*. Colonies were identified to species based on the original description by Dana, 1846, supported by subsequent descriptions as well as images of the holotype and live colonies (Veron and Pichon 1980; Veron 2000; Terraneo et al. 2014). From each site, between 18 and 23 samples were taken from 4 to 6 m depth using a cutter (Table S1). We kept at least 5 m apart from sample to sample in order to avoid sampling genetically identical colonies. All samples were preserved in 100% molecular grade ethanol and stored at – 80 °C immediately after collection. Genomic DNA was extracted using Qiagen DNeasy Blood and Tissue Kit. Post-extraction, gel electrophoresis test was carried out in order to ensure that samples were clean from RNA or proteins. DNA quantification was performed using a Qubit 3 Fluorometer.

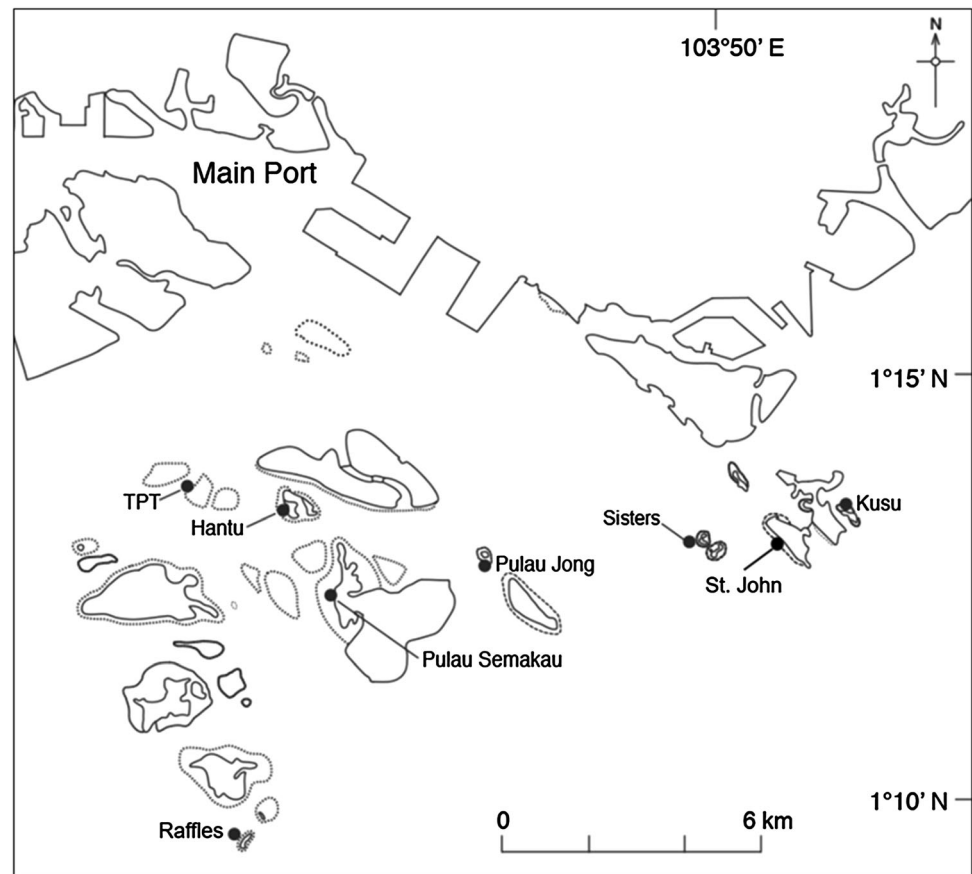
NextRAD library preparation and sequencing

All 144 samples were genotyped via nextRAD genotyping-by-sequencing (SNPsaurus, LLC), following library preparation as detailed in Russello et al. (2015). Briefly, DNA (~ 12 ng) was first fragmented and adapter-ligated with the Nextera DNA Library Prep Kit (Illumina, Inc). Fragmented DNA was then amplified with one of the primers matching the adapter and extending nine nucleotides into the genomic DNA with the selective sequence 5'–GTGTAGAGG–3'. Thus, only fragments starting with a sequence that can be hybridised by the selective sequence of the primer would be efficiently amplified. The nextRAD libraries were then sequenced on three HiSeq 4000 lanes for 150-bp single-end reads (University of Oregon).

Genotyping and quality control

The genotyping analysis used custom scripts (SNPsaurus, LLC) that trimmed the reads using bbduk (BBTools package, Brian Bushnell, Walnut Creek, CA, USA) (see Supplementary File 1). Next, all remaining reads were mapped to the *Pachyseris speciosa* genome (Bongaerts et al. 2021; downloaded from <http://reefgenomics.org>) (see Supplementary File 1). Genotype calling was performed using Samtools and bcftools (Li et al. 2009) and compiled in Variant Call Format (VCF) files using custom parameters (see Supplementary File 1). The VCF files were filtered to remove alleles with a population frequency of less than 3%. SNPs that were heterozygous in all samples, or had more than two alleles in a sample were also removed. PGDSpider (version 2.1.1.5) (Lischer and Excoffier 2012) was used to reformat the VCF files for downstream analyses. The remaining SNPs were evaluated for significant deviations from Hardy–Weinberg equilibrium and linkage using arlecore (version 3.5.2.2), with SNPs that deviated in more than five a priori populations removed as in Bongaerts et al. (2017). The *clonecorrect* function in R package poppr (version 2.8.1) (Kamvar et al. 2014, 2015) was used to remove potential clones from the dataset, with clonal groups reduced to a single representative per population. Finally, only SNPs with 1% missing data and samples with < 15% missing data were retained to ensure high-quality downstream analyses (see Afiq-Rosli et al. 2021). Three datasets with varying filtering parameters were assembled for analysis: overall dataset (all SNPs), neutral dataset (SNPs under selection removed) and outlier dataset (only SNPs identified as under selection). BayeScan (version 2.1) (Foll and Gaggiotti 2008) using default parameters (see Supplementary File 1) and Bayes factor cut-off of 0.05 were used to identify SNPs under possible selection.

Fig. 1 A map of all seven sampling sites at the offshore islands of Singapore



Genetic structuring and connectivity analyses

To assess genetic structure for each dataset, Bayesian clustering analysis was performed in STRUCTURE version 2.3.4 for up to seven possible genetic clusters (K) according to the total number of collection sites. We considered correlated allele frequencies in the admixture model, using sampling locations as priors, and ran 10 iterations of 100,000 MCMC repetitions with the first 10,000 as burn-in (Gilbert et al. 2012; Janes et al. 2017). MCMC convergence, where α values reached equilibrium, was examined using the *Data plot* option in STRUCTURE (Porrás-Hurtado et al. 2013). Variation of K values was then summarised and plotted in CLUMPAK (Kopelman et al. 2015). The optimal K was determined by examining the $\ln Pr(X|K)$ and ΔK plots (Pritchard and Wen 2003; Evanno et al. 2005; Janes et al. 2017). Principal component analysis (PCA) was performed in the R package SNPRelate version 1.18 to identify clusters without relying on population genetic models (Jombart et al. 2010).

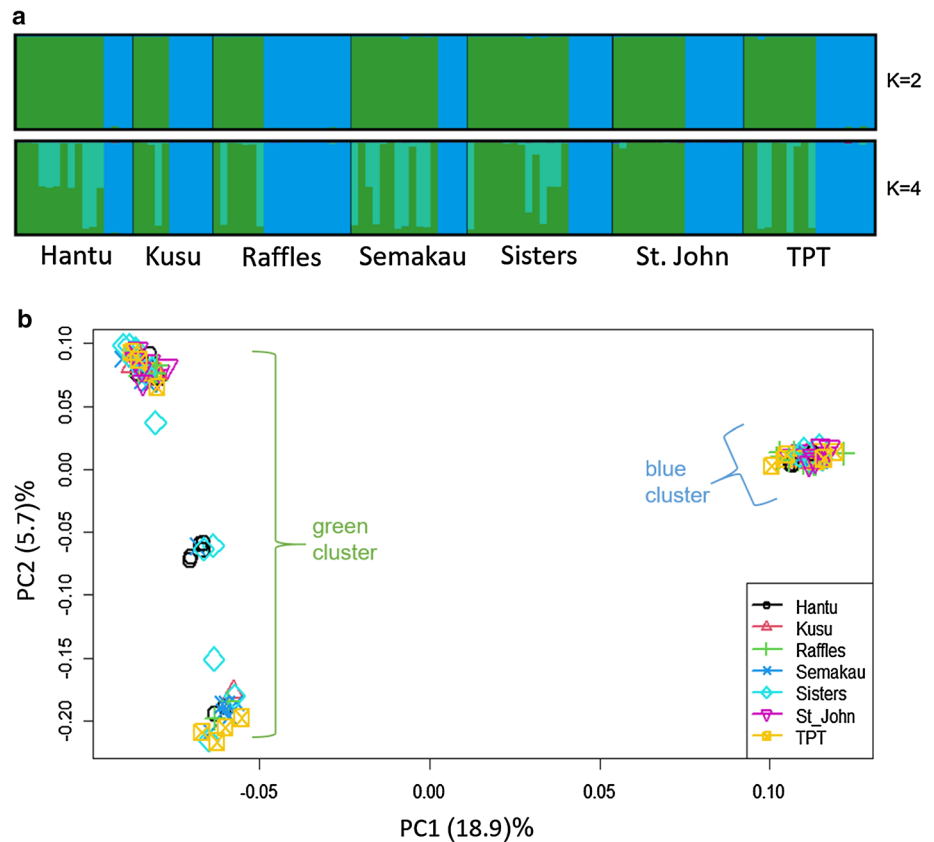
An individual-based analysis grounded on detecting deviations from the isolation-by-distance (IBD) models (Keis et al. 2013; Tang et al. 2018) was used to characterise barriers of and corridors for dispersal of each lineage using R package ResDisMapper (Tang et al. 2019). First,

distributions of genetic distance (Nei's standard genetic distance) and geographic distance (both measured in GenAlEx v 6.5) were checked using two modelling methods—linear and nonlinear—before a best-fit method based on R^2 value was chosen for IBD residual calculation for each pair of individuals. Resistance values, together with their corresponding statistical significance over the landscape, were then calculated and visualised using default settings.

Identification of distinct lineages

In order to assess the relationship of our samples within the recently uncovered *P. speciosa* species complex (Bongaerts et al. 2021), we employed the cleaved amplified polymorphic sequence (CAPS) assay. This assay was designed to rapidly assign individuals to one of the three cryptic lineages that occur sympatrically in East Australia. Genomic DNA for each sample was amplified with three separate primer pairs (Pspe-GRN, Pspe-BLU and Pspe-RED), and amplicons were digested with restriction enzymes (HhaI, HaeIII and Taq α 1, respectively) following reaction conditions described in Bongaerts et al. (2021). The lengths of restriction fragments were then determined via agarose gel electrophoresis and used to assign samples

Fig. 2 Analysis of 8590 SNPs found across samples of *Pachyseris speciosa* from Singapore. **a** STRUCTURE plot of ancestry proportions with $K = 2$ and $K = 4$ depicting two main clusters (*green* and *blue*) that were not site specific. Within the *green* cluster two subclusters could be observed (*dark* and *light green*). **b** Principal component analyses (PCAs) of the *blue* and the *green* clusters showed separation on PC1 (18.9% variations)



to one of the three clusters (Bongaerts et al. 2021) (see Fig. S1).

We also compared representative samples from our main clusters through joint variant calling and a maximum likelihood tree. For this comparison, we included three samples from each of our two main genetic clusters and six samples from each of the six main clusters (“green”, “blue”, “red”, “dark green”, “dark blue” and “purple”) in Bongaerts et al. (2021). RAxML version 8.2.12 (Stamatakis 2014) was used to infer a maximum likelihood phylogeny based on the SNP data with invariant sites removed. We applied an ascertainment bias correction for the omission of invariant sites (Lewis 2001; Leaché et al. 2015) to perform tree searches using 50 random starting trees and bootstrap resampling with 1000 replicates.

Results

Sequencing of the nextRAD libraries resulted in an average of 3.01 million reads per sample that mapped to the reference ($n = 144$) and genotype calling initially yielded 19,716 biallelic SNPs. After quality control to remove SNPs that were linked, deviated from Hardy–Weinberg equilibrium or had more than 1% missing data per SNP, removing colonies with more than 15% missing data per

sample, and following minimal representation filtering, we retained 8590 biallelic SNPs ($n = 140$). *clonecorrect* under default parameters did not identify any clones. BayeScan identified 32 outlier SNPs. PCA and STRUCTURE analyses with or without SNPs identified as putatively under selection did not alter assignments of individuals to populations, and because of this, we opted to use the larger dataset for subsequent analyses.

PCA and STRUCTURE clearly showed that samples were clustered into two distinct lineages that were not site specific (Fig. 2), possibly representing cryptic species. The CAPS assay yielded clearly distinct restriction fragment length patterns for the two lineages (Fig. S1; Table S1). Specifically, one of the lineages had the diagnostic mutation for the blue cluster described by Bongaerts et al. (2021), as indicated by the restriction digest of the *Pspe*-BLU amplicon by the *Hae*III enzyme into two 100–150 bp bands, whereas no digestion was observed for the other lineage. None of the samples had the diagnostic mutation of the “red” or “green” lineage, as indicated by consistent digestion observed for all samples with *Pspe*-Red-Taq α 1 (*not* “red”) and no digestion observed for *Pspe*-GRN *Hha*I (*not* “green”) (Fig. S1; Table S1). It must be noted the CAPS assay was designed to target specifically GBR lineages, and was not diagnostic for the “dark green” and “dark blue” lineages in Okinawa (Bongaerts et al. 2021).

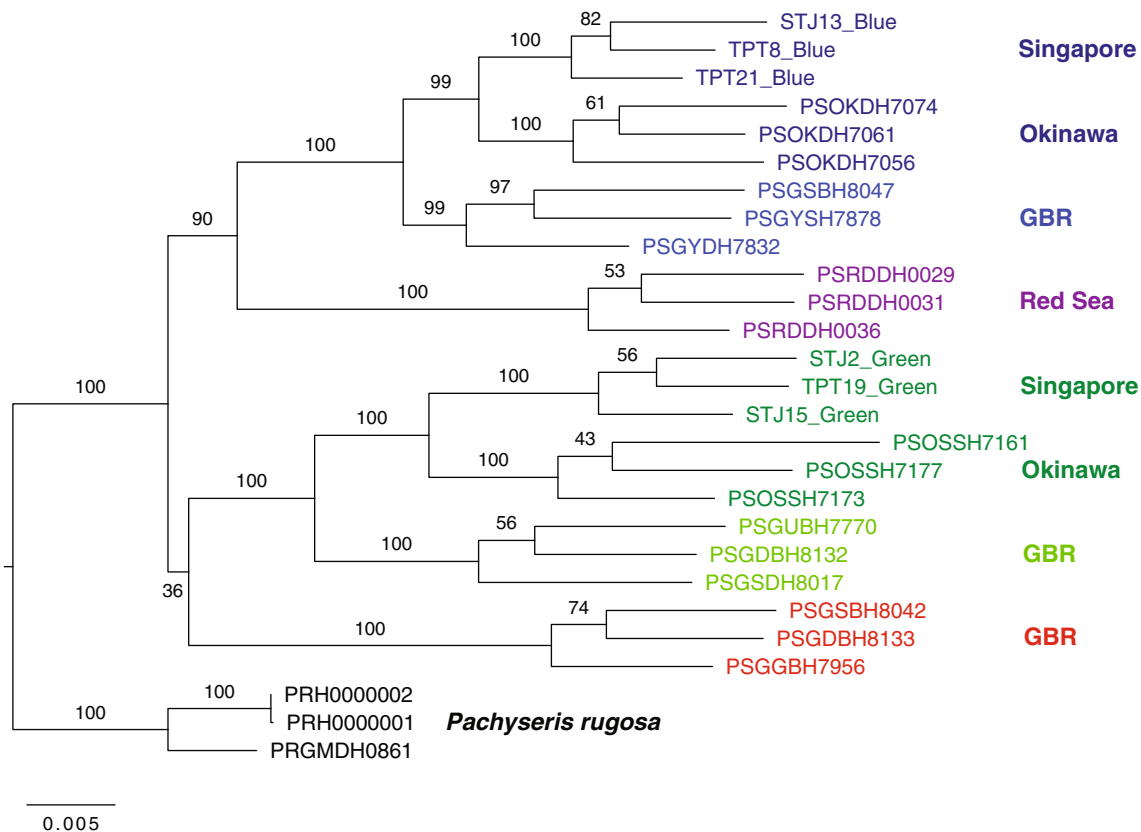


Fig. 3 Maximum likelihood tree of representative samples of the *green* and *blue* lineages from Singapore showing clustering with samples from the “dark green” and “dark blue” clusters in Okinawa from Bongaerts et al. (2021)

We therefore conducted joint variant calling and maximum likelihood analysis with representative samples from Bongaerts et al. (2021), which indicated our lineages to be most closely related to the “dark green” and “dark blue” clusters (which appear to be geographic subclusters of the “green” and “blue” lineages) (Fig. 3; Table S1). We therefore analysed the two lineages (*green* and *blue*) separately, in order to detect genetic clustering within the two lineages with identical filtering steps as the overall dataset.

Based on 6979 and 6562 biallelic SNPs (including 45 and 38 outlier SNPs detected by BayeScan) for the *green* ($n = 70$) and *blue* ($n = 47$) lineages, respectively, global mean F_{ST} was higher in the *green* lineage ($F_{ST} = 0.0142$) compared to *blue* lineage ($F_{ST} = 0.0037$). Evanno’s method and PCA showed that the most likely “K” is two for the *green* lineage (Fig. 4a, b; Fig. S2a). For this number of populations, STRUCTURE plots showed that St. John comprises exclusively of a *dark green* subcluster (not to be confused with the “dark green” cluster in Bongaerts et al. 2021) and that Semakau and TPT comprise mainly the *light green* subcluster (Fig. 4a). PCA and STRUCTURE showed no geographic structuring of colonies within the *blue* lineage (Fig. 4c, d; Fig. S2b). ResDisMapper identified a

dispersal corridor at the southern periphery of the islands along the Singapore Strait for both lineages (Fig. 5a, b).

Discussion

The aim of this study was to characterise the *Pachyseris speciosa* species complex and its population genetic structure in Singapore using a genotyping-by-sequencing approach (nextRAD; Russello et al. 2015). Based on sequencing of 144 colonies that were identified as *P. speciosa* based on conventional taxonomy (Dana 1846; Veron and Pichon 1980; Veron 2000; Terraneo et al. 2014) from seven sites 2–15 km apart, we found two clearly distinct lineages (i.e. *green* and *blue*) that were sympatric at each of the seven sampling sites (Fig. 2). This separation into two lineages was supported through a CAPS assay and clustering analyses based on shared variants, with the latter indicating relatedness to the “dark green” and “dark blue” clusters from Okinawa identified in Bongaerts et al. (2021) (Fig. 3). Our results greatly extend the geographic range of these recently uncovered *P. speciosa* species, further confirming their status as distinct and widespread species.

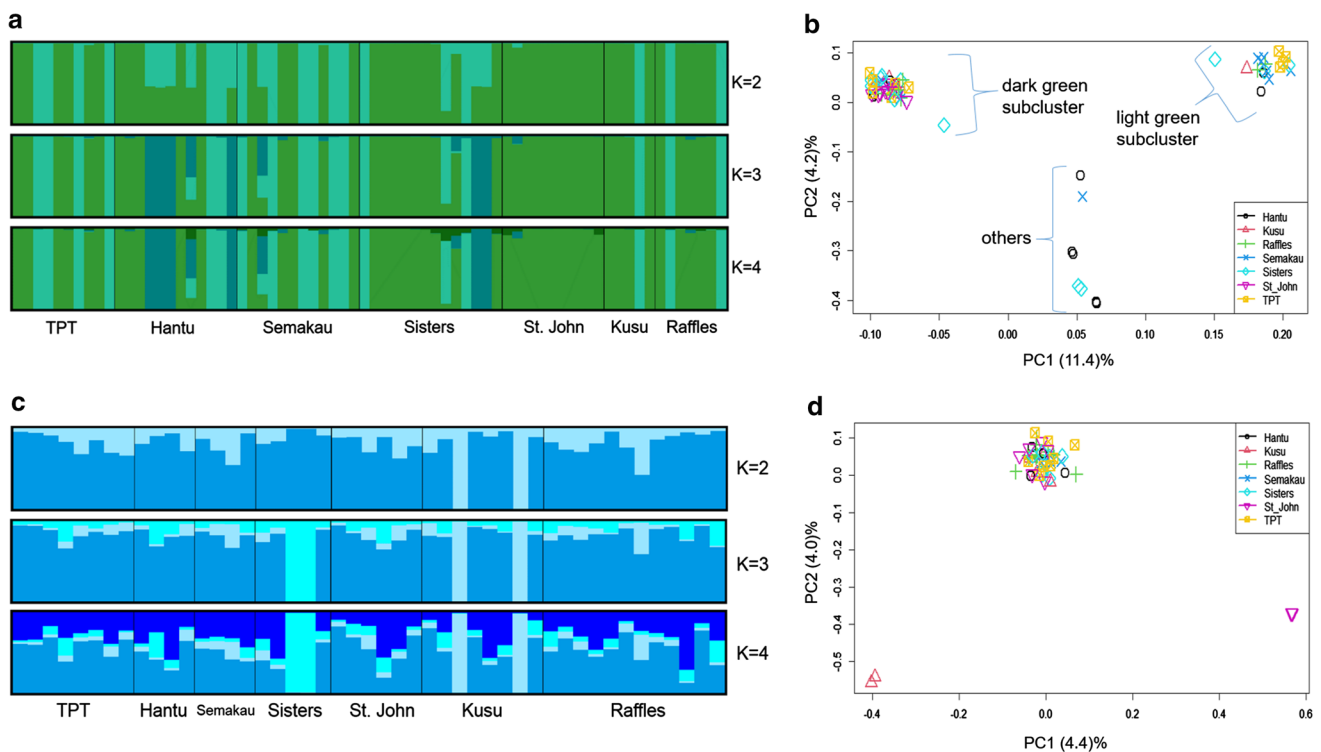


Fig. 4 Analysis of the *green* and *blue* clusters with 8590 SNPs. **a** STRUCTURE plot of ancestry proportions from $K = 2$ to $K = 4$ with the best model depicting two main subclusters (*dark* and *light green*) that were not site specific. St. John has a 100% proportion of the *dark green* subcluster. Semakau has the highest proportion of the *light green* subcluster (54%). **b** Independent principal components

(PCs) are separated primarily into two subclusters on PC1 (11.4% variations) with a few mosaics from Hantu, Sisters and Semakau. **c** STRUCTURE plot of ancestry proportions from $K = 2$ to $K = 4$ with the best model depicting one population across all sites within Singapore's *blue* cluster. **d** Principal components (PCs) showing one cluster with a few mosaics from Kusu and St. John

The population structuring within each of the two lineages reveals an interesting pattern: the *blue* lineage seems to be one panmictic population, with only a few outliers in St. John and Kusu Island, while the *green* lineage has unexplained substructuring (Fig. 4). The low genetic structure of the *blue* lineage across all geographic sites is similar to other broadcasting spawners (e.g. Porto-Hannes et al. 2015; Bongaerts et al. 2017; Eckert et al. 2019) and more specifically in Singapore (Tay et al. 2015). Gene flow mechanisms of coral species are dependent mostly upon their life history traits, as broadcast spawners' populations are expected to be more connected due to the long pelagic larval duration of broadcasted larvae compared to brooders (Serrano et al. 2016; Underwood et al. 2018). Reproductive patterns of *P. speciosa* in Singapore have never been documented. Australian *P. speciosa* species were reported to be gonochoric spawners, and the different lineages showed different timing of gamete release. It is possible that the different genetic patterns of the Singapore lineages could be linked to variations in the timing and mode of gamete release. Furthermore, changes in current regimes associated with tidal cycles, storms and seasonal monsoon along the Singapore Strait (Sin et al. 2016) may influence

gene flow and drive the observed differences in genetic structures of the two *P. speciosa* lineages. The two lineages of *P. speciosa*—showing such distinct population genetic and gene flow patterns between them—support the species-level divergence inferred from the SNP data in this work and in Bongaerts et al. (2021), which found four distinct lineages including the two found here.

ResDisMapper analyses showing barriers vs. corridors to gene flow between sites indicate that connectivity between the western sites and between eastern and western sites is limited and could be observed only between the eastern sites and Raffles and Hantu (Fig. 5). The population distinction between the western and eastern populations and among the western populations is concerning and could be due to the massive reclamation and development of the area in the last 60 years. Fringing and patch reefs, mangroves, sandy and rocky shores were major coastal features in this area prior to development in the 1960's (Chou et al. 2019). Yet, the distribution of coral reefs has been greatly reduced by landfill construction (Chou and Tan 2007), the expanding port facilities and terminals (Sin et al. 2016) and the reclamation and development of offshore islands (Tay et al. 2018). These extensive coastal

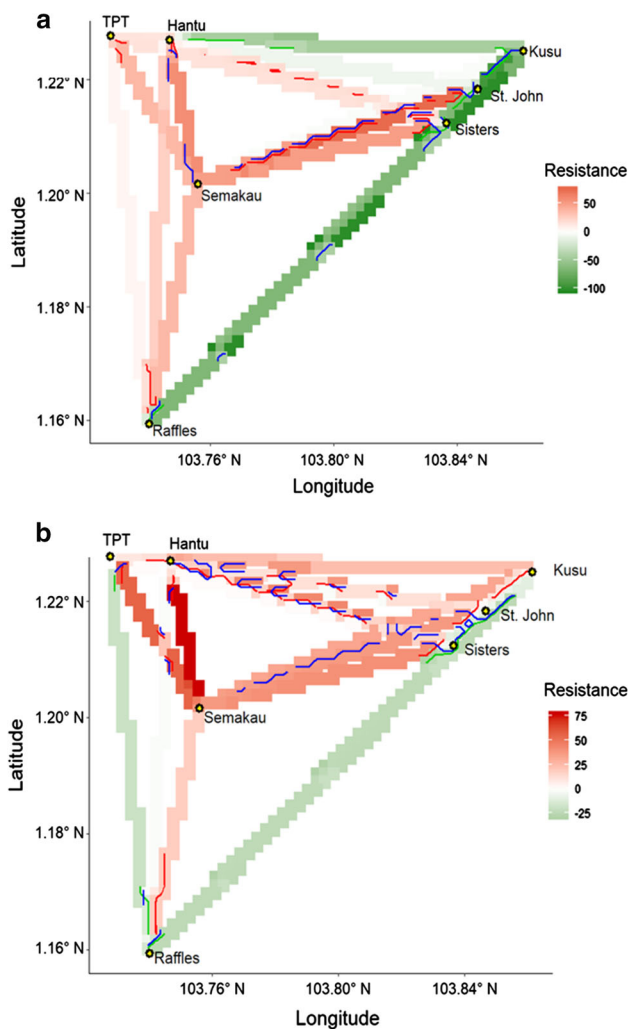


Fig. 5 Resistance map produced by ResDisMapper for **a** green lineage and **b** blue lineage of *Pachyseris speciosa*. Areas with resistance values that are higher/lower than those from a null distribution with high probability and lie within the red/green contours represent a significant barrier/corridor. Areas within the blue contours have resistance values with high probability of being positive or negative (high “certainty”). Yellow circles indicate sampling points

changes have resulted in rapid declines in area and quality of reef habitats (Hilton and Manning 1995), especially those adjacent to the western cluster of islands due to their proximity to the intensive urban activities. The increase in land area could have reduced water flow at the western islands, or increased introduction of sediments, nutrients, heavy metals and organic chemicals (Goh and Chou 1997; Sin et al. 2016) and led to filtering of more tolerant genotypes.

Considering most islands are isolated (i.e. showing barriers between them and the others), there may be a need for these results to inform future developments to consider enhancing physical and biological connectedness among the western island cluster. Such actions will promote

biological connectivity and resilience, especially since coral recruitment is at low levels in the Singapore Strait (Bauman et al. 2015). Relatedly, recent genotyping of the endosymbionts of *P. speciosa* suggests that the two lineages do not have divergent dominant Symbiodiniaceae types (Jain et al. 2020; Smith et al. 2020). Singapore’s reefs provide habitat for a diverse coral assemblage (Guest et al. 2016), yet a strong selective pressure caused by the turbid water along the Singapore Strait possibly limits the diversity of the associated endosymbiont community. Interestingly, detailed characterisation of the bleaching susceptibility of the two lineages also showed no clear difference as both lineages have similar responses to bleaching (Jain et al. 2020).

The subclustering within the green lineage (i.e. Figure 4a, b), possibly promoted by the barriers to gene flow (i.e. Figure 5a), may help explain the cryptic lineages of *P. speciosa* in other geographic sites. If these processes do scale up to the global level, i.e. at larger geographic scale and over longer time, these minute population differentiations could provide more opportunities for isolation of lineages, especially over the 10-million-year history of the three cryptic lineages (Bongaerts et al. 2021). We note that there are three other nominal species currently considered to be junior synonyms of *P. speciosa* (Veron and Pichon 1980; Scheer and Pillai 1983). *Agaricia levicollis* Dana (1846) has a non-specific type locality referring to Southeast Asia (‘East Indies’, Dana 1846, p. 338), while *Pachyseris haimeii* Quelch, 1886, and *Pachyseris clementei* Nemenzo, 1955, were described from Tahiti (French Polynesia) and Puerto Galera (Philippines), respectively. Localities of *Agaricia levicollis* and *P. clementei* are within the range of the green and blue clusters discovered between Bongaerts et al. (2021) and the present study. Detailed taxonomic work integrating these genomic results, morphological differences between these nominal species, and more geographically resolved collections in the Central Indo-Pacific are needed to ascertain potential relationships with these junior synonyms.

Population genetics and connectivity among reefs play a vital role in shaping regional patterns of reef biodiversity and recovery following disturbance (Bongaerts et al. 2010, 2017; Sheets et al. 2018). This research highlights how a small reef system less than 15 km across all sites sampled can have highly sympatric distributions, furthermore showing distinct subclustering of a cryptic lineage.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00338-021-02160-4>.

Acknowledgements We thank Sudhanshi S. Jain, Adi Zweifler, Eviatar Weizman and Inbal Ayalon for assistance in field and laboratory work. This research was supported by the National Research

Foundation, Prime Minister's Office, Singapore and the Israel Science Foundation under their 2nd Joint Grant Call (NRF2017NRF-ISF002-2658; Grant Number 2658/17).

Declarations

Conflict of interest The author declares that there is no conflict of interest.

References

- Afiq-Rosli L, Wainwright BJ, Gajanur AR, Lee AC, Ooi SK, Chou LM, Huang D (2021) Barriers and corridors of gene flow in an urbanised tropical reef system. *Evol Appl*. <https://doi.org/10.1111/eva.13276>
- Andrews KR, Norton EL, Fernandez-Silva I, Portner E, Goetze E (2014) Multilocus evidence for globally distributed cryptic species and distinct populations across ocean gyres in a mesopelagic copepod. *Mol Ecol* 23:5462–5479
- Appeltans W, Ah Yong ST, Anderson G, Angel MV, Artois T, Bailly N, Bamber R, Barber A, Bartsch I, Berta A, Błazewicz-Paszkowycz M, Bock P, Boxshall G, Boyko CB, Brandão SN, Bray RA, Bruce NL, Cairns SD, Chan TY, Cheng L, Collins AG, Cribb T, Curini-Galletti M, Dahdouh-Guebas F, Davie PJF, Dawson MN, De Clerck O, Decock W, De Grave S, De Voogd NJ, Domning DP, Emig CC, Erséus C, Eschmeyer W, Fauchald K, Fautin DG, Feist SW, Franssen CHJM, Furuya H, Garcia-Alvarez O, Gerken S, Gibson D, Gittenberger A, Gofas S, Gómez-Daglio L, Gordon DP, Guiry MD, Hernandez F, Hoeksema BW, Hopcroft RR, Jaume D, Kirk P, Koedam N, Koenemann S, Kolb JB, Kristensen RM, Kroh A, Lambert G, Lazarus DB, Lemaitre R, Longshaw M, Lowry J, MacPherson E, Madin LP, Mah C, Mapstone G, McLaughlin PA, Mees J, Meland K, Messing CG, Mills CE, Molodtsova TN, Mooi R, Neuhaus B, Ng PKL, Nielsen C, Norenburg J, Opreko DM, Osawa M, Paulay G, Perrin W, Pilger JF, Poore GCB, Pugh P, Read GB, Reimer JD, Rius M, Rocha RM, Saiz-Salinas JL, Scarabino V, Schierwater B, Schmidt-Rhaesa A, Schnabel KE, Schotte M, Schuchert P, Schwabe E, Segers H, Self-Sullivan C, Shenkar N, Siegel V, Sterrer W, Stöhr S, Swalla B, Tasker ML, Thuesen EV, Timm T, Todaro MA, Turon X, Tyler S, Uetz P, Van Der Land J, Vanhoorne B, Van Ofwegen LP, Van Soest RWM, Vanaverbeke J, Walker-Smith G, Walter TC, Warren A, Williams GC, Wilson SP, Costello MJ (2012) The magnitude of global marine species diversity. *Curr Biol* 22:2189–2202
- Arrigoni R, Terraneo TI, Galli P, Benzoni F (2014) Lobophylliidae (Cnidaria, Scleractinia) reshuffled: Pervasive non-monophyly at genus level. *Mol Phylogenet Evol* 73:60–64
- Arrigoni R, Berumen ML, Stolarski J, Terraneo TI, Benzoni F (2019) Uncovering hidden coral diversity: a new cryptic lobophylliid scleractinian from the Indian Ocean. *Cladistics* 35:301–328
- Arrigoni R, Berumen ML, Terraneo TI, Caragnano A, Bouwmeester J, Benzoni F (2015) Forgotten in the taxonomic literature: Resurrection of the scleractinian coral genus *Sclerophyllia* (Scleractinia, Lobophylliidae) from the Arabian Peninsula and its phylogenetic relationships. *Syst Biodivers* 13:140–163
- Arrigoni R, Berumen ML, Mariappan KG, Beck PSA, Hulver AM, Montano S, Pichon M, Strona G, Terraneo TI, Benzoni F (2020) Towards a rigorous species delimitation framework for scleractinian corals based on RAD sequencing: the case study of *Leptastrea* from the Indo-Pacific. *Coral Reefs* 39:1001–1025
- Baird HP, Miller KJ, Stark JS (2011) Evidence of hidden biodiversity, ongoing speciation and diverse patterns of genetic structure in giant Antarctic amphipods. *Mol Ecol* 20:3439–3454
- Bauman AG, Guest JR, Dunshea G, Low J, Todd PA, Steinberg PD (2015) Coral settlement on a highly disturbed equatorial reef system. *PLoS One* 10:e0127874
- Benzoni F, Arrigoni R, Stefani F, Pichon M (2011) Phylogeny of the coral genus *Plesiastrea* (Cnidaria, Scleractinia). *Contrib Zool* 80(4):231–249
- Benzoni F, Stefani F, Stolarski J, Pichon M, Mitta G, Galli P (2007) Debating phylogenetic relationships of the scleractinian *Psammocora*: Molecular and morphological evidences. *Contrib Zool* 76:35–54
- Benzoni F, Arrigoni R, Zoologica S, Dohrn A, Waheed Z, Stefani F (2014) Phylogenetic relationships and revision of the genus *Blastomussa* (Cnidaria: Anthozoa: Scleractinia) with description of a new species. *Raffles Bull Zool* 62:358–378
- Bickford D, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I (2007) Cryptic species as a window on diversity and conservation. *Trends Ecol Evol* 22:148–155
- Bongaerts P, Riginos C, Brunner R, Englebert N, Smith SR, Hoegh-Guldberg O (2017) Deep reefs are not universal refuges: Reseeding potential varies among coral species. *Sci Adv* 3:e1602373
- Bongaerts P, Riginos C, Ridgway T, Sampayo EM, van Oppen MJH, Englebert N, Vermeulen F, Hoegh-Guldberg O (2010). Genetic divergence across habitats in the widespread coral *Seriatopora hystrix* and its associated *Symbiodinium*. *PLoS One* 5:e10871
- Bongaerts P, Cooke I, Ying H, Wels D, Den SH, Hernandez-Agreda A, Brunner CA, Dove S, Englebert N, Eyal G, Forêt S, Grinblat M, Hay KB, Harii S, Hayward DC, Lin Y, Mihaljević M, Moya A, Muir P, Sinniger F, Smallhorn-West P, Torda G, Ragan MA, Van-Oppen MJH, Hoegh-Guldberg O (2021) Cryptic diversity masks ecologically distinct coral species on tropical reefs. *Curr Biol* 31:2286–2298
- Browne NK, Tay J, Todd PA (2015) Recreating pulsed turbidity events to determine coral-sediment thresholds for active management. *J Exp Mar Bio Ecol* 466:98–109
- Browne NK, Precht E, Last KS, Todd PA (2014) Photo-physiological costs associated with acute sediment stress events in three near-shore turbid water corals. *Mar Ecol Prog Ser* 502:129–143
- Chadè I, Mcdonald-Madden E, Mccarthy MA, Wintle B, Linkie M, Possingham HP (2008) When to stop managing or surveying cryptic threatened species. *PNAS* 105:13936–13940
- Chevalier JP (1975) Les scléactiniaires de la Mélanésie française (Nouvelle Calédonie, Iles Chesterfield, Iles Loyauté, Nouvelles Hébrides). Deuxième partie. *Expédition Française sur les Récifs Coralliens de la Nouvelle Calédonie* 7:1–407
- Chou LM, Tan KPP (2007) Conserving reefs beside a marine landfill in Singapore. *Coral Reefs* 26:719
- Chou LM, Huang D, Tan KS, Toh TC, Goh BPL, Tun K (2019) Singapore. In: Sheppard CRC (ed) *World seas: an environmental evaluation, vol II. The Indian Ocean to the Pacific*. Academic Press, London, pp 539–558
- Chow GSE, Chan YKS, Jain SS, Huang D (2019) Light limitation selects for depth generalists in urbanised reef coral communities. *Mar Environ Res* 147:101–112
- Costello MJ, Wilson S, Houlding B (2012) Predicting total global species richness using rates of species description and estimates of taxonomic effort. *Syst Biol* 61:871–883
- Dana JD (1846) *U.S. Exploring Exped (1838–1842). Vol. VII. Zoophytes*. C. Sherman. 740 pp. Available from: http://www.sil.si.edu/digitalcollections/ussex/navigation/ScientificText/USEXEx19_08select.cfm.
- Dikou A, van Woesik R (2006) Survival under chronic stress from sediment load: Spatial patterns of hard coral communities in the southern islands of Singapore. *Mar Pollut Bull* 52:1340–1354

- Eckert RJ, Studivan MS, Voss JD (2019) Populations of the coral species *Montastraea cavernosa* on the Belize Barrier Reef lack vertical connectivity. *Sci Rep* 9:1–11
- Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software structure: a simulation study. *Mol Ecol* 14:2611–2620
- Fišer C, Robinson CT, Malard F (2018) Cryptic species as a window into the paradigm shift of the species concept. *Mol Ecol* 27:613–635
- Foll M, Gaggiotti O (2008) A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: A Bayesian perspective. *Genetics* 180:977–993
- Frederick Grasse J, Maciolek NJ (1992) Deep-sea species richness: regional and local diversity estimates from quantitative bottom. *Am Nat* 139:313–341
- Fukami H, Budd AF, Paulay G, Sole-Cava A, Allen CC, Iwao K, Knowlton N (2004) Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals. *Nature* 427:829–832
- Fukami H, Chen CA, Budd AF, Collins A, Wallace C, Chuang YY, Chen C, Dai CF, Iwao F, Sheppard C, Knowlton N (2008) Mitochondrial and nuclear genes suggest that stony corals are monophyletic but most families of stony corals are not (Order Scleractinia, Class Anthozoa, Phylum Cnidaria). *PLoS One* 3:e3222
- 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. *Mol Phylogenet Evol* 109:430–446
- Gilbert KJ, Andrew RL, Bock DG, Franklin MT, Moore B, Kane NC, Rennison DJ, Veen T, Vines TH (2012) Recommendations for utilizing and reporting population genetic analyses: the reproducibility of genetic clustering using the program STRUCTURE. *Mol Ecol* 604:822–2416
- Goh BPL, Chou LM (1997) Heavy metal levels in marine sediments of Singapore. *Environ Monit Assess* 97:131–141
- Grundt HH, Kjørner S, Borgen L, Rieseberg LH, Brochmann C (2006) High biological species diversity in the Arctic flora. *PNAS* 106:972–975
- Guest JR, Tun K, Low J, Vergés A, Marzinelli EM, Campbell AH, Bauman AG, Feary DA, Chou LM, Steinberg PD (2016) 27 years of benthic and coral community dynamics on turbid, highly urbanized reefs off Singapore. *Sci Rep* 6:36260
- Hilton MJ, Manning SS (1995) Conversion of coastal habitats in Singapore: Indications of unsustainable development. *Environ Conserv* 22:307–322
- Hoeksema, BW, Cairns S (2020) World List of Scleractinia. *Pachyseris* Milne Edwards & Haime, 1849. World Register of Marine Species [<http://www.marinespecies.org/aphia.php?p=taxdetails&id=1363>]
- Huang D, Meier R, Todd PA, Chou LM (2009) More evidence for pervasive paralogy in scleractinian corals: Systematic study of Southeast Asian Faviidae (Cnidaria; Scleractinia) based on molecular and morphological data. *Mol Phylogenet Evol* 50:102–116
- Huang D, Benzoni F, Arrigoni R, Baird AH, Berumen ML, Bouwmeester J, Chou LM, Fukami H, Licuanan WY, Lovell ER, Meier R, Todd PA, Budd AF (2014) Towards a phylogenetic classification of reef corals: the Indo-Pacific genera *Merulina*, *Goniastrea* and *Scapophyllia* (Scleractinia, Merulinidae). *Zool Scr* 43:531–548
- Hughes TP, Connolly SR, Keith SA (2013) Geographic ranges of reef corals (Cnidaria: Anthozoa: Scleractinia) in the Indo-Pacific. *Ecology* 94:1659
- Jain SS, Afiq-Rosli L, Feldman B, Levy O, Phua JW, Wainwright BJ, Huang D (2020) Homogenization of endosymbiont communities hosted by equatorial corals during the 2016 mass bleaching event. *Microorganisms* 8:1370
- Janes JK, Miller JM, Dupuis JR, Malenfant RM, Gorrell JC, Cullingham CI, Andrew RL (2017) The K=2 conundrum. *Mol Ecol* 26:3594–3602
- Jombart T, Devillard S, Balloux F (2010) Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genet* 11:94
- Kamvar ZN, Tabima JF, Grünwald NJ (2014) Poppr: An R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. *PeerJ* 2:e281
- Kamvar ZN, Brooks JC, Grünwald NJ (2015) Novel R tools for analysis of genome-wide population genetic data with emphasis on clonality. *Front Genet* 6:208
- Keis M, Remm J, Ho SYW, Davison J, Tammelaht E, Tumanov IL, Saveljev AP, Männil P, Kojola I, Abramov AV, Margus T, Saarma U (2013) Complete mitochondrial genomes and a novel spatial genetic method reveal cryptic phylogeographical structure and migration patterns among brown bears in north-western Eurasia. *J Biogeogr* 40:915–927
- Kerr AM, Baird AH, Hughes TP (2011) Correlated evolution of sex and reproductive mode in corals (Anthozoa: Scleractinia). *Proc R Soc B* 278:75–81
- Kitahara MV, Cairns SD, Stolarski J, Miller DJ (2013) Deltocyathidae, an early-diverging family of robust corals (Anthozoa, Scleractinia). *Zool Scr* 42:201–212
- Kitahara MV, Cairns SD, Stolarski J, Blair D, Miller DJ (2010) A comprehensive phylogenetic analysis of the Scleractinia (Cnidaria, Anthozoa) based on mitochondrial CO1 sequence data. *PLoS One* 5:e11490
- Kitahara MV, Stolarski J, Cairns SD, Benzoni F, Stake JL, Miller DJ (2012) The first modern solitary Agariciidae (Anthozoa, Scleractinia) revealed by molecular and microstructural analysis. *Invertebr Syst* 26:303–315
- Kopelman NM, Mayzel J, Jakobsson M, Rosenberg NA, Mayrose I (2015) Clumpak: A program for identifying clustering modes and packaging population structure inferences across K. *Mol Ecol Resour* 15:1179–1191
- Ladner JT, Palumbi SR (2012) Extensive sympatry, cryptic diversity and introgression throughout the geographic distribution of two coral species complexes. *Mol Ecol* 21:2224–2238
- Lamarck JBP (1815) *Les polypes*. Hist Nat des animaux sans vertèbres, Paris
- Lang JC (1984) Whatever works: the variable importance of skeletal and non-skeletal characters in scleractinian taxonomy. *Palaeontogr Am* 54:18–44
- Leaché AD, Banbury BL, Felsenstein J, de Oca ANM, Stamatakis A (2015) Short tree, long tree, right tree, wrong tree: new acquisition bias corrections for inferring SNP phylogenies. *Syst Biol* 64:1032–1047
- Lewis PO (2001) A likelihood approach to estimating phylogeny from discrete morphological character data. *Syst Biol* 50:913–925
- Li H, Handsaker B, Wysoker A, Fennell T, Ruan J, Homer N, Marth G, Abecasis G, Durbin R (2009) The sequence alignment/map format and SAMtools. *Bioinformatics* 25:2078–2079
- Lischer HEL, Excoffier L (2012) PGDSpider: an automated data conversion tool for connecting population genetics and genomics programs. *Bioinformatics* 28:298–299
- Mora C, Tittensor DP, Adl S, Simpson AGB, Worm B (2011) How many species are there on earth and in the ocean? *PLoS Biol* 9:e1001127
- Nygren A (2014) Cryptic polychaete diversity: A review. *Zool Scr* 43:172–183
- Paz-García DA, Hellberg ME, García-de-León FJ, Balart EF (2015) Switch between morphospecies of *Pocillopora* corals. *Am Nat* 186:434–440

- Pfenninger M, Schwenk K (2007) Cryptic animal species are homogeneously distributed among taxa and biogeographical regions. *BMC Evol Biol* 7:121
- Porras-Hurtado L, Ruiz Y, Santos C, Phillips C, Carracedo Á, Lareu MV (2013) An overview of structure: applications, parameter settings, and supporting software. *Front Genet* 4:1–13
- Porto-Hannes I, Zubillaga AL, Shearer TL, Bastidas C, Salazar C, Coffroth MA, Szmant AM (2015) Population structure of the corals *Orbicella faveolata* and *Acropora palmata* in the Mesoamerican Barrier Reef System with comparisons over Caribbean basin-wide spatial scale. *Mar Biol* 162:81–98
- Pritchard JK, Wen W (2003) Documentation for STRUCTURE Software: Version 2. Chicago: University of Chicago Press. Retrieved from: http://web.stanford.edu/group/pritchardlab/software/structure2_1.html
- Richards ZT, Berry O, van Oppen MJH (2016) Cryptic genetic divergence within threatened species of *Acropora* coral from the Indian and Pacific Oceans. *Conserv Genet* 17:577–591
- Russello MA, Waterhouse MD, Etter PD, Johnson EA (2015) From promise to practice: pairing non-invasive sampling with genomics in conservation. *PeerJ* 3:e1106
- Scheer G, Pillai CSG (1983) Report on the stony corals from the Red Sea. *Zoologica (Stuttgart)* 133:1–198
- Scheffers BR, Joppa LN, Pimm SL, Laurance WF (2012) What we know and don't know about Earth's missing biodiversity. *Trends Ecol Evol* 27:501–510
- Schmidt-Roach S, Lundgren P, Miller KJ, Gerlach G, Noreen AME, Andreakis N (2013) Assessing hidden species diversity in the coral *Pocillopora damicornis* from Eastern Australia. *Coral Reefs* 32:161–172
- Serrano XM, Baums IB, Smith TB, Jones RJ, Shearer TL, Baker AC (2016) Long distance dispersal and vertical gene flow in the Caribbean brooding coral *Porites astreoides*. *Sci Rep* 6:21619
- Sheets EA, Warner PA, Palumbi SR (2018) Accurate population genetic measurements require cryptic species identification in corals. *Coral Reefs* 37:549–563
- Sheppard CRC, Sheppard ALS (1991) Corals and coral communities of Saudi Arabia. *Fauna Arab* 12:1–170
- Sites JW, Marshall JC (2003) Delimiting species: A Renaissance issue in systematic biology. *Trends Ecol Evol* 18:462–470
- Sin TM, Ang HP, Buurman J, Lee AC, Leong YL, Ooi SK, Steinberg P, Teo SLM (2016) The urban marine environment of Singapore. *Reg Stud Mar Sci* 8:331–339
- Smith EG, Gurskaya A, Hume BCC, Voolstra CR, Todd PA, Bauman AG, Burt JA (2020) Low Symbiodiniaceae diversity in a turbid marginal reef environment. *Coral Reefs* 39:545–553
- Souter P (2010) Hidden genetic diversity in a key model species of coral. *Mar Biol* 157:875–885
- Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312–1313
- Stefani F, Benzoni F, Yang SY, Pichon M, Galli P, Chen CA (2011) Comparison of morphological and genetic analyses reveals cryptic divergence and morphological plasticity in *Stylophora* (Cnidaria, Scleractinia). *Coral Reefs* 30:1033–1049
- Tang Q, Fung T, Rheindt FE (2019) ResDisMapper: An R package for fine-scale mapping of resistance to dispersal. *Mol Ecol Resour* 20:819–831
- Tang Q, Low GW, Lim JY, Gwee CY, Rheindt FE (2018) Human activities and landscape features interact to closely define the distribution and dispersal of an urban commensal. *Evol Appl* 11:1598–1608
- Tay JY, Wong SK, Chou LM, Todd PA (2018) Land reclamation and the consequent loss of marine habitats around the Ayer Islands, Singapore. *Nature in Singapore* 11:1–5
- Tay YC, Noreen AME, Suharsono CLM, Todd PA (2015) Genetic connectivity of the broadcast spawning reef coral *Platygyra sinensis* on impacted reefs, and the description of new microsatellite markers. *Coral Reefs* 34:301–311
- Terraneo TI, Berumen ML, Arrigoni R, Waheed Z, Bouwmeester J, Caragnano A, Stefani F, Benzoni F (2014) *Pachyseris inattesa* sp. n. (Cnidaria, Anthozoa, Scleractinia): a new reef coral species from the Red Sea and its phylogenetic relationships. *ZooKeys* 433:1–30
- Todd PA (2008) Morphological plasticity in scleractinian corals. *Biol Rev* 8:315–337
- Todd PA, Sidle RC, Lewin-Koh NJI (2004) An aquarium experiment for identifying the physical factors inducing morphological change in two massive scleractinian corals. *J Exp Mar Bio Ecol* 299:97–113
- Toonen RJ, Puritz JB, Forsman ZH, Whitney JL, Fernandez-Silva I, Andrews KR, Bird CE (2013) ezRAD: a simplified method for genomic genotyping in non-model organisms. *PeerJ* 1:e203.
- Underwood JN, Richards ZT, Miller KJ, Puotinen ML, Gilmour JP (2018) Genetic signatures through space, time and multiple disturbances in a ubiquitous brooding coral. *Mol Ecol* 27:1586–1602
- Veron JEN (2000) Corals of the World. Aust Inst Mar Sci. Townsville
- Veron JEN (2002) New species described in Corals of the World (Vol. 11). Aust Inst Mar Sci. Townsville
- Veron JEN, Pichon M (1980) Scleractinia of Eastern Australia, III: families Agaraciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectiniidae, Caryophylliidae, Dendrophylliidae. *Aust Inst Mar Sci Monogr Ser* 4:1–422
- Warner PA, Van Oppen MJH, Willis BL (2015) Unexpected cryptic species diversity in the widespread coral *Seriatopora hystrix* masks spatial-genetic patterns of connectivity. *Mol Ecol* 24:2993–3008
- Wells JW (1956) Scleractinia. In: Moore RC (ed) Treatise on invertebrate paleontology, Part F, Coelenterata: Boulder, Colo. Geol Soc Am and Univ Kansas Press, pp F328–F444
- Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu Rev Ecol Evol Syst* 34:273–309
- Wong JSY, Chan YKS, Ng CSL, Tun KPP, Darling ES, Huang D (2018) Comparing patterns of taxonomic, functional and phylogenetic diversity in reef coral communities. *Coral Reefs* 37:737–750

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.