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REPORT

Evidence of host-associated divergence from coral-eating snails (genus *Coralliophila*) in the Coral Triangle

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Abstract We studied how host-associations and geography shape the genetic structure of sister species of marine snails *Coralliophila radula* (A. Adams, 1853) and *C. violacea* (Kiener, 1836). These obligate ectoparasites prey upon corals and are sympatric throughout much of their ranges in coral reefs of the tropical and subtropical Indo-Pacific. We tested for population genetic structure of snails in relation to geography and their host corals using mtDNA (COI) sequences in minimum spanning trees and AMOVAs. We also examined the evolutionary relationships of their *Porites* host coral species using maximum likelihood trees of RAD-seq (restriction site-associated DNA sequencing) loci mapped to a reference transcriptome. A maximum likelihood tree of host corals revealed three distinct clades. *Coralliophila radula* showed a pronounced genetic break across the Sunda Shelf ($\Phi_{CT} = 0.735$) but exhibited no genetic structure with respect to host. *C. violacea* exhibited significant geographic structure ($\Phi_{CT} = 0.427$), with divergence among Hawaiian populations, the Coral Triangle and the Indian Ocean. Notably, *C. violacea* showed evidence of ecological divergence; two lineages were associated with different groups of host coral species, one widespread found at all sites, and the other restricted to the Coral Triangle. Sympatric populations of *C. violacea* found on different suites of coral species were highly divergent ($\Phi_{CT} = 0.561$, $d = 5.13\%$), suggesting that symbiotic relationships may contribute to lineage diversification in the Coral Triangle.

Keywords Marine gastropod · Parasite · Sister species · *Porites* · RAD-seq

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Introduction

Our understanding of evolution in marine ecosystems is framed by theories developed in terrestrial environments (Miglietta et al. 2011). Historically, researchers have invoked geographic-based models of speciation without gene flow (i.e. allopatry) to explain the majority of diversity in terrestrial systems (Barraclough and Vogler 2000). However, such models are not a natural fit for the marine realm (Palumbi 1994; Puebla 2009). Most marine organisms have planktonic larvae that increase the potential for gene flow between geographically separated regions (Riginos and Liggins 2013). Even species with relatively modest mean dispersal distances can have dispersal kernels with long tails (Kinlan and Gaines 2003), providing sufficient genetic connectivity to limit population divergence (Slatkin 1987), even across broad geographic scales.

While uncommon, geographic barriers to gene flow in the ocean do exist, albeit with varying degrees of permeability. Landmasses are the most obvious, isolating biota in

different ocean basins (Briggs and Bowen 2013), both currently (e.g. Isthmus of Panama, see Lessios 2008 for review) and in the past (e.g. Sunda Shelf, see Ludt and Rocha 2015 for review). However, vast expanses of open-ocean can isolate remote archipelagos like Hawai'i (e.g. Polato et al. 2010; Iacchei et al. 2016; Waldrop et al. 2016) or populations spanning the Eastern Pacific Barrier (e.g. Baums et al. 2012). Additionally, large freshwater outflows like the Amazon can form barriers to gene flow for shallow-water marine species (Rocha 2003).

Dispersal barriers are critical to the evolution and distribution of marine biodiversity, including in the world's most diverse marine ecosystem, the Coral Triangle (Barber et al. 2011; Carpenter et al. 2011; Gaither et al. 2011; Gaither and Rocha 2013). Low sea levels during the Pliocene and Pleistocene (Williams and Benzie 1998), and more recent phenomena such as the Halmahera Eddy (Kool et al. 2011), create potent dispersal barriers for various reef organisms (see Barber et al. 2011 and Carpenter et al. 2011 for reviews). Still, allopatric divergence alone may be insufficient to explain the Coral Triangle's exceptional species diversity. Processes such as ecological divergence and assortative mating could promote divergence with gene flow, but remain relatively unexplored in marine systems (Krug 2011; Miglietta et al. 2011).

Ecological divergence is the evolution of reproductive isolation among populations driven by opposing selection in ecological niches or environments (Schluter and Conte 2009). While widely documented in terrestrial ecosystems, ecological barriers to gene flow in the ocean have only recently been reported (Krug 2011; Bird et al. 2012). In terrestrial and freshwater systems, ecological divergence often takes place in sympatry via assortative mating in different microhabitats or on different hosts in species with strong symbioses (Hatfield and Schluter 1999; Matsubayashi et al. 2010). Evidence suggests that ecological factors (Johannesson et al. 2010; Bird et al. 2011; Prada and Hellberg 2013; Moura et al. 2015) including symbiotic relationships (Munday et al. 2004; Sotka 2005; Faucci et al. 2007; Prada et al. 2014b; Fritts-Penniman 2016) may similarly drive ecological divergence in the marine environment.

Marine snails in the genus *Coralliophila* are symbionts of anthozoans (Oliverio et al. 2009). The sister species *C. radula* and *C. violacea* (Oliverio et al. 2009) are ectoparasites, exhibiting obligate relationships with corals in the family Poritidae (Fujioka and Yamazato 1983). These snails are sedentary and feed suctorially on photosynthetic products sent by corals to regenerate injured sites (Oren et al. 1998). As adults they live in groups and rarely move (Soong and Chen 1991; Oren et al. 1998). Dispersal is achieved via planktonic larvae brooded by protandrous hermaphroditic females (Soong and Chen 1991). Both species have extensive geographic ranges, occurring sympatrically in coral reefs throughout the tropical and subtropical Indo-Pacific.

The purpose of this study was to enhance our understanding of the evolutionary processes generating marine biodiversity in the Coral Triangle. Specifically, we tested the hypothesis that co-distributed populations of *C. radula* and *C. violacea* would exhibit concordant patterns of phylogeographic structure, patterns that resulted from physical processes shaping the phylogeography of other marine organisms in the Coral Triangle. However, because parasitic relationships with poritid host corals create the possibility of ecological divergence, we first tested for genetic structure that could result from ecological segregation among sympatric populations of snails utilising different host corals.

Materials and methods

Field sampling

During 2011–2013, we collected *Coralliophila radula* and *C. violacea* from Indo-Pacific locations ($N = 14$ and $N = 17$ respectively, Table 1, Fig. 1). These sites span the Sunda Shelf Barrier, an area where phylogeographic structure is commonly observed (Barber et al. 2011), and also include known areas of isolation (i.e. Hawai'i). At each site, we collected 1–15 *C. radula* and 1–16 *C. violacea* from 1–6 colonies of each host coral species ($N = 1$–4) (Table 2). In total, we collected 235 *C. radula* and 328 *C. violacea* from 114 coral colonies (Table 2), representing 12 named *Porites* species (Fig. 2). Approximately 50–100% of each snail's foot tissue was preserved in 95% ethanol and stored at room temperature for DNA analysis.

Porites corals are notoriously difficult to identify in situ because of their morphological plasticity and small corallites (Forsman et al. 2015), while genetically similar colonies can have vastly different morphologies and vice versa (Forsman et al. 2009, 2015; Prada et al. 2014a). Therefore, to define coral species both morphologically and genetically, we collected detailed information about each snail's host; tagged photos of coral colonies in situ; took macrophotos with a transparent ruler to measure corallites; and sampled tissues for genetic analysis.

DNA extraction and sequencing

We sequenced 1–16 snails from each coral colony. We extracted DNA using 10% Chelex™ (BioRad, Hercules, CA, USA) (Walsh et al. 2013) and DNeasy® Blood and Tissue Kit (Qiagen, Valencia, CA, USA) and then amplified a 668-bp-length fragment of COI mtDNA using primers HCO-2198, LCO-1490 (Folmer et al. 1994).

Table 1 Sampling locations for *Coralliophila radula*, *C. violacea*. Coordinates are in decimal degrees. Location numbers correspond to those in Fig. 1

Location	Region	Country	Province/State	Latitude	Longitude
1. Vavvaru	Indian Ocean	Maldives	North Province	5.419	73.358
2. Pulau Weh	Indian Ocean	Indonesia	Aceh	5.887	95.348
3. Pulau Keluang	Indian Ocean	Indonesia	Aceh	5.129	95.294
4. Pulau Pagang	Indian Ocean	Indonesia	Sumatra	− 1.157	100.352
5. Hòn Mun	Coral Triangle	Vietnam	Nha Trang	12.170	109.308
6. Pemuteran	Coral Triangle	Indonesia	Bali	− 8.140	114.654
7. Nusa Penida	Coral Triangle	Indonesia	Bali	− 8.675	115.513
8. Pulau Mengyatan	Coral Triangle	Indonesia	East Nusa Tenggara	− 8.557	119.685
9. Wangi–Wangi	Coral Triangle	Indonesia	South Sulawesi	− 5.269	123.519
10. Díli	Coral Triangle	Timor-Leste	Timor Island	− 8.477	125.911
11. Lembeh	Coral Triangle	Indonesia	North Sulawesi	1.479	125.251
12. Bunaken	Coral Triangle	Indonesia	North Sulawesi	1.612	124.783
13. Dumaguete	Coral Triangle	Philippines	Negros Oriental	9.332	123.312
14. Ticao	Coral Triangle	Philippines	Luzon	12.628	123.706
15. Raja Ampat	Coral Triangle	Indonesia	West Papua	− 0.559	130.672
16. Manokwari	Coral Triangle	Indonesia	West Papua	− 0.888	134.085
17. Ka'a'awa	Hawai'i	USA	O'ahu	21.584	− 157.887

Regions were used for AMOVA analyses

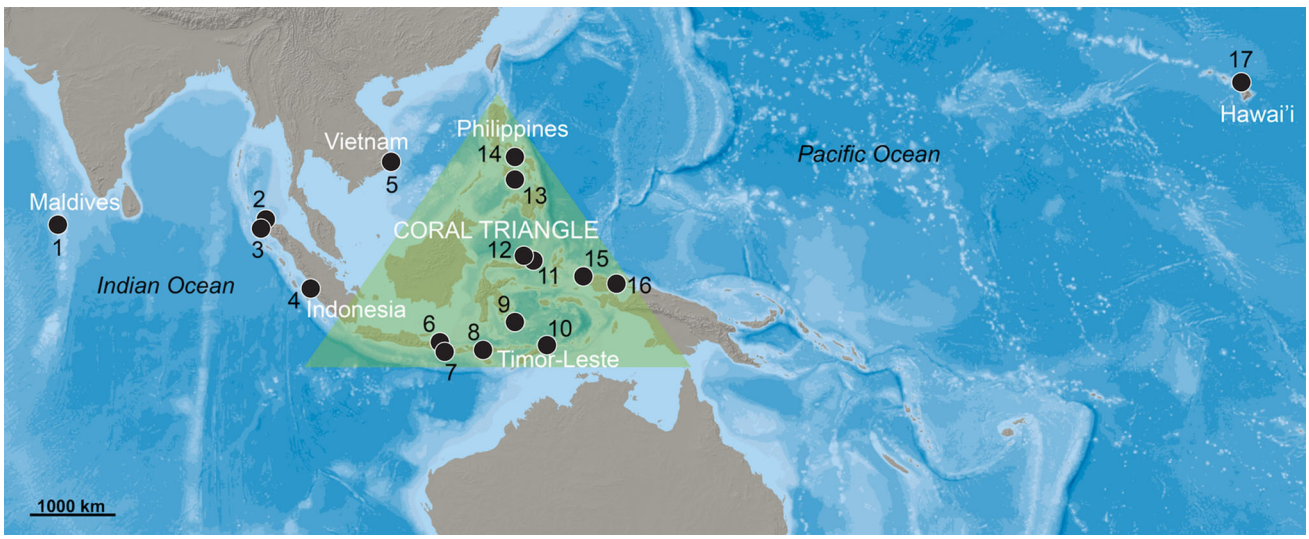


Fig. 1 Population sampling locations across the Indo-West Pacific for ectoparasitic snails (*Coralliophila radula*, *C. violacea*) and on a suite of host corals (*Porites* spp.). Location names and coordinates are shown in Table 1

Following an initial denaturation at 94 °C for 1.5 min, the thermocycling parameters were as follows: 94 °C for 30 secs, 50 °C for 30 secs and 72 °C for 45 secs for 35 cycles with a final 10-min extension at 72 °C. All PCR product clean up and DNA sequencing was done by the University of California, Berkeley DNA Sequencing Facility.

We extracted coral DNA using DNeasy® Blood and Tissue Kit (Qiagen, Valencia, CA, USA). Only extractions with high-quality DNA at high enough concentrations were chosen ($N = 51$) for library preparation. We chose to sequence coral using a restriction site-associated DNA sequencing (RAD-seq) approach because recent work has shown that these data have a greater potential of resolving relationships within *Porites* than more commonly used genes such as ITS or COI (Forsman et al. 2017). Coral Illumina libraries were prepared according to methods detailed in the BestRAD protocol (Ali et al. 2016) using the SbfI restriction enzyme, and sequenced using a Next-Seq 500 (Illumina, Inc.) sequencer on a mid-output 300 cycle with paired-end reads. All library preparation and sequencing was conducted at the Eagle Fish Genetics Laboratory.

Table 2 Number of mitochondrial cytochrome oxidase I (COI) sequences from *Coralliophila radula* and *C. violacea* at each location collected from available host corals

Location	Collection host (N)	*C. radula*	*C. violacea*
1. Vavvaru	*P. lobata*	21	13
	P. rus	5	–
	P. attenuata	17	–
2. Pulau Weh	*P. annae*	–	1
	P. lobata	4	22
	P. rus	4	3
3. Pulau Keluang	*P. lobata*	–	3
4. Pulau Pagang	*P. lobata*	–	2
	P. lutea	–	3
5. Hòn Mun	*P. lobata*	–	33
6. Pemuteran	*P. attenuata*	15	–
	P. cylindrica	5	17
	P. lobata	10	15
	P. negrosensis	3	5
7. Nusa Penida	*P. cylindrica*	–	5
	P. lobata	7	9
8. Pulau Mengyatan	*P. cylindrica*	–	8
	P. lobata	12	8
	P. nigrescens	–	2
9. Wangi–Wangi	*P. attenuata*	16	–
	P. cylindrica	–	1
10. Díli	*P. lobata*	3	2
11. Lembeh	*P. cylindrica*	–	12
	P. lobata	4	9
	P. tuberculosus	–	14
12. Bunaken	*P. cylindrica*	–	18
	P. lobata	6	23
13. Dumaguete	*P. cylindrica*	18	22
	P. lobata	15	32
14. Ticao	*P. lobata*	26	8
15. Raja Ampat	*P. attenuata*	20	7
	P. lobata	6	4
	P. lutea	–	1
	P. rus	6	–
16. Manokwari	*P. lobata*	1	–
	P. lutea	5	12
17. Ka'a'awa, Hawai'i	*P. compressa*	–	12
	P. evermanni	5	4
	P. lutea	1	1
	P. solida	–	2

Example photo vouchers of host coral species are shown in Fig. 2

RAD-seq data processing

Coral reads were processed using the iPyrad v0.7.17 pipeline (http://ipyrad.readthedocs.io/) (see Appendix S2 for parameter input file). Sequence data were demultiplexed, low-quality base calls were filtered out, and adapter sequences removed and dereplicated. To focus on coral genes and exclude any DNA from symbiotic micro-organisms, we then mapped reads to a reference transcriptome (*Porites lobata* available at reefgenomics.org, Bhattacharya et al. 2016) using the programme BWA v0.7.16 (Li and Durbin 2009). From there, highly similar reads were clustered together and aligned. Then, the joint estimate of heterozygosity and sequencing error rates were

calculated and used in consensus base calling. Any samples that did not sequence well were removed from further analyses ($N = 11$). Only loci with less than 20% missing data across taxa were kept, and reads were thinned to one single-nucleotide polymorphism (SNP) per locus to removed linked loci.

Data analysis

Determining host coral identities and evolutionary relationships

To identify coral species, test for cryptic diversity and determine phylogenetic relationships among corals, we aligned our sequences (see Table S1 in Appendix S1) using the iPyrad pipeline and exported alignments in PHYLIP format to Geneious v11 (Kearse et al. 2012). Maximum likelihood analyses were performed using RAxML v8.2.11 with 1000 rapid bootstraps.

Ecological and geographic analyses of genetic structure of Coralliophila

For the snails, we aligned and edited complementary sequences, and confirmed translations in Geneious (Kearse et al. 2012). Sequences were aligned using the MAFFT plugin in Geneious. We trimmed final sequence alignments to 576 bp for *C. radula* and 617 bp for *C. violacea* and then reduced all sequences to unique haplotypes using FaBox v1.41 (Villesen 2007). We calculated standard diversity statistics (haplotype and nucleotide diversity) in Arlequin v3.5 (Excoffier and Lischer 2011).

Since genetic structure in the two *Coralliophila* could be partitioned by host coral or geography, we tested for divergence associated with corals in sympatry. As a first pass to visually examine for genetic structure, we built phylogenetic trees for each snail species using the RAxML plugin in Geneious and labelled each tip with the associated host coral and location. After inspecting these trees, *C. violacea* showed clear partitioning based on groups of host coral species. These two groupings corresponded to the major clades (clade 1, clade 2/3) present in the *Porites* RAD-seq tree (Fig. 3). Given the well-documented taxonomic challenges in *Porites* (Forsman et al. 2009, 2015; Prada et al. 2014a) and possible cryptic species, we opted to group host coral supported clades (Fig. 3) that were seen in both the *Porites* tree and the *C. violacea* tree, using these groupings (Gold = clade 1, Green = clade 2/3) for all tests of genetic structure in relation to host coral. We created minimum spanning trees (MSTs) using Gephi v 0.8.2 (Bastian et al. 2009) based on pairwise differences calculated in Arlequin, only including haplotypes from populations where *C. radula* and *C. violacea* were found on different host coral clades (Gold = clade 1, Green = clade 2/3) at the same location. To formally, test for structure based on host we plotted coral groups onto MSTs and analysed molecular variance (AMOVA) in Arlequin, partitioning the genetic data by coral group. To estimate the relative contributions of geographic divergence versus divergence in sympatry, we calculated pairwise Φ_{ST} values among locations within host-associated lineages, and then calculated pairwise Φ_{ST} between host-associated populations within individual sampling locations.

To test for phylogeographic partitions, we constructed MSTs and then plotted the resulting haplogroups onto a map of the study area. We then ran AMOVAs with and without a priori geographic partitions to test for genetic structure related to divergence related to isolation across the Sunda Shelf with significance determined by 100,000 random replicates.

Results

Of the snail species, *C. radula* was less abundant (235 vs. 328), found at fewer locations (14 vs. 17; Table 2) and found on fewer coral species (8 vs. 12; Table 2). The sister species of *Coralliophila* exhibited ecological niche overlap in the coral species they inhabited, sharing at least seven named host coral species (Table 2). In addition, looking at the hosts that they shared, *Coralliophila* spp. were found in syntopy on about half of all the sampled coral colonies.

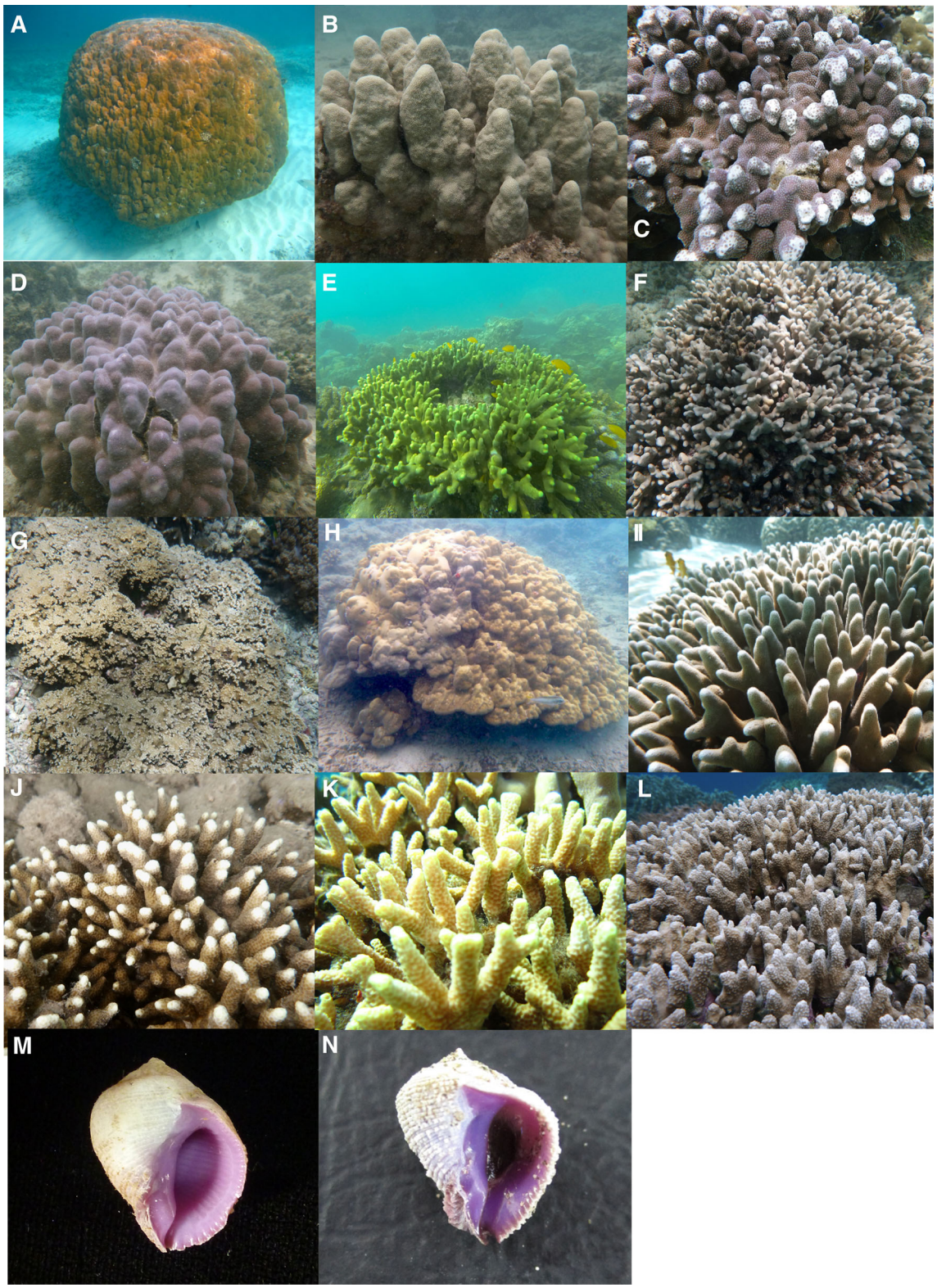
Sequences and genetic diversity

We successfully sequenced the DNA of 11 named species of *Porites* from 40 colonies using RAD-seq and the dataset was deposited in the Dryad Data Repository (https://doi.org/10.5061/dryad.jv853v1) (Appendix S1). We obtained 235 COI sequences from *C. radula* (567 bp) and 328 from *C. violacea* (617 bp), yielding totals of 192 and 296 unique haplotypes, respectively. All sequences were deposited in GenBank (Accession numbers: MG917096–MG917657).

Both snail species had high haplotype diversity (*C. radula*: $h = 0.966$–1.00 and *C. violacea*: $h = 0.900$–1.00, Table 3) in all populations except one: *C. violacea* (Pulau Keluang; $h = 0.667$, Table 3). Nucleotide diversity was low in both species (*C. radula*: $\pi = 0.011$–0.024 and *C. violacea*: $\pi = 0.011$–0.040), although across all locations *C. violacea* had a higher average number of polymorphic sites ($N = 67/617$ bp) than *C. radula* ($N = 41/567$ bp).

Phylogenetics of host coral species

The RAxML tree of 40 *Porites* coral RAD sequences (Table S1 in Appendix S1, Fig. 3) resolved some of the named species as reciprocally monophyletic (i.e. *P. rus, P.*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◀**Fig. 2** Photo vouchers of the host coral species (**a**–**l**) of **m** *C. violacea* (Kiener, 1836) and **n** *C. radula* (A. Adams, 1855). Photos and tissue samples of each coral colony were taken. **a** *Porites lobata* (Dana, 1846), Bali, Indonesia. **b** *Porites solida* (Forskål, 1775), Hawai'i, USA. **c** *P. annae* (Crossland, 1952), Aceh, Indonesia. **d** *P. evermanni* (Vaughan, 1907), Hawai'i, USA. **e** *P. attenuata* (Nemenzo, 1955), Bali, Indonesia. **f** *P. compressa* (Dana, 1846), Hawai'i, USA. **g** *P. rus* (Forskål, 1775), North Sulawesi, Indonesia. **h** *P. lutea* (Milne Edwards and Haime, 1851) Sumatra, Indonesia. **i** *P. cylindrica* (Dana, 1846), East Nusa Tenggara, Indonesia. **j** *P. nigrescens* (Dana, 1848), Sumatra, Indonesia. **k** *P. negrosensis* (Veron, 1990) Bali, Indonesia. **l** *P. tuberculosis* (Veron, 2000) North Sulawesi, Indonesia. Coral species were identified using Veron (2000) and for *P. evermanni* Forsman et al. (2015)

annae, P. evermanni). At a deeper level, three well-supported clades were apparent. Clade 1 included three species with branching morphologies *P. cylindrica*, *P. negrosensis* and *P. nigrescens*. These colonies were not reciprocally monophyletic to the named species level, but this could be due to cryptic diversity. Clade 2 was composed of three species with nodular growth forms of varying sizes: *P. annae, P. evermanni* and *P. rus*. All three species were well supported. Clade 3 contained named species of various morphologies including massive types *P. lobata*, *P. lutea* and *P. solida*, as well as two named branching species *P. attenuata* and *P. compressa*. While colonies from the same species clustered together, they did not have high support values.

Analysis of ecological divergence in *Coralliophila*

To investigate the genetics of snails for structure in relation to host coral, we first built MSTs of haplotypes from locations where snails from *Porites* groups (Gold = clade 1, Green = clade 2/3) were sampled. There was no evidence of genetic structure in relation to host in *C. radula* (Fig. 4a), which we confirmed with AMOVA analyses ($\Phi_{CT} = -0.018$, $p = 1.000$, Table 4).

In contrast, the MST of *C. violacea* on sympatric hosts showed two lineages (A and B) largely concordant with host groups (Gold = clade 1, Green = clade 2/3; Figs. 2, 3). Lineage A of *C. violacea* (Fig. 4b) was found predominately on nine named species of *Porites* (*P. annae, P.*

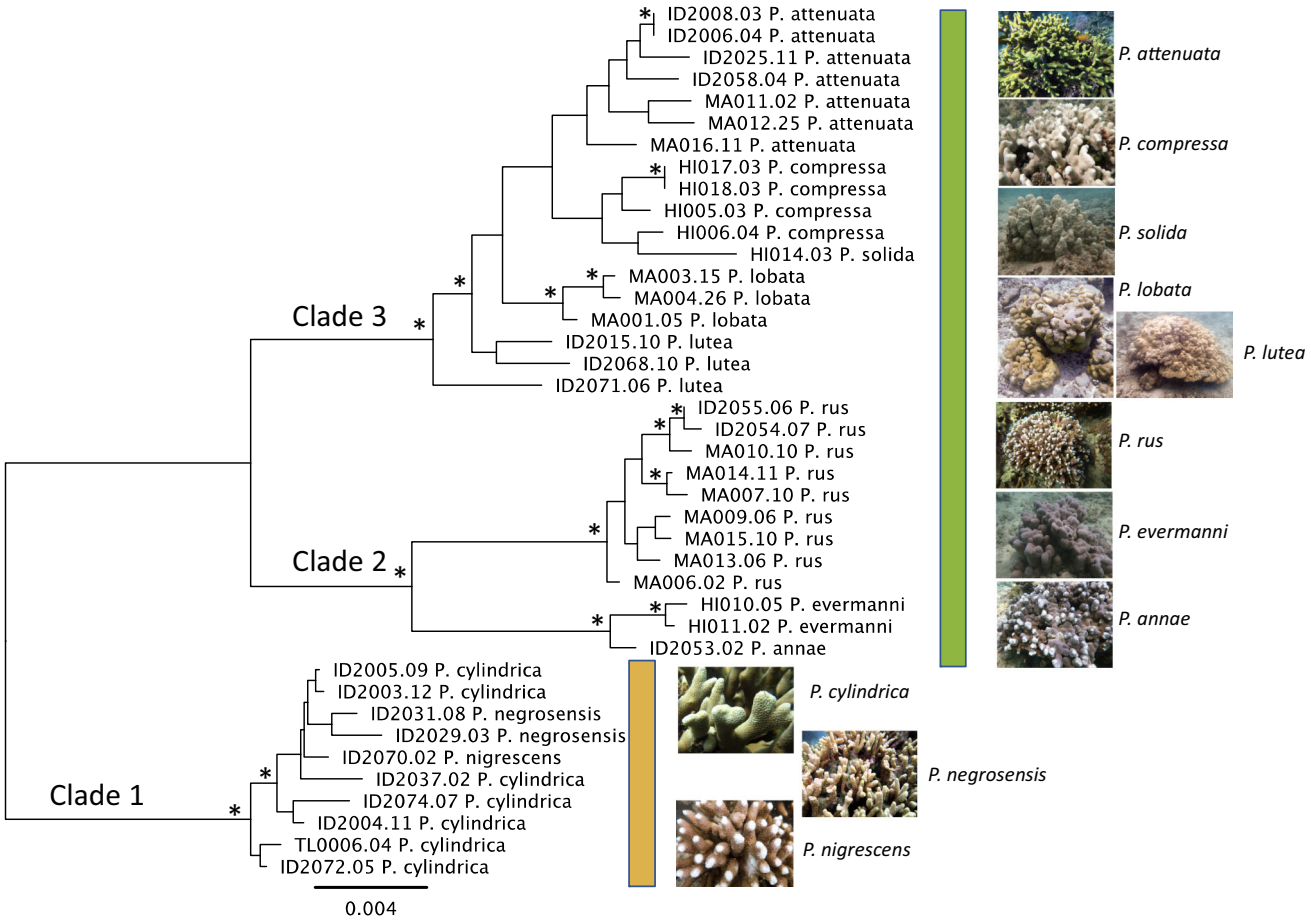

Fig. 3 RAxML phylogenetic tree of 40 RAD sequences (10,882 bps) mapped to the transcriptome of *P. lobata*, from 11 named *Porites* species. Tip labels are the sample code followed by the species name. * = nodes with > 80% bootstrap support. Green and Gold groups are those observed to be used by divergent lineages of *C. violacea*

Table 3 *Coralliophila radula* and *C. violacea*

Location	*C. radula*				*C. violacea*			
	N	*h*	π (%)	θs	N	*h*	π (%)	θs
1. Vavvaru	43	0.996	0.011	15.716	13	0.987	0.013	4.573
2. Pulau Weh	10	0.978	0.013	10.251	26	0.988	0.015	16.510
3. Pulau Keluang					3	0.667	0.021	12.667
4. Pulau Pagang					5	0.900	0.032	21.600
5. Hòn Mun					33	0.987	0.011	16.509
6. Pemuteran	33	0.966	0.014	17.248	37	1.000	0.035	21.598
7. Nusa Penida	6	1.000	0.017	11.825	14	1.000	0.035	25.156
8. Pulau Mengyatan	12	0.970	0.012	9.272	18	1.000	0.037	21.805
9. Wangi–Wangi	17	0.993	0.017	16.860	2	1.000	0.040	24.000
10. Díli	3	1.000	0.013	7.333	35	0.998	0.029	23.797
11. Lembeh	4	1.000	0.012	7.636	41	0.999	0.036	26.645
12. Bunaken	6	1.000	0.024	15.766	54	0.999	0.034	7.346
13. Dumaguete	33	0.998	0.013	15.030	8	1.000	0.021	0.000
14. Ticao	25	0.993	0.016	14.036	7	0.952	0.029	21.633
15. Raja Ampat	32	0.990	0.017	17.630	12	1.000	0.022	19.537
16. Manokwari	6	1.000	0.023	14.891	19	1.000	0.020	7.550
17. Ka'a'awa	5	1.000	0.016	8.640	13	0.987	0.013	4.573

Population level summary statistics and neutrality test statistics

attenuata, *P. compressa*, *P. evermanni*, *P. lobata, P. lutea, P. rus*, *P. solida*) belonging to the Green group of *Porites* (clade 2/3, Fig. 3). Lineage B of *C. violacea* (Fig. 4b) was found on three different named *Porites* species (*P. cylindrica*, *P. negrosensis* and *P. nigrescens*), from the Gold group of *Porites* (clade 1, Fig. 3) as well as *P. tuberculosus*. AMOVA also showed marked genetic differentiation between hosts in sympatry (Φ_{CT} = 0.561, $p = 0.003$, $d = 5.13\%$, Table 4), but no geographic structure among populations within host ($\Phi_{SC} = 0.003$, $p = 0.328$, Table 4). Despite these distinctions, we found occasional mismatches between *C. violacea* mtDNA background and their host (Fig. 4b). Some *C. violacea* collected from *Porites* clade 1 species fell in MST lineage A (mean = 11.7%, Fig. 4b). However, we identified only one mismatch the other way, when host corals were sympatric (Fig. 4b).

Phylogeographic analyses of *Coralliophila*

Because there was no ecological divergence observed in *C. radula,* we tested for phylogeographic structure using all haplotypes. The MST revealed three deeply divergent haplogroups separated by 18 or more steps that were concordant with geography (Fig. 5). The red group was restricted to the Indian Ocean. The blue group was the most common, present at all sites in the Pacific Ocean. The yellow group was rarest and found only within the Coral Triangle.

Due to the strong genetic associations by host coral group in *C. violacea*, we tested for phylogeographic structure separately within samples collected from each coral group. The MST of *C. violacea* collected from *Porites* clade 2/3 distinguished six haplogroups (Fig. 6). The blue group was most common, present at all sites, and dominated Coral Triangle sites. The red group dominated sites in the Indian Ocean (> 75%). The yellow group was found almost exclusively within the Coral Triangle with the exception of Pulau Weh and was concordant with snails found on hosts of the mismatched genetic group. The purple group was restricted to Hawai'i. There were also two rare, but divergent, haplogroups (turquoise, pink) only seen at sites within the Coral Triangle (Hòn Mun, Ticao, Díli and Bunaken).

Non-hierarchical AMOVAs of all haplotypes showed significant genetic structure in *C. radula* ($\Phi_{ST} = 0.531$, $P = 0.000$; Table 4) and *C. violacea* ($\Phi_{ST} = 0.213$, $P = 0.000$; Table 4). The per cent variation in *C. radula* was almost equal among (53%) and within (47%) populations. However, in *C. violacea* more variation was present within (79%) than among (21%) populations (Table 4).

Hierarchical AMOVA analyses comparing *C. radula* populations from the Indian Ocean, and the Coral Triangle + Hawai'i, spanning the Sunda Shelf, revealed a prominent genetic break ($\Phi_{CT} = 0.735$, $P = 0.011$, 5% sequence divergence), with the most variation (74%) between ocean basins (Table 4). However, only 0.5% of

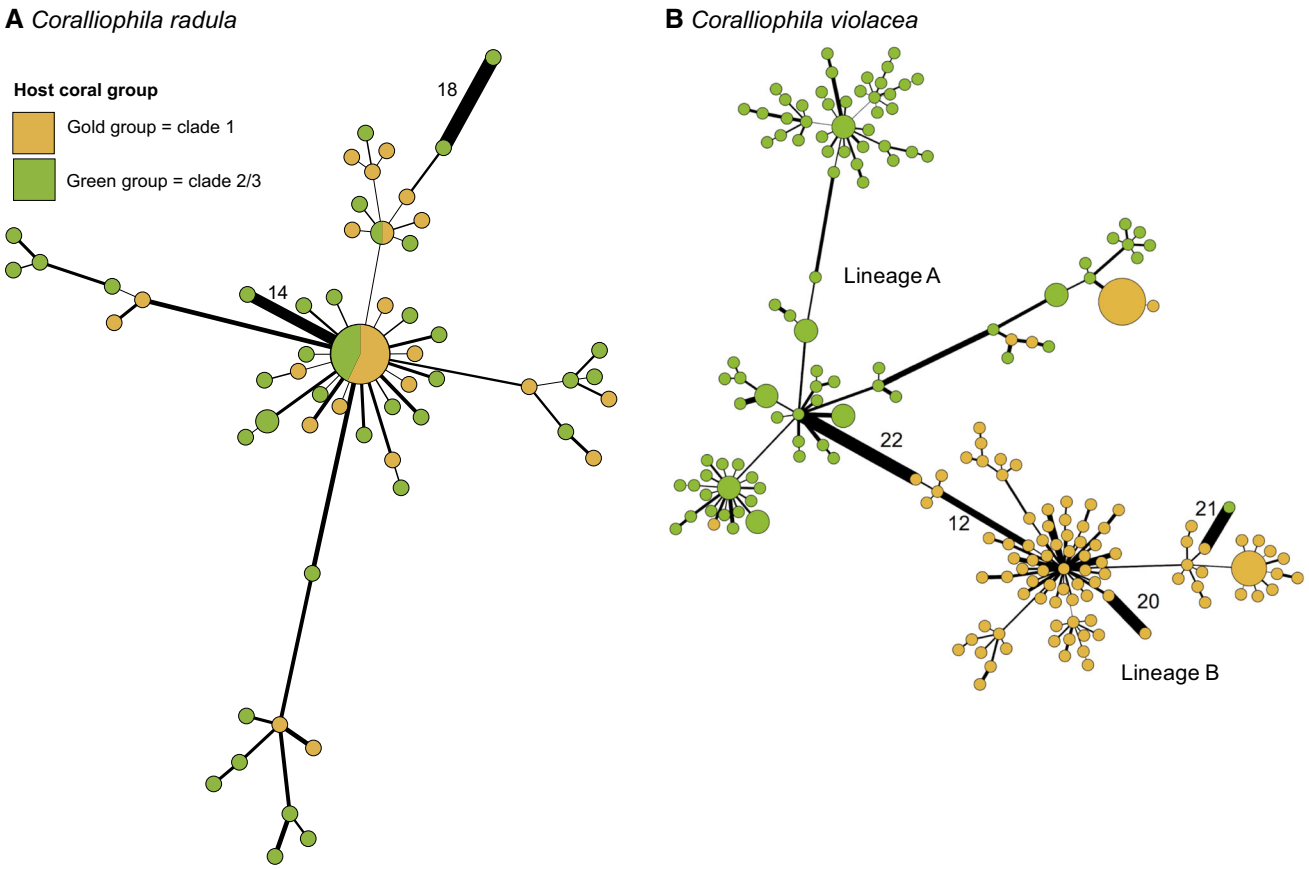

Fig. 4 Sympatric host coral groups (colours same as in Fig. 3) plotted onto minimum spanning trees of **a** 57 COI haplotypes from 65 *Coralliophila radula*. Haplogroups separated by more than 13 steps are indicated with numbers. **b** 188 COI haplotypes from 200 *C. violacea*. Circles sizes are proportional to the frequency of haplotypes. Haplogroups separated by more than 20 steps are indicated with numbers. Line thickness scales with the number of mutational steps between haplogroups

Table 4 *Coralliophila* AMOVA results testing hypotheses about (a) non-hierarchical, (b) host: sympatric populations of *C. radula* and *C. violacea* with snails from each host coral group, and (c) geography: *C. radula* (Indian Ocean, Coral Triangle + Hawai'i); *C. violacea* from *Porites* species in the Green group (clade 2/3) (Indian Ocean, Coral Triangle, Hawai'i)

Source of variation	*C. radula*			*C. violacea*		
	Fixation indices	*P* values	% var.	Fixation indices	*P* values	% var.
(a) Non-hierarchical						
Among populations	**Φ_{ST} 0.531**	**0.000**	53.10	**Φ_{ST} 0.213**	**0.000**	78.72
Within populations			46.90			21.28
(b) Host						
Between hosts	Φ_{CT} − 0.018	1.000	− 1.08	**Φ_{CT} 0.561**	**0.003**	56.14
Among populations	Φ_{SC} 0.022	0.055	2.22	Φ_{SC} 0.003	0.328	0.13
Within populations	Φ_{ST} 0.004	0.165	99.58	**Φ_{ST} 0.563**	**0.000**	43.73
(c) Geography				*C. violacea*		
				Porites Green group (clade 2/3)		
Between regions	**Φ_{CT} 0.735**	**0.011**	73.49	**Φ_{CT} 0.427**	**0.002**	42.65
Among population	**Φ_{SC} 0.018**	**0.039**	0.46	**Φ_{SC} 0.056**	**0.000**	3.19
Within population	**Φ_{ST} 0.740**	**0.000**	26.04	**Φ_{ST} 0.458**	**0.000**	54.16

Significant values are in bold type

the variation was among populations within oceans ($\Phi_{SC} = 0.018$, $p = 0.039$, Table 4). More isolated populations like Hawai'i were significantly different from a few populations in the Coral Triangle (Dumaguete, Pemuteran, Pulau Mengyatan) but only marginally so (pairwise $\Phi_{ST} = 0.120$–0.140, Table 5).

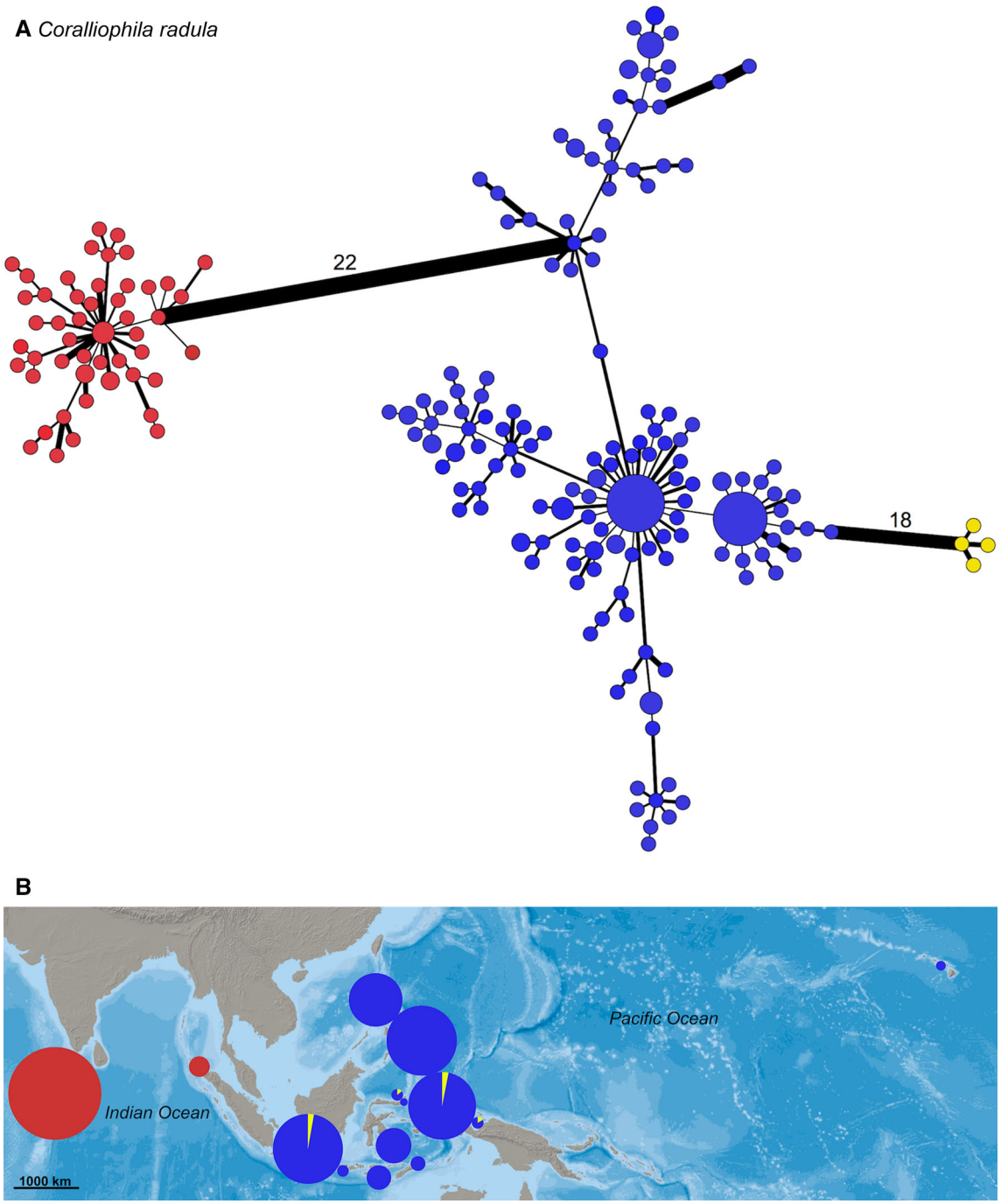

Fig. 5 *Coralliophila radula.* **a** Minimum spanning tree of COI haplotypes. Circle size corresponds to haplotype frequency. Haplogroups with 18 or more mutational steps between them are coloured. Line thickness scales with the number of mutational steps between haplogroups. **b** Map showing the geographic distribution of haplogroups. Circle size corresponds to the number of individuals sampled at each location

Where sample sizes were sufficient, a non-hierarchical AMOVA of *C. violacea* from *Porites* clade 1 in the Coral Triangle showed no significant genetic structure among populations (2% var.; $\Phi_{ST} = 0.020$, $P = 0.091$). However, a couple of pairwise Φ_{ST} distances were significant: populations in Lembeh were different from Komodo ($\Phi_{ST} = 0.048$), and South Bali ($\Phi_{ST} = 0.109$).

Because Hawaiian populations of *C. violacea* from *Porites* species in the Green group (clade 2/3) were distinct in the MST (Fig. 6), we defined three partitions: (1) Indian Ocean, (2) Coral Triangle and (3) Hawai'i for AMOVAs.

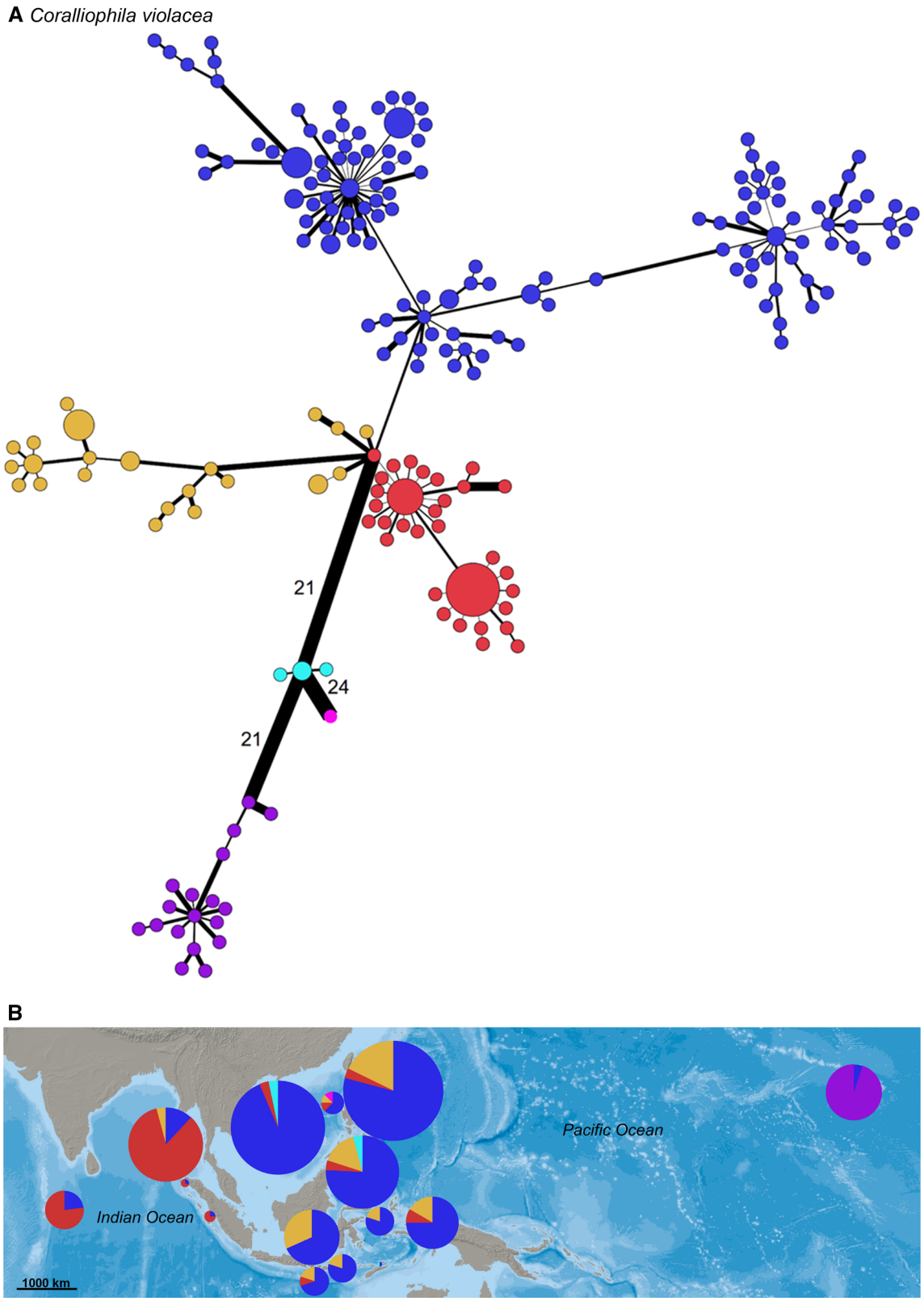

Fig. 6 *Coralliophila violacea* collected from *Porites* species in the Green group (clades 2/3) only. **a** Minimum spanning tree of 204 COI haplotypes from 234 snails. Circle size corresponds to the number of individuals with that haplotype. Haplotypes are coloured by groups with 21 or more mutational steps between them, or groups of haplotypes dominating a geographic area. **b** Map showing the geographic distribution of haplogroups. Circle size corresponds to the number of individuals sampled at each location

Table 5 *Coralliophila radula*. Pairwise population ΦST comparisons

Location	Indian Ocean		Coral Triangle + Hawai'i											
	1	2	6	7	8	9	10	11	12	13	14	15	16	17
1. Vavvaru	0													
2. Pulau Weh	0.017	0												
6. Pemuteran	**0.773**	**0.741**	0											
7. Nusa Penida	**0.778**	**0.721**	− 0.021	0										
8. Pulau Mengyatan	**0.790**	**0.760**	− 0.012	− 0.010	0									
9. Wangi–Wangi	**0.762**	**0.709**	− 0.011	− 0.050	− 0.012	0								
10. Díli	**0.792**	**0.748**	− 0.061	− 0.117	− 0.116	− 0.089	0							
11. Lembeh	**0.802**	**0.763**	0.090	0.033	**0.117**	0.039	0.106	0						
12. Bunaken	**0.749**	**0.666**	0.017	− 0.032	0.015	0.000	− 0.099	0.061	0					
13. Dumaguete	**0.788**	**0.762**	0.006	0.004	0.002	0.009	− 0.032	**0.094**	0.036	0				
14. Ticao	**0.761**	**0.715**	**0.033**	− 0.029	0.024	0.006	− 0.068	0.042	0.017	**0.026**	0			
15. Raja Ampat	**0.757**	**0.711**	**0.018**	− 0.017	0.022	0.007	− 0.048	0.012	0.000	0.001	− 0.001	0		
16. Manokwari	**0.746**	**0.662**	0.026	− 0.031	0.014	0.012	− 0.121	0.093	− 0.092	**0.073**	0.031	0.041	0	
17. Ka'a'awa, Hawai'i	**0.775**	**0.719**	**0.119**	0.023	**0.122**	0.069	− 0.028	0.114	0.043	**0.140**	0.005	0.071	0.013	0

Significant values are in bold type

Genetic structure was strong ($\Phi_{CT} = 0.427$, $P = 0.002$, Table 6) with 43% of the variation among regions (Table 6). Snails from Hawai'i were the most genetically distinct, resulting in the highest pairwise Φ_{ST} values ($\Phi_{ST} = 0.475$–0.689, Table 6). Populations from Hòn Mun in Vietnam were also genetically distinct from all other populations except Díli in Timor-Leste ($\Phi_{ST} = 0.081$–0.447, Table 6).

Discussion

Although phylogeographic studies in the Coral Triangle typically focus on allopatric divergence, results from the corallivorous snail *C. violacea* showed evidence for ecological divergence via host-shifting. Two lineages of *C. violacea* were strongly concordant with the groups of *Porites* species from which these snails were collected. Even within locations, there was genetic divergence among snails collected from different groups of host coral species. Given the high prevalence of symbioses in coral reef ecosystems, the recovery of ecological divergence in *C. violacea* suggests that ecology could be an important driver of lineage diversification in the epicentre of marine biodiversity, the Coral Triangle (e.g. Hoeksema 2007; Gaither and Rocha 2013).

Both *C. radula* and *C. violacea* showed evidence of phylogeographic structure across the Sunda Shelf, as predicted for ecologically similar, sympatrically distributed sister taxa. This classic phylogeographic pattern is observed in a wide diversity of Indo-Pacific marine taxa (Carpenter et al. 2011; Barber et al. 2011; Bowen et al. 2013) and is typically attributed to eustatic sea level fluctuations. In addition to divergence across the Sunda Shelf, *C. violacea* populations in Hawai'i were also highly divergent from all other locations, indicating divergence at both the centre and in more isolated areas of this species' geographic range (see Bowen et al. 2013).

Ecological barriers

Within the Coral Triangle, two sympatric haplogroups of *C. violacea* were concordant with host coral groups. Ecological divergence among populations inhabiting sympatric host taxa is commonly reported for terrestrial species, particularly phytophagous insects such as fruit flies (Bush 1969), pea aphids (Peccoud et al. 2009), butterflies (Fordyce 2010) and stick insects (Nosil et al. 2012). However, marine studies have not typically found evidence for genetic structure among populations on different, sympatrically distributed hosts (e.g. Sotka et al. 2003; Johnston et al. 2012; Li and O'Foighil 2012), with the exception of sponge-dwelling snapping shrimp (Duffy 1996), and *Phestilla* nudibranchs that are also parasites of *Porites* (Fritts-Penniman 2016). However, ecological barriers have been reported at the species level in *Symbiodinium* and their anthozoan hosts (LaJeunesse 2005; Bongaerts et al. 2011).

Table 6 *Coralliophila violacea* collected from *Porites* species in the Green group (clades 2/3) only. Pairwise population ΦST comparisons

Location	Indian Ocean				Coral Triangle											Hawai'i
	1	2	3	4	5	6	7	8	10	11	12	13	14	15	16	17
1. Vavvaru	0															
2. Pulau Weh	− 0.021	0														
3. Pulau Keluang	− 0.040	− 0.016	0													
4. Pulau Pagang	0.085	0.082	− 0.103	0												
5. Hòn Mun	**0.340**	**0.375**	**0.385**	**0.447**	0											
6. Pemuteran	**0.227**	**0.287**	**0.201**	**0.279**	**0.170**	0										
7. Nusa Penida	**0.166**	**0.229**	0.102	**0.168**	**0.178**	0.002	0									
8. Pulau Mengyatan	**0.328**	**0.383**	**0.292**	**0.322**	**0.336**	**0.032**	0.039	0								
10. Díli	**0.357**	**0.448**	0.158	0.305	0.261	0.234	0.150	0.328	0							
11. Lembeh	**0.230**	**0.299**	**0.170**	**0.244**	**0.114**	− 0.021	− 0.030	0.039	0.104	0						
12. Bunaken	0.150	0.206	0.102	0.178	**0.111**	− 0.011	− 0.016	**0.064**	0.086	− 0.028	0					
13. Dumaguete	**0.207**	**0.259**	**0.193**	**0.244**	**0.183**	− 0.014	− 0.018	− 0.010	0.242	− 0.005	0.015	0				
14. Ticao	**0.194**	**0.258**	0.146	**0.218**	**0.183**	− 0.047	− 0.078	0.001	0.182	− 0.040	− 0.039	− 0.049	0			
15. Raja Ampat	**0.176**	**0.249**	0.076	**0.171**	**0.106**	0.066	0.035	**0.137**	− 0.108	0.006	0.015	**0.089**	0.032	0		
16. Manokwari	**0.183**	**0.246**	0.134	**0.224**	**0.081**	0.016	− 0.007	0.126	0.102	− 0.003	0.000	0.037	− 0.026	0.008	0	
17. Ka'a'awa, Hawai'i	**0.671**	**0.708**	**0.640**	**0.657**	**0.689**	**0.635**	**0.597**	**0.648**	**0.475**	**0.602**	**0.579**	**0.624**	**0.615**	**0.538**	**0.599**	0

Significant values are in bold type

While sympatric populations of parasites from different hosts can be genetically distinct, frequently they can still exchange genes (Dres and Mallet 2002). Indeed, the small number of mismatched mtDNA haplotypes on the *C. violacea* host MST could be the result of either incomplete lineage sorting, or current/historical gene flow. However, even reduced gene flow resulting from segregation by the host can, over time, result in speciation (Matsubayashi et al. 2010). Phylogenetic studies of symbiotic marine taxa have discovered host-specific cryptic species in anemone dwelling snapping shrimp (Hurt et al. 2013) and anthozoan-associated barnacles (Tsang et al. 2009), snails (Gittenberger and Gittenberger 2011), nudibranchs (Faucci et al. 2007; Fritts-Penniman 2016) and fishes (Munday et al. 2004; Litsios et al. 2012; Tornabene et al. 2013).

The significant genetic patterns we report in *C. violacea* could be the result of different host-associated haplogroups having distinct host preferences and experiencing differential selection. Previous studies have hinted at host preferences in *C. violacea* (Fujioka and Yamazato 1983), as well as differential selection on different host morphologies (Chen et al. 2004). However, those studies did not characterise the genetics of the host corals, making their results difficult to interpret in the context of this work. It also emphasises the importance of collecting both host and symbiont data for DNA testing, especially given the challenges of coral taxonomy and possibility of cryptic species.

It is not clear what mechanisms are driving the strong association between the divergent *C. violacea* haplogroups and their assemblages of host corals. However, possibilities may include: (1) larval settlement cues as found with corallivorous *Phestilla* nudibranchs (Ritson-Williams et al. 2009), (2) differences in nutritional quality (Yamashiro et al. 1999; Baums et al. 2003), or (3) potential secondary metabolites/pigments development (Wang et al. 2008) due to reduced physical defences (Connell 1973). Whether the mechanism is secondary metabolites, settlement cues, or nutrients, interactions between parasites and hosts are most likely chemically mediated, representing a fruitful avenue of research for understanding the ecological and evolutionary dynamics of host-parasite associations.

Geographic barriers

Co-distributed species with equivalent ecologies and life histories should be impacted in similar ways by broadly acting physical processes (Avise 2000; Marko and Hart 2011). Both *C. radula* and *C. violacea* exhibited strong genetic divergence between Indian and Pacific Ocean populations spanning the Sunda Shelf. During the Pleistocene, sea levels repeatedly dropped by 100–140 m, cyclically exposing the Sunda Shelf, and creating a partial barrier between the two oceans that lasted for ~ 15,000–30,000 years (Voris 2000). Genetic structure among marine organism populations spanning the Sunda Shelf is typically attributed to these sea level changes (Gaither and Rocha 2013), and numerous marine molluscs show phylogeographic structure across this region (Crandall et al. 2008; DeBoer et al. 2008; Kochzius et al. 2008; Nuryanto and Kochzius 2009).

The 5% COI sequence divergence we observed in *C. radula* suggests that separation across the Sunda Shelf began at the latest in the Pliocene/Pleistocene (~ 2.5 Ma) assuming a heuristic molecular clock with a conservative divergence rate of 1%/myr for molluscan COI (Marko 2002; 0.7–1.2%/myr). Therefore, time dependency of substitution rates in other marine invertebrates from this region yield estimates of 2.3–6.7%/myr (Crandall et al. 2011), suggesting that divergence could have occurred less than 1 Ma. Either way, these values place divergence within periods of modern glacial cycles and resulting sea level fluctuations.

The genetic isolation of Hawaiian populations of *C. violacea* is seen in many other Indo-Pacific species (summarised in Gaither et al. 2011), and the levels of population structure we saw were also similar to other findings (COI, $\Phi_{ST} = 0.08–0.89$; Skillings et al. 2011). Yet surprisingly, there was only weak genetic structure between populations of the sister species *C. radula* in Hawai'i and a few Coral Triangle populations. It remains unclear why species with nearly identical ecological niches and life history strategies, and which inhabit the same hosts and overlap in the majority of their geographic ranges, would have concordant patterns in one part of their range, but discordant patterns in the other. It is unlikely that they differ drastically in planktonic larval duration, so possible explanations include different population demographics, and/or the timing of colonisation or expansion into different parts of their ranges. For example, as evidenced by star polytomies in MSTs and relative abundances, *C. radula* may have experienced recent population expansions in the Coral Triangle, whereas *C. violacea* may have expanded in the Indian Ocean. Similarly, subtle ecological differences might structure populations in ways we cannot untangle without information about individuals (e.g. microhabitat) for each specimen collected. For instance, while both species were found on the host coral colonies, they may specialise on different microhabitats (Fernández-González et al. 2015) or nutrients within a host.

A tale of two species

As with the discordant phylogeographic structure between *C. radula* and *C. violacea,* it is puzzling why *C. violacea* has diverged on different host corals, while *C. radula* has not. There are two possible explanations. First, the two

snail species may be responding differently to the same selective pressures because of different evolutionary histories affecting the genetic background upon which selection acts (Prunier et al. 2012). Second, *C. radula* may in fact be diverging on different hosts and selection is occurring in the face of gene flow at certain loci, but this process began too recently or is too weak to be evident in neutral loci. Previous studies reported adaptations to different hosts by herbivorous marine invertebrates, and genetically mediated differences in fitness on hosts (e.g. Sotka et al. 2003), yet could not find any genetic structure in mtDNA. Finally, differences in fitness and selection between host-associated populations could be maintained under on-going gene flow, a process demonstrated in numerous other systems (e.g. Mullen and Hoekstra 2008). To help settle this question, whole-genome or reduced representation sequencing of *C. violacea* is needed to look for candidate loci under selection and estimate gene flow among populations.

Allopatric speciation was such a dominant model of speciation, that early terrestrial studies reporting sympatric speciation mediated by ecological differences (*ecological speciation*) were met with scepticism (Bird et al. 2011). Today, however, a growing body of the literature indicates ecological speciation is more common than previously thought. While studies of ecological divergence in the ocean are still in their infancy, the pervasiveness of obligate host relationships in the marine environment suggests that ecologically mediated divergence and speciation could be important in the evolution of marine biodiversity, particularly in hyper-diverse regions like the Coral Triangle.

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Compliance with ethical standards

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

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