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Integrating cryptic diversity into coral evolution, symbiosis and conservation

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Understanding how diversity evolves and is maintained is critical to predicting the future trajectories of ecosystems under climate change; however, our understanding of these processes is limited in marine systems. Corals, which engineer reef ecosystems, are critically threatened by climate change, and global efforts are underway to conserve and restore populations as attempts to mitigate ocean warming continue. Recently, sequencing efforts have uncovered widespread undescribed coral diversity, including 'cryptic lineages'—genetically distinct but morphologically similar coral taxa. Such cryptic lineages have been identified in at least 24 coral genera spanning the anthozoan phylogeny and across ocean basins. These cryptic lineages co-occur in many reef systems, but their distributions often differ among habitats. Research suggests that cryptic lineages are ecologically specialized and several examples demonstrate differences in thermal tolerance, highlighting the critical implications of this diversity for predicting coral responses to future warming. Here, we draw attention to recent discoveries, discuss how cryptic diversity affects the study of coral adaptation and acclimation to future environments, explore how it shapes symbiotic partnerships, and highlight challenges and opportunities for conservation and restoration efforts.

Modern sequencing technologies have uncovered pervasive undescribed cryptic diversity—the presence of genetically distinct but morphologically similar lineages—across the tree of life, suggesting standing genetic diversity may be severely underestimated[1,2]. This is especially true for corals—the engineers of modern coral reefs—whose morphological plasticity and potential for hybridization presents challenges in taxonomic classification (Box 1)[3,4]. Understanding cryptic coral diversity is important because coral reefs are critically threatened by climate change, and global efforts to conserve and restore reefs are underway as we devise strategies to mitigate ocean warming[5,6]. Left undetected, cryptic lineages complicate ecological studies, conservation strategies and assessments of diversity.

Here, we define cryptic coral lineages as species complexes of multiple morphologically highly similar, or visually indistinguishable, groups that overlap in range yet exhibit signatures of barriers to gene flow[7]. These genetic lineages can represent either undescribed species diversity or, in some cases, described nominal species that were synonymized in taxonomic revisions[8] (Box 1). Identifying cryptic coral lineages using traditional molecular approaches is challenging due to different evolutionary rates for genetic markers, incomplete lineage sorting and reticulate evolution or introgressive hybridization among corals[9–12]. Yet, recent advancements in genome-wide sequencing technologies have revealed that cryptic coral lineages are ubiquitous in nature[13–16] (Box 2).

Studies of coral reef responses to disturbances often do not account for the presence of cryptic diversity, perhaps because morphologically similar colonies are presumed to be functionally similar[17–19]. Yet, recent work has shown that cryptic lineages can exhibit strong

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BOX 1

An introduction to cryptic diversity and coral systematics

The concept of cryptic lineages was first introduced by Mayr[2], who referred to them as 'sibling species'. Despite a lack of clear criteria, cryptic lineages are currently reported across almost all taxonomic groups, from unicellular eukaryotes to vertebrates[1]. Evolutionary processes that prevent or erode detectable morphological change—and may therefore result in cryptic lineage evolution—can be classified into four categories[197,198]: (1) recent divergence, indicating that insufficient time has passed for morphological differences to accumulate[7]; (2) parallelism, which occurs when phylogenetically unrelated species occupied common morpho-spaces and evolved into near-identical morphologies[7,199]; (3) convergence, which describes independent evolution of similar morphologies from dissimilar ancestors[7,199]; and (4) stasis, indicating the retention of high degrees of morphological similarity, in which ancestral traits (that is, symplesiomorphies) exist for millions of years[7]. Each of these forces probably contributes to cryptic lineage evolution, but their relative contributions require further exploration[197].

Cryptic lineages may be particularly prevalent among corals because taxonomy was historically based on skeletal morphology, but morphological plasticity and trait convergence among sister species impede the disentanglement of coral diversity[75,200–203]. Moreover, coral phylogenetic relationships explored via mitochondrial markers in the late twentieth and early twenty-first centuries offered low resolution to discern taxa in species-rich genera[204], causing described species (for example, Pacific *Acropora*) to be considered junior synonyms during taxonomic revisions[205]. Therefore, cryptic diversity uncovered using next-generation sequencing may in some cases correspond to described species that were incorrectly synonymized[127].

Although cryptic coral lineages are increasingly reported, the term 'cryptic diversity' has been used inconsistently, either to describe newly discovered genetic variation within described species (for example, refs. 14,24,38,113), to differentiate morphologically indistinguishable described species within a genus (for example, refs. 19,206) or to indicate newly uncovered lineages for which diagnostic traits were ambiguous or not assessed (for example, refs. 8,21,155). Therefore, it is often unclear whether newly reported cryptic lineages are truly cryptic (that is, no diagnostic traits). Of 102 identified articles, 33 reported potential morphological differences between 2 or more cryptic lineages (in 13 stony coral and 4 soft coral genera; Table 1 and Supplementary Table 1). However, some of these traits may only differ between some lineages in a complex, and due to partial overlap in trait values often require expert evaluation. Quantified traits that have been found to differ among some cryptic taxa include branch morphology and growth form (*Acropora*[111,112,127,144], *Heliopora*[55,187,190,191] and *Seriatopora*[181]), microskeletal features (*Coelastrea*[149], *Eunicia*[40], *Favia*[151], *Fungia*[154], *Pachyseris*[13], *Paramuricea*[193], *Plesiastrea*[162], *Plexaura*[196], *Psammocora*[179] and *Stylophora*[184,185]), nematocyst morphology (*Galaxea*[113,114,155,156]), and combinations of gross morphology and microskeletal features (*Orbicella*[160,207], *Porites*[163,177] and *Pocillopora*[56,163]; but see refs. 164–166). Only 4 studies reported that quantified traits were entirely unrelated to genetic lineages[140,164–166], and the majority (n=65) did not report morphological assessments. Overall, these findings suggest that some sets of morphological traits can help to 'decrypt' coral lineages and, in combination with genetic data, aid assignment of species names. However, researchers must also account for morphological plasticity by sampling corals across environmental gradients.

differentiation in functional traits, including responses to elevated temperatures[14,19–23]. Some lineages also appear to associate with distinct algal symbionts (family Symbiodiniaceae)[20,24–26]. This variation has critical implications for understanding and predicting coral responses to future warming, given that warming oceans are the primary driver of coral bleaching—a disruption of the symbiosis between corals and their algal symbionts—and can cause widespread mortality[27,28]. Here, we discuss five key topics in coral biology relevant to coral reef persistence under rapid ocean warming that are affected by the presence of this ubiquitous cryptic diversity.

Ubiquity and distributions of cryptic coral lineages

Evidence for the existence of cryptic coral lineages was summarized 30 years ago[29] for 5 coral genera. Since then, cryptic lineages have been reported in at least 18 stony coral and 6 octocoral genera across ocean basins (Table 1 and further detail in Supplementary Table 1; based on 102 retrieved articles). Initial molecular surveys suggest that cryptic diversity also probably exists in additional families and genera[30–36]. Available data indicate that, although cryptic coral lineages often co-occur in reef systems[20,37,38], they frequently segregate across environmental gradients and exhibit patterns consistent with ecological specialization[15–17,21,39] (Fig. 1 and Table 1). For 19 genera (out of 24), environmental gradients such as depth, habitat type (for example, nearshore versus offshore) and latitude have emerged as predictors of cryptic lineage distributions[13,16,17,21,40–43] (Table 1). These variables are often correlated with other attributes including temperature, light availability, wave exposure and terrestrial (nutrients and sediments from runoff) as well as oceanic (upwelling, currents) influences (Table 1 and Fig. 1), suggesting that a combination of abiotic characteristics interact to shape the environmental niche required to host a cryptic lineage.

The evolution and ecology of depth-segregated cryptic coral lineages has been extensively studied in the gorgonian *Eunicea flexuosa*[40]. In *E. flexuosa*, two lineages are specialized to different depths, and migrant corals are selected out of the population before reproductive maturity[40,44,45] (Fig. 1a). Similar patterns of environmental filtering across depths have been observed in other taxa (Table 1), including the reef-building coral *Seriatopora hystrix* on the Great Barrier Reef[43,46] and *Montastraea cavernosa* and *Siderastrea siderea* in the Caribbean, with lineages occurring sympatrically but some found only at specific depth ranges[16,47] (for example, deep; ~20 m). Broad geographic sampling of the *Pachyseris speciosa* species complex also revealed cryptic lineages that occurred sympatrically but differed in their depth distributions along the Great Barrier Reef and western Coral Sea[13].

Differences in distributions among cryptic lineages are also evident at larger spatial scales, including across latitudes (Fig. 1b). For example, lineages of the widespread coral genus *Acropora* were first discovered in *A. hyacinthus*[38]. Since then, seven *A. hyacinthus* lineages have been uncovered across the Pacific, with some coexisting within sites and others exhibiting spatial distribution differences across wider geographic scales[38,41,48,49]. Whether the same mechanisms govern the evolution of cryptic lineages across both small (for example, depth, habitat type) and large (for example, latitude) spatial scales remains unclear.

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BOX 2

Identifying cryptic coral lineages using molecular tools

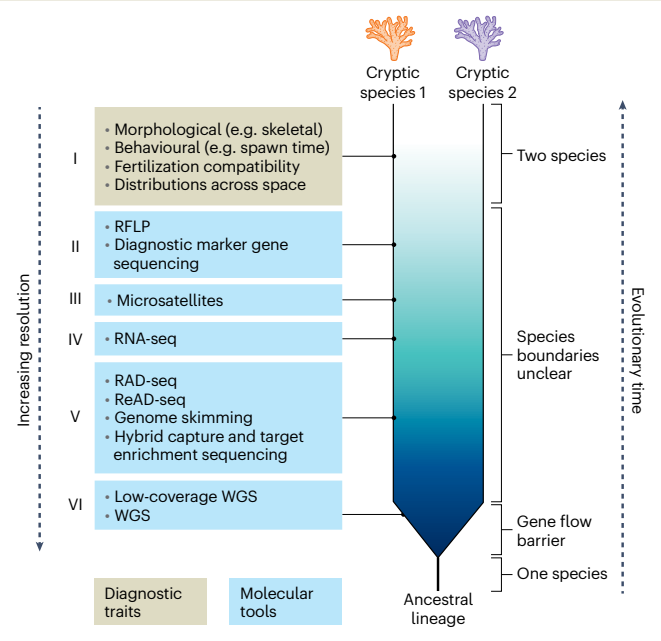
Coral taxonomy based on colony morphology is challenged by a dearth of diagnostic traits distinguishing related species (arrow I in the Box figure). Yet, molecular studies have transformed our ability to identify species via phylogenies from molecular sequencing data[29,32,208,209] (arrows II–VI; Supplementary Table 1), especially with recent advancements in genome-wide SNP-based approaches (arrows V–VI).

'Classic' molecular markers used to delineate cryptic lineages include allozymes and diverse mitochondrial, ribosomal and nuclear markers (for example, *Cytb*, *ITS* and *PaxC*), with variable resolution due to different rates of evolution (arrow II)[32,204,210,211]. These tools are now readily available and relatively inexpensive, facilitating cryptic lineage identification. However, these low-resolution methods may not always be informative due to low evolutionary rates in mitochondrial DNA[204], the multi-copy nature of ribosomal DNA and—in some taxonomic groups—hybridization among species, coupled with recent diversification events resulting in low genetic separation[9,11,12]. In such cases, the discovery and identification of cryptic lineages requires phylogenomic delineation based on microsatellites (arrow III) or transcriptome sequencing (arrow IV), but genome-wide SNPs provide the highest resolution (arrows V–VI). Relatively affordable tools for genome-wide SNP identification include restriction-site associated DNA sequencing (RAD-seq), reductively amplified DNA sequencing (ReAD-seq), genome skimming, and hybrid capture and target enrichment sequencing (arrow V)[209,212]. Whole genome sequencing (WGS) and low-coverage WGS provide even higher resolution to detect very recently diverged lineages (arrow VI)[212]. These tools can also provide additional insight into the ecology and evolution of lineages, for example, by identifying loci under selection[20,163].

Molecular analyses typically include multivariate statistical clustering methods developed to disentangle genetic population structure[213–216]. Genetically distinct populations (that is, groups with low gene flow) that occur sympatrically (that is, in the same larval crossing range) can generally be assumed to represent evolutionary lineages[217]. For reference, some recent genome-wide SNP-based surveys in diverse genera reported F_{ST} values between sympatric cryptic coral lineages ranging between 0.06 and 0.7, but most comparisons exceeded 0.1[13,14,16,21,98]. Calculation of F_{ST} values between co-occurring populations can thus be a helpful tool to detect lineages, but note that retrieved values strongly differ depending on the system, as well as the markers and filters used[218].

To assign lineages at remote sites where sequencing facilities or funding are less available, researchers can design rapid sequencing-independent tools, such as restriction fragment length polymorphism (RFLP), based on existing marker gene or SNP data. Such assays have been developed to distinguish cryptic lineages of *Pocillopora*[206], *Galaxea fascicularis*[114] and *Pachyseris speciosa*[13]. When paired with low-cost rapid DNA extraction methods such as the HotSHOT approach[219] (<US$0.10 per sample, ~1 hour per plate), these assays can provide lineage classifications within hours. The development of such assays for additional lineages will increase the accessibility of tools to quantify cryptic diversity and will help to accelerate scientific discovery. However, comprehensive genetic analysis must also be conducted at a given locality to ensure that additional cryptic diversity is not masked by a lack of unique restriction sites.

Tools to identify and characterize cryptic coral lineages. Available diagnostic tools range from low-resolution observational (I) and molecular (II and III) tools that support the identification of highly diverged cryptic lineages, to more data-rich tools that provide increased power to distinguish more recently diverged lineages, albeit often at higher monetary costs (IV–VI). RNA-seq, RNA sequencing. Figure adapted from ref. 88, CC BY 4.0; adapted with permission from ref. 220, Taylor & Francis, and ref. 221, Society of Systematic Biologists.



Evidence for functional differences relevant to ocean warming

High functional diversity and redundancy, as well as the persistence of corals with particular traits, may buffer reefs from the impacts of climate change[18]. In particular, adaptations that enable survival in shallow habitats with higher and more variable temperatures may underpin increased tolerance to temperature stress[50] (for example, lagoon specialist lineage in Fig. 1). Of the 102 articles examined here (Table 1 and Supplementary Table 1), 21 reported potential functional differences among cryptic lineages that are relevant to survivorship in future climate change conditions. This includes 10 genera (8 stony coral and 2 octocoral genera) with reported evidence for differences in growth rates[51,52], photophysiology[23,46], energy stores[13,23] and gene expression patterns[53], stress response genes under selection[20,54,55] and environmental filtering underpinning lineage distributions[16,24,44–46]. Of these 21 articles, 11 reported direct evidence for variation in thermal tolerance[14,19–23,25,39,51,56,57] and 2 reported a lack of heat tolerance differences between lineages (quantified either as equivalent bleaching frequencies during an ongoing marine heatwave[58] or similar recovery rates following bleaching[59]). An additional 14 studies reported differences in reproductive mode or phenology among cryptic lineages, and the remaining 64 articles did not report data informing potential functional differences between lineages. Clearly, additional work is needed to understand the functional significance of cryptic lineages under climate change conditions.

Table 1 | Summary of coral genera for which evidence for sympatric cryptic lineages has been reported

Genus	Likely environmental drivers of cryptic lineage structure	Functional and morphological differences between cryptic lineages	Microbial community	References
Stony corals				
Acropora	Habitat type[20,37] (backreef versus fore reef, inshore versus offshore), temperature[20,41,49], latitude[37,41,48,49], longitude[140] and geographic isolation[49]	Differences in thermal tolerance[20] (but see ref. 59), growth rate[51], spawning phenology[110–112,141–143], branch and corallite morphology[111,112,127,144], and reduced fertilization between lineages[48] Stress response genes under selection[20]	S: some lineages may be more likely to associate with *Durusdinium*[20] (but see refs. 59,143), diversity was structured from nearshore to offshore in *A. tenuis*[37] B: ND	20,37,38,41,48,49,51,59, 110–112,127,140–148
Agaricia	Depth[4,98]	ND	S: structured by depth, not cryptic lineage per se[98] B: ND	4,98
Coelastrea	Latitude[149]	Differences in corallite morphology and reproductive mode[149]	S: ND B: ND	149
Favia	Habitat type[150] (reef versus seagrass), depth[150,151] and geographic isolation[152]	Differences in corallite morphology[151]	S: ND B: ND	150–152
Fungia	Geographic isolation[153]	Differences in mode of reproduction[153] and corallum morphology[154]	S: ND B: ND	153,154
Galaxea	Depth (perhaps only at some locations)[155]	Differences in corallite size and shape[155], nematocyst morphology[113,114,156] and spawning time[114] Cross fertilization between lineages is rare[113]	S: ND B: ND	113,114,155–157
Leptoseris	Depth[4]	ND	S: ND B: ND	4
Madracis	Depth[42,158]	ND	S: some lineages host symbionts that do not associate with other lineages[42,158,159], or may host different symbionts at certain depths[159] B: ND	42,158,159
Montastraea	Habitat type[16] (inshore versus offshore) and depth[16,47]	ND	S: symbionts may be structured by depth in some locations, but it is unclear whether there are differences between lineages[47] B: ND	16,47
Orbicella	Depth and physical disturbance[160]	Differences in thermal tolerance[14], calice size[160], colony morphology, growth rates and oxygen isotope ratios[52]	S: lineages of *O. faveolata* have different levels of symbiont fidelity[14] B: ND	14,52,160
Pachyseris	Depth[13]	Differences in corallite morphology, energy stores, tissue thickness and reproductive phenology[13]	S: no differences between lineages[13] B: differed among regions, not lineages[13]	13,161
Plesiastrea	Latitude[162]	Differences in corallite morphology[162]	S: ND B: ND	162
Pocillopora	Habitat type[54] (reef flat versus slope), depth[17,19,26,163], temperature[17,163] and oceanographic factors[164,165]	Differences in thermal tolerance[19,25,56], morphology[56,163] (but see refs. 164–166) and potentially reproductive mode (*P. damicornis*)[167] Stress response genes under selection[54]	S: evidence for cophylogeny between host and symbiont[26,165,167], some lineage-specific symbionts[167] and some lineages may be more likely to associate with *Durusdinium*[25,26,165] B: may differ between some lineages[54]	17,19,25,26,54,56,163–172
Porites	Habitat type[21,39,53,173–177] (inshore versus offshore), depth[163,173], geographic distance[173], temperature[163] and potentially latitude[39]	Differences in thermal tolerance[21,39,57] (but see ref. 58), gross[163] and corallite morphology[53,177], and gene expression[53]	S: evidence for cophylogeny between host and symbiont[57,58], some lineage-specific symbionts[178] (but see[39]) and depth zonation in some locations[173] B: ND	21,39,53,57,58,163, 173–178
Psammocora	ND	Potential differences in corallite morphology[179]	S: ND B: ND	179
Seriatopora	Habitat[46,180,181] (exposed versus sheltered) and depth[43,182,183]	Differences in branch morphology[181] and photo-physiology[46] Environmental filtering also suggests functional differences[46]	S: differences between lineages[43,46], some lineage-specific symbionts[181] and some structuring across depths[43,182] B: ND	43,46,180–183

Table 1 (continued) | Summary of coral genera for which evidence for sympatric cryptic lineages has been reported

Genus	Likely environmental drivers of cryptic lineage structure	Functional and morphological differences between cryptic lineages	Microbial community	References
Siderastrea	Habitat type[16,23] (inshore versus offshore) and depth[16]	Differences in thermal tolerance, skeletal morphology, and energy stores[23] Environmental filtering also suggests functional differences[16]	S: some lineages may be more likely to host *Durusdinium*, some lineage-specific symbionts[23] B: accessory microbiomes differed between lineages[23] (note that samples were taken after common garden experiment)	16,23
Stylophora	Temperature[94] and geographic distance[184,185]	Differences in thermal tolerance[22] Potential differences in gross[186] and corallite morphology[184,185] (but see refs. 184,186)	S: differences between some lineages[94,185], as well as variation by environment[94] B: differences in *Endozoicomonas* amplicon sequence variants between some lineages, as well as by environment[94]	22,94,184–186
Octocorals				
Eunicea	Depth[15,24,40,44,45]	Differences in sclerite morphology and skeletal densities[24,40] Environmental filtering also suggests functional differences[24,44,45] Limited hybridization between lineages[45]	S: lineages host distinct populations of *Breviolum minutum*[15,24] B: ND	15,24,40,44,45
Heliopora	Habitat type[55,187,188], depth[187] and oceanographic factors[187,189]	Differences in reproductive phenology[55] and colony morphology[55,187,190,191] Fixed nucleotide differences in stress response genes[55]	S: ND B: ND	55,187–191
Leiopathes	Potentially habitat (slope) or oceanographic factors[192]	Hypothesized differences in reproductive strategies[192]	S: ND B: ND	192
Paramuricea	Depth or oceanographic factors[193,194]	Differences in sclerite morphology[193] and coloration[195]	S: ND B: ND	193–195
Plexaura	ND	Differences in sclerite morphology and reproductive phenology[196]	S: lineages host distinct species of *Breviolum*[196] B: ND	196
Sinularia	ND	ND	S: ND B: ND	10

S, symbiont (Symbiodiniaceae); B, bacterial community; ND, no data. Based on 102 articles retrieved by reviewing the top 100 results (and references therein) from Google Scholar searches for each of the following queries: 'coral cryptic lineage', 'coral' species complex population cryptic -fish' and 'coral' cryptic species -fish' (results retrieved 8 March, 24 May and 31 May 2023, respectively). In total, 300 results were reviewed, plus references therein. See Supplementary Table 1 for more details.

A frequently used approach to test for variation in thermal tolerance among coral taxa is to conduct common garden heat challenge experiments. To date, three studies have used such manipulative experiments to compare responses to elevated temperatures among cryptic lineages. So far, results point to remarkable levels of response variation: lineages of *Orbicella faveolata*[14,60] and *S. siderea*[23] in Panama, and genetically distinct populations of *Stylophora pistillata* from the Red Sea each showed differences in heat tolerance that may inform long-term population responses to ocean warming. However, findings in *S. pistillata* were based on acute heat stress assays, and the authors did not strictly define these populations as cryptic lineages[22].

Another avenue to compare thermal tolerances between cryptic lineages is to capitalize on 'natural' bleaching events by sampling morphologically similar colonies with variable bleaching levels. Such sampling of *A. hyacinthus* in American Samoa revealed that one lineage ('HE') in backreef habitats—which are characterized by higher daily mean temperatures and higher variability—experienced less bleaching than other co-occurring lineages[20]. Low-coverage whole genome sequencing (Box 2) revealed two highly diverged loci, one of which encoded genes associated with thermal stress responses[20,61]. Additionally, during a thermal anomaly in Mo'orea, 72% of *Pocillopora* colonies bleached; however, 12 sympatric haplotypes were uncovered, and mortality following bleaching was largely restricted to a single haplotype ('haplotype 11'; 86% of mortality)[19]. These patterns were consistent with *Pocillopora damicornis* at Heron Island, Australia, where a lineage dominating the reef flat (analogous to the lagoon habitat in Fig. 1) showed signatures of local adaptation in cellular stress response genes[54]. In addition, historical bleaching frequencies were analysed in *Porites* cf. *lobata* colonies sampled in Palau by comparing stress bands deposited in coral skeletons. Four cryptic lineages were uncovered; of these, two lineages had reduced bleaching frequencies and, similar to *A. hyacinthus* lineage 'HE' distributions[31], were more abundant in warmer habitats[21].

In cases in which thermal tolerance has not been explicitly tested, other quantitative traits may inform responses to elevated temperatures. Traits that correlate with thermal tolerance include propensity for heterotrophy[62,63], morphology, growth rates[64,65], tissue thickness, nutrient stores[66] and Symbiodiniaceae cell densities[67]. Although studies linking phenotypic traits with functional differences in cryptic lineages are rare, in Panamanian *S. siderea*, a lineage with higher baseline energy stores, increased growth rates, and higher symbiont and chlorophyll *a* densities, maintained elevated photochemical efficiencies during a heat challenge[23]. Depth-stratified lineages of *P. speciosa* similarly varied in tissue thickness, nutrient stores, photosynthetic pigment concentrations and skeletal structure[13], but thermal tolerance was not tested. Lineage-specific differences in skeletal traits may be an important but overlooked coral trait that can underpin local adaptation by affecting photoharvesting potential (as in ref. 68), especially in depth-segregated lineages[53,54]. Recent advancements in morphological tools, including microscopy and three-dimensional scanning, offer opportunities for identification of morphological traits associated with thermal tolerance that may also aid delineation and description of lineages in some groups[69–72].

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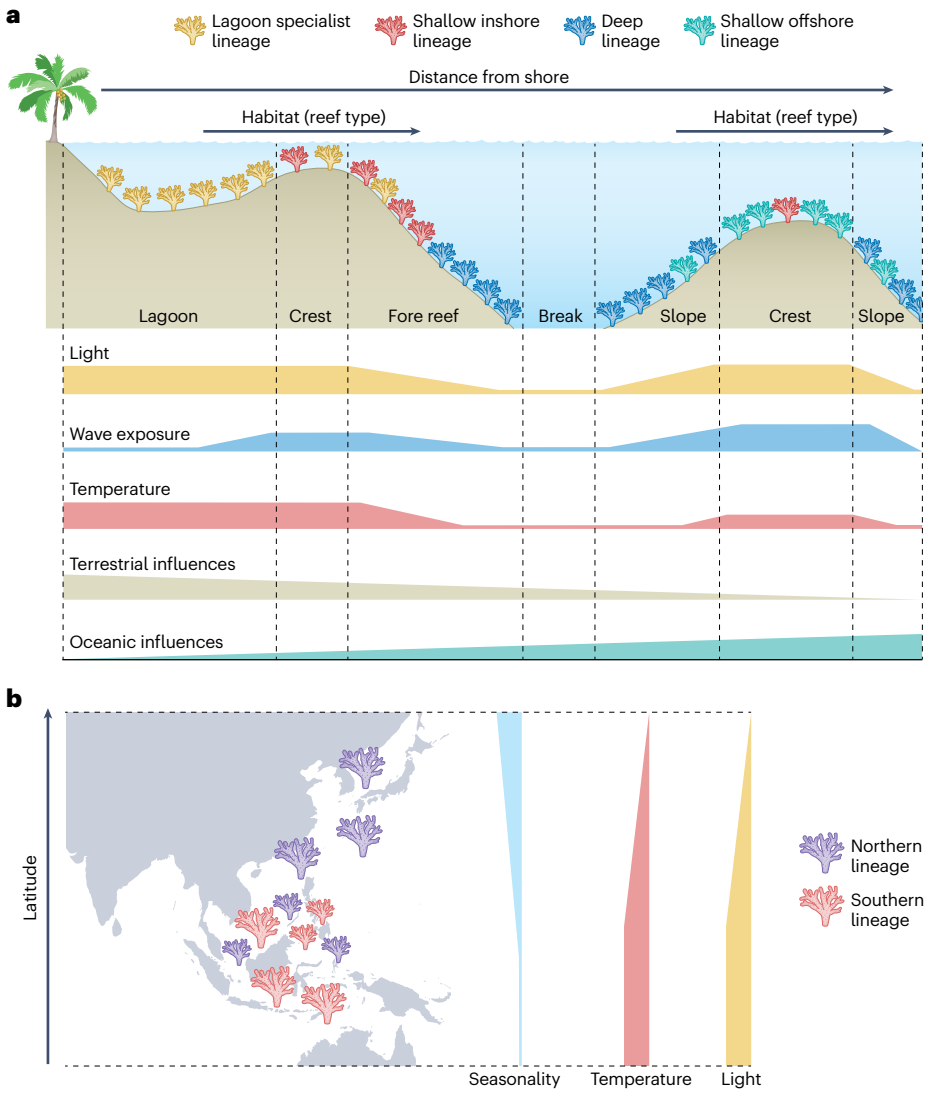

Fig. 1 | Hypothetical distributions of cryptic coral lineages. a, Cryptic lineages are often structured along environmental gradients including distance from shore, habitat type and depth. **b**, Cryptic lineages can also be structured along latitudinal gradients, with associated changes in seasonality, temperature and light availability. Coral icon colours indicate distinct cryptic lineages. Terrestrial influences may include nutrients, sediments and freshwater from runoff; oceanic influences may include currents and upwelling of deep water. Dissolved oxygen concentrations may also vary between habitats, and are often low in nearshore shallow environments. Seasonality may include temporal variation in temperature, light and nutrient availability, among other factors.

One key question is whether thermal tolerance carries any trade-offs, for example, in growth or fecundity. Reduced growth rates and lower skeletal densities have been identified as a trade-off in heat-tolerant lineages of *A. hyacinthus* and *Porites*, for example[21,51,53,73]. However, in cases where heat-tolerant lineages occur primarily in marginal or extreme environments, differences in growth could also be explained by low pH, which can reduce calcification[21,50]. The environmental conditions experienced by lineages at smaller scales are also important, as light intensity and other abiotic variables can vary greatly within the three-dimensional reef environment. Additional work is needed to identify trade-offs in lineages with increased thermal tolerance, as well as how interactions between morphology, physiology and environmental conditions shape thermal tolerance.

In summary, a growing body of literature provides evidence for functional differences between cryptic lineages with relevance to survival under future ocean warming. This development underscores the need to explicitly consider the presence of cryptic lineages when designing studies. Quantifying functional differences is critical for predicting coral responses to future climate change and can inform management plans—especially for traits such as thermal tolerance. Manipulative experiments and opportunistic sampling of cryptic lineages across habitats in additional coral genera, along with linking correlated phenotypic traits, will increase our understanding of the link between cryptic lineages, traits and persistence under future ocean warming conditions.

Patterns of microbial community diversity among cryptic coral lineages

The composition of coral-associated microbial communities, including algal symbionts (that is, Symbiodiniaceae), bacteria and other microbial entities (for example, archaea, fungi, viruses or apicomplexans) are critical drivers of responses to environmental change[74–78]. Associations with specific algal symbiont species allow corals to occupy distinct niches along environmental gradients (Fig. 2) and have functional consequences for thermal tolerance[79,80], growth[81] and susceptibility to disease[82,83]. Variation in bacterial communities can also modulate coral health and acclimatization potential[76,84–87]. Yet, studies on cryptic coral lineages often do not include surveys of algal symbionts (Symbiodiniaceae communities were characterized in 31 of 102 articles surveyed) or bacterial associates (bacterial communities were characterized in 5 of

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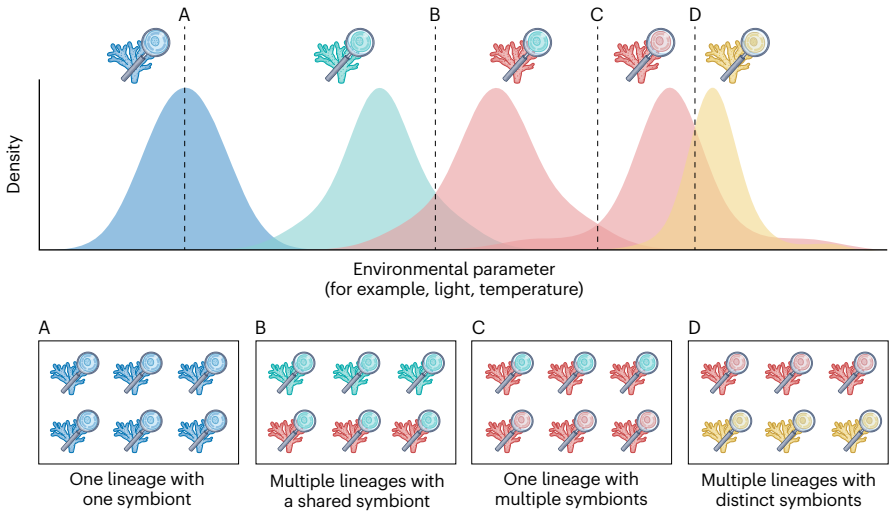

Fig. 2 | Hypothetical distributions of four cryptic coral lineages with several algal symbionts (Symbiodiniaceae) across an environmental gradient. Some lineages with high symbiont fidelity may associate with specialized algal symbionts that are absent in other lineages (for example, the blue and orange lineages). Other lineages may share algal symbionts (red and green lineages sharing the green symbiont). Promiscuous lineages may associate with multiple algal symbionts, extending their potential range (red lineage). Dashed vertical lines A–D indicate hypothetical sampling sites and the corresponding rectangles demonstrate how observed patterns of symbiont diversity is confounded by the presence of cryptic lineages. For example, sampling at site B captures two co-occurring cryptic lineages (green and red) with the same symbiont species, whereas site C captures only one cryptic lineage (red) but with two symbiont species. Characterizing cryptic lineages is therefore important for understanding patterns of Symbiodiniaceae diversity and vice versa.

102 reports; Table 1). To date, of the 24 identified coral genera harbouring putative cryptic lineages, studies in 13 characterized algal symbiont populations (11 of 18 stony coral genera; 2 of 6 octocoral genera; Table 1), whereas bacterial communities have been explored in only 4 genera (4 of 18 stony coral genera; 0 of 6 octocoral genera; Table 1).

Thus far, at least three lineage-specific scenarios for host–algal symbiont associations have emerged (Table 1): (1) algal symbiont species hosted by each lineage overlap, but there are differences in the relative proportions of colonies that host each symbiont species (for example, all green lineage colonies host green symbionts, but the red lineage colonies host either green or red symbionts in Fig. 2); (2) each lineage has high fidelity for a different algal symbiont (for example, orange and blue lineages in Fig. 2); and (3) no discernable differences in algal symbiont community patterns exist between lineages (for example, green symbiont hosted by red and green lineages in Fig. 2).

Evidence for scenario 1 has been identified in *A. hyacinthus*, *S. siderea*, *Pocillopora* spp. and *O. faveolata*, with implications for bleaching responses (Table 1). Promiscuous lineages appear to be more thermally tolerant for both *A. hyacinthus* and *S. siderea*[20,23]. In these cases, colonies with increased thermal tolerance were more likely to host *Durusdinium* (a genus of Symbiodiniaceae containing strains linked to increased thermal tolerance), suggesting higher promiscuity promotes thermal tolerance by shifting to more thermally resistant symbionts when it is advantageous. This is further evidenced by one lineage of *Pocillopora* spp. in the eastern tropical Pacific showing higher propensity to shift to *Durusdinium* symbionts than a co-occurring lineage, resulting in increased survivorship during a bleaching event[25].

Support for scenario 2 has been reported for depth-stratified lineages of *E. flexuosa* and *Madracis pharensis*, where each lineage associated with distinct algal symbionts[24,42]. Additionally, a survey of host–symbiont associations in Mo'orea uncovered a pattern of cophylogeny between five cryptic species of *Pocillopora* and specific *Cladocopium* (another genus within Symbiodiniaceae) species[26]. Similarly, the reef flat lineage of *P. damicornis* (discussed in the previous section) hosted distinct *Cladocopium* strains compared with a nearby lineage inhabiting the reef slope[54], suggesting that ecological specialization can involve both the coral host and its algal symbiont. Although high symbiont fidelity itself may not be maladaptive, certain host–symbiont associations might be costly under rapidly changing environments. For example, three cryptic lineages of massive *Porites* in Kiritimati that showed a pattern of cophylogeny with their symbionts exhibited differential survival after a heatwave, with one lineage showing higher mortality[57]. In the rare cases where colonies from this lineage survived, they had shifted to a symbiont common in the other two lineages, showcasing erosion of this tight partnership[57].

Evidence for scenario 3 has been reported from *P. speciosa*, which exhibits tight fidelity with *Cladocopium goreaui* regardless of lineage or environment[13]. A recent study[59] observed similar patterns, with all lineages of *Acropora aspera* associating with *Cladocopium* symbionts regardless of sampling location (that is, intertidal versus subtidal; but note that symbiont diversity was only characterized at the genus level). Additionally, another study[39] demonstrated that two cryptic species of *Porites* differed in their bleaching responses despite associating with the same dominant algal symbiont species. These studies highlight the complexity that cryptic lineages introduce even when algal symbiont communities are similar. However, it is important to acknowledge that genetic tools available for coral hosts are more sophisticated than those currently available for Symbiodiniaceae, potentially limiting our ability to capture detailed patterns of symbiont genetic diversity[88].

As a result of variation in symbiont associations between cryptic lineages, sampling coral populations in a given habitat may be confounded by the presence of multiple lineages with differing symbiont fidelity or promiscuity (as shown in Fig. 2 rectangles A–D). Moreover, it is possible that a combination of these patterns occurs within a single coral species complex (that comprises all closely related lineages), complicating these patterns amongst cryptic lineages. Understanding patterns of algal symbiont communities across cryptic lineages can also be complicated by the mode of symbiont transmission. For example, vertically transmitting species may be more likely to associate with particular algal symbiont species, which can lead to co-evolution[26], while horizontally transmitting species may inherently exhibit more variable symbiont communities[89–92]. Surveys of algal symbiont diversity among cryptic lineages should therefore be conducted along environmental gradients, especially in areas where multiple lineages coexist, to disentangle lineage- and environment-specific patterns of symbiont associations.

Bacterial microbiome structure and flexibility have been shown to differ across the coral phylogeny and may facilitate acclimatization to local environments[84,85,93]. Based on the limited data available, microbiome structure and flexibility may also differ among cryptic coral lineages. For example, low-abundance bacterial taxa, but not core microbiomes, differed between two *S. siderea* lineages (note that microbiomes were sampled after a common garden experiment, possibly resulting in microbiome convergence)[23]. Additionally, patterns of bacterial diversity differed among lineages of *S. pistillata* along a broad geographic range in the Red Sea[94]. Specifically, amplicon sequence variants belonging to *Endozoicomonas*, which are emerging as important coral associates (for example, refs. 95,96), exhibited different patterns of relative abundance across lineages and environments[94]. By contrast, bacterial communities across *P. speciosa* cryptic lineages were primarily structured by region, and not by lineage[13]. Comparative surveys of bacterial diversity across cryptic coral lineages and environments are needed to better understand these patterns and their potential functional roles.

Overall, cryptic coral lineages exhibit divergent strategies regarding associations with Symbiodiniaceae and bacterial communities. Cryptic lineages often differ in their algal symbiont associations, as well as in their ability to associate with different symbionts along environmental gradients (Fig. 2). Although data are limited, emerging patterns suggest that cryptic lineages may also associate with distinct bacterial communities, or have different levels of microbiome flexibility, potentially affecting their resistance to anthropogenic disturbances. Functional studies combining cryptic lineage delineation with microbial community profiling are needed to identify susceptible host–microorganism pairings[97].

Processes that promote, maintain and structure cryptic coral diversity

Understanding the mechanisms that generate and maintain cryptic lineages remains a key research priority and can ultimately inform how speciation occurs more broadly (Box 1). The co-occurrence of cryptic coral lineages over relatively small spatial scales suggests the potential for gene flow between lineages. In fact, the five studies to date that have modelled historical gene flow between cryptic lineages have each demonstrated a pattern of divergence with gene flow[15,16,37,41,98]. If these cryptic lineages occur sympatrically and exhibit historical gene flow, why have they not collapsed into a single species?

There are many hypothesized scenarios of divergence with gene flow (for example, ref. 99); we outline some here that may be important in the context of cryptic speciation in corals and other marine taxa. Broadly speaking, populations can diverge with gene flow if there is strong selection, a period of strict geographic isolation followed by secondary contact, or a combination of some degree of spatial segregation and divergent selection[100,101]. Divergence owing to selection is particularly evident when the genetic loci subjected to divergent ecological selection coincide with those contributing to intrinsic reproductive barriers (reviewed in ref. 102). Transient separation of coral populations, resulting from geological changes such as sea-level fluctuations[103], can persist long enough to drive reproductive isolation before ranges overlap during secondary contact. However, lineages can also diverge on the same reef when separated by oceanographic barriers imposed by depth, bathymetric factors or currents (Fig. 1). For example, differences in gamete packaging (Table 1) can affect gamete buoyancy[104], potentially leading to distinct patterns of gamete mixing and affecting gene flow between depth-stratified lineages. Furthermore, lineages that occur primarily at inshore sites may experience low flow[105], isolating gametes and leading to low cross-fertilization with offshore populations.

Once some degree of reproductive isolation is achieved, species boundaries can be maintained in sympatry via prezygotic or postzygotic isolation. Prezygotic barriers can include mismatches of sperm–egg interacting proteins[106–109], temporal variation in spawning (for example, refs. 110–112) or small windows of overlap, but low[48,113,114] to no fertilization success[115,116] (Table 1). When inter-lineage hybridization does occur, postzygotic barriers could lead to hybrid sterility or inviability. For example, backcrosses of inter-lineage hybrids showed reduced fertilization rates in *A. hyacinthus*[48]. Hybrid sterility or inviability may be caused by incompatibilities of certain combinations of alleles at different loci (for example, Bateson–Dobzhansky–Muller incompatibilities[117]), or differential selection across habitats resulting in the immigrant inviability (see first section). Bateson–Dobzhansky–Muller incompatibilities can accumulate during reproductive isolation and represent alleles that, while functional in their lineage-specific genetic backgrounds, cause fitness loss when combined in hybrids[117]. Reproductive barriers, selection in the early life-history stages, and genomic incompatibilities could act independently or synergistically to increase reproductive isolation among lineages. As divergence increases, reproductive isolation also increases, eventually leading to fully incompatible gametes, inviable embryos or sterile hybrids.

Genomic islands of divergence (IoDs; that is, genomic regions with high differentiation) between coral lineages[15,16,41] offer insight into the evolutionary processes responsible for the origin and maintenance of cryptic lineages. IoDs have been referred to as 'speciation islands', because during divergence with gene flow they are predicted to form around genomic regions involved in local adaptation or reproductive isolation[118,119]. Alternatively, IoDs can emerge without gene flow and represent ancient balanced polymorphisms that were sieved in the descendent lineages. In this scenario, each lineage carries the haplotype that selection favoured in their respective habitat, in addition to genes with adaptive significance. This pattern contrasts with the rest of the genome where there may be little to no differentiation between lineages[120]. Another alternative is IoD formation without gene flow via either genetic hitchhiking or background selection in regions of low recombination[121]. In this case, IoDs have no function in adaptation. Although some support exists for IoDs in the octocoral *E. flexuosa* probably as a result of adaptation to depth[15], the three models of IoD formation require more testing and represent useful avenues for future research.

The development of reproductive barriers between lineages is probably a complex process driven by multiple factors. Cases have been made for all scenarios of divergence with gene flow in lineage differentiation outlined above[15,37,98]. Future research investigating contemporary reproductive barriers by studying reproductive phenology and inter-lineage crosses and backcrosses are warranted. No studies to date have investigated inter-lineage hybrid fitness and only one[48] has examined hybrid sterility in cryptic lineages. Natural history observations, including spawn timing, egg size and buoyancy, and cross-fertilization assays will be key to determining the factors driving cryptic lineage persistence in corals. Additionally, using demographic tools on existing single nucleotide polymorphism (SNP) data[16,122,123] can disentangle divergence scenarios and reveal genomic signatures associated with the evolution of cryptic coral lineages through time across environments (Box 2).

Challenges and opportunities presented by cryptic diversity

The prevalence of cryptic coral lineages and paucity of knowledge surrounding their relative distributions profoundly limits biodiversity estimations, which can lead to dramatic underestimation of biodiversity loss following large-scale mortality events and complicates assessments of reef diversity in response to disturbances. The presence of cryptic lineages can also cloud interpretations of 'winners' and 'losers' during coral bleaching events[64,124]. For example, not accounting for the presence of cryptic lineages would have led to the conclusion that massive *Porites* had relatively low mortality during a severe bleaching episode compared with other species in the same region[125].

Yet, sequencing revealed that one lineage experienced 75% mortality island-wide, while overall mortality of other massive *Porites* lineages was only 20%[57]. Systematic quantification of cryptic lineages, their distributions and their microbial partners over large environmental scales is needed to identify baseline levels of biodiversity, understand coral bleaching patterns, predict future coral distributions, and design successful conservation and restoration efforts.

Going forward, we have identified five questions that are critical for understanding the processes shaping cryptic speciation in corals and their repercussions for coral reef management:

1. How much of our understanding of coral ecology and evolution is confounded by the presence of diverse cryptic lineages?
2. How often do cryptic lineages differ in thermal tolerance (and other key adaptations) across the anthozoan tree of life, and what are the trade-offs?
3. How do patterns of symbiont and microbiome associations shape ecological functions and evolutionary trajectories of cryptic lineages, and what are the relative contributions of host, symbiont and microbiome to these differences?
4. What are the biophysical and molecular mechanisms driving cryptic lineage divergence, and how do they evolve and coexist in sympatry?
5. How can cryptic species be harnessed to bolster coral conservation and restoration?

Given that cryptic lineages represent distinct evolutionary units with unique functional traits, it is important to explicitly account for them when designing studies and conducting analyses. In population genetics studies, cryptic lineages must first be identified and then partitioned into lineages to accurately assess effective population sizes, fixation index (F_{ST}), gene flow and so on (for example, refs. 4,13,16,41). We also strongly advocate for the use of molecular tools to identify cryptic lineages in ecological studies, and especially when quantifying species responses to climate change[14,20,21,39,56,57]. Assessing host lineages is probably equally important to the identification of Symbiodiniaceae species within corals[14,20,25,39,88], and when conducted in concert, these host–symbiont pairings have the potential to transform our understanding and propel the field forward. That said, molecular tools can be laborious and expensive, and represent a substantial barrier to research progress. When possible, we encourage the development of low-cost rapid tools for lineage identification, including diagnostic morphological traits (Box 1) or rapid genetic assays (Box 2). Observational data such as reproductive compatibility and larval development and settlement dynamics are also essential to understanding cryptic coral lineages. Low-cost resources will increase accessibility, equity and inclusion, and will maximize research capital to better understand how cryptic diversity may shape coral reef responses under future global change.

When reporting the presence of cryptic lineages, we urge the use of clear and consistent language to prevent confusion. We suggest using the term 'cryptic lineage' when distinct sympatric populations are identified. Newly identified lineages awaiting formal descriptions should have voucher specimens, field images and reference sequence data (or archived DNA) to examine potential morphological differences between putatively cryptic species[8,126]. Additionally, newly uncovered cryptic lineages should be compared with junior species synonyms to prevent the assignment of novel names to previously described species[8,127]. Extraction of ancient DNA may facilitate comparison to historic voucher specimens if tissue samples are not available[128]. Integration among datasets and international collaboration to provide access to resources will prevent the duplication of work, and facilitate discoveries of phylogenetically informative characters and genes to develop a more robust taxonomic framework. In some genera, taxonomic revisions may be necessary.

Given the uneven distributions of cryptic lineages, conservation strategies should aim to preserve coral diversity across diverse habitat types, including marginal habitats such as shallow lagoons that tend to harbour lineages adapted to elevated temperatures[5] (Fig. 1). The designation of marine protected areas, for example, may help mitigate the effects of climate change by eliminating compounding local stressors, including pollution and overfishing[129,130]. Such local conservation efforts may facilitate natural dispersal and range expansion of thermally tolerant lineages as temperatures increase, and may in some cases provide genetic rescue[5,131,132].

As practitioners and scientists increasingly discuss coral translocations[133], it is critical to recognize that ecological specialization of cryptic lineages may strongly influence coral transplant success (for example, ref. 16). Not accounting for this may lead to widespread mortality of transplanted corals[44], which is costly in terms of coral loss, effort and funding. Additionally, if transplantation goals are aimed at increasing local genetic diversity via cross-fertilization of local corals with transplants, these cryptic lineages may not interbreed due to a variety of pre- and postzygotic mechanisms (discussed in the previous section).

In cases where lineages can hybridize, estimates of standing genetic diversity upon which selection can act may currently be misrepresented, resulting in an underestimation of the evolutionary potential of many coral species complexes. Hybridization between closely related non-cryptic species has been proposed to promote reticulate evolution in corals[11,12]. For example, *Acropora palmata* and *A. cervicornis* can successfully hybridize to form *A. prolifera*[107,134], and these hybrids can become dominant on Caribbean reefs[135,136]. If different lineages can cross-fertilize, even via ex situ spawning efforts, this recombination of genomes might offer novel genetic variation.

Finally, it is important to acknowledge that the level of crypsis recently reported in corals is by no means exclusive to cnidarians or marine taxa. Cryptic lineages have been identified in many eukaryotic phyla, ranging from amoebae[137] to elephants[138]. The pervasiveness of hidden diversity in the tree of life[139] suggests that this diversity may affect ecosystem function and responses to anthropogenic change. Leveraging this cryptic diversity can bolster conservation and restoration efforts, especially in critically endangered ecosystems such as coral reefs. We therefore hope that these findings provide cautious optimism for coral reef conservation in the Anthropocene and encourage researchers to reevaluate research priorities for coral biology and conservation.

References

1. Mayo, S. J. & Monro, A. K. *Cryptic Species: Morphological Stasis, Circumscription, and Hidden Diversity* (Cambridge Univ. Press, 2022).
2. Mayr, E., Linsley, E. G. & Usinger, R. L. *Methods and Principles of Systematic Zoology* (McGraw-Hill, 1953).
3. Bickford, D. et al. Cryptic species as a window on diversity and conservation. *Trends Ecol. Evol.* **22**, 148–155 (2007).
4. Gijsbers, J. C. et al. Global phylogenomic assessment of *Leptoseris* and *Agaricia* reveals substantial undescribed diversity at mesophotic depths. *BMC Biol.* **21**, 147 (2023).
5. Colton, M. A. et al. Coral conservation in a warming world must harness evolutionary adaptation. *Nat. Ecol. Evol.* **6**, 1405–1407 (2022).
6. Epstein, N., Bak, R. P. M. & Rinkevich, B. Applying forest restoration principles to coral reef rehabilitation. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **13**, 387–395 (2003).
7. Struck, T. H. et al. Finding Evolutionary Processes Hidden in Cryptic Species. *Trends Ecol. Evol.* **33**, 153–163 (2018).
8. Bonito, V. E., Baird, A. H., Bridge, T., Cowman, P. F. & Fenner, D. Types, topotypes and vouchers are the key to progress in coral taxonomy: Comment on Wepfer et al. (2020). *Mol. Phylogenet. Evol.* **159**, 107104 (2021).
9. Hobbs, J.-P. A. et al. Hybridisation and the evolution of coral reef biodiversity. *Coral Reefs* **41**, 535–549 (2022).

10. Quattrini, A. M. et al. A next generation approach to species delimitation reveals the role of hybridization in a cryptic species complex of corals. *BMC Evol. Biol.* **19**, 116 (2019).
11. Vollmer, S. V. & Palumbi, S. R. Hybridization and the evolution of reef coral diversity. *Science* **296**, 2023–2025 (2002).
12. Willis, B. L., Van Oppen, M. J. H., Miller, D. J., Vollmer, S. V. & Ayre, D. J. The role of hybridization in the evolution of reef corals. *Annu. Rev. Ecol. Evol. Syst.* **37**, 489–517 (2006).
13. Bongaerts, P. et al. Morphological stasis masks ecologically divergent coral species on tropical reefs. *Curr. Biol.* **31**, 2286–2298 (2021).
14. Gómez-Corrales, M. & Prada, C. Cryptic lineages respond differently to coral bleaching. *Mol. Ecol.* **29**, 4265–4273 (2020).
15. Prada, C. & Hellberg, M. E. Speciation-by-depth on coral reefs: sympatric divergence with gene flow or cryptic transient isolation? *J. Evol. Biol.* **34**, 128–137 (2021).
16. Rippe, J. P., Dixon, G., Fuller, Z. L., Liao, Y. & Matz, M. Environmental specialization and cryptic genetic divergence in two massive coral species from the Florida Keys Reef Tract. *Mol. Ecol.* **30**, 3468–3484 (2021).
17. Johnston, E. C., Wyatt, A. S. J., Leichter, J. J. & Burgess, S. C. Niche differences in co-occurring cryptic coral species (*Pocillopora* spp.). *Coral Reefs* **41**, 767–778 (2022).
18. Elmqvist, T. et al. Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* **1**, 488–494 (2003).
19. Burgess, S. C., Johnston, E. C., Wyatt, A. S. J., Leichter, J. J. & Edmunds, P. J. Response diversity in corals: hidden differences in bleaching mortality among cryptic *Pocillopora* species. *Ecology* **102**, e03324 (2021).
20. Rose, N. H. et al. Genomic analysis of distinct bleaching tolerances among cryptic coral species. *Proc. R. Soc. B.* **288**, 20210678 (2021).
21. Rivera, H. E. et al. Palau's warmest reefs harbor thermally tolerant corals that thrive across different habitats. *Commun. Biol.* **5**, 1394 (2022).
22. Voolstra, C. R. et al. Contrasting heat stress response patterns of coral holobionts across the Red Sea suggest distinct mechanisms of thermal tolerance. *Mol. Ecol.* **30**, 4466–4480 (2021).
23. Aichelman, H. *Exploring Coral Symbiosis Under Climate Change Stress Across Spatial and Temporal Scales*. PhD dissertation, Boston Univ. (2023).
24. Prada, C. et al. Cryptic diversity hides host and habitat specialization in a gorgonian–algal symbiosis. *Mol. Ecol.* **23**, 3330–3340 (2014).
25. Palacio-Castro, A. M. et al. Increased dominance of heat-tolerant symbionts creates resilient coral reefs in near-term ocean warming. *Proc. Natl Acad. Sci. USA* **120**, e2202388120 (2023).
26. Johnston, E. C., Cunning, R. & Burgess, S. C. Cophylogeny and specificity between cryptic coral species (*Pocillopora* spp.) at Mo'orea and their symbionts (Symbiodiniaceae). *Mol. Ecol.* **31**, 5368–5385 (2022).
27. Hoegh-Guldberg, O. Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshw. Res.* **50**, 839–866 (1999).
28. Weis, V. M. Cellular mechanisms of cnidarian bleaching: stress causes the collapse of symbiosis. *J. Exp. Biol.* **211**, 3059–3066 (2008).
29. Knowlton, N. Sibling species in the sea. *Annu. Rev. Ecol. Evol. Syst.* **189**, 189–216 (1993).
30. Arrigoni, R., Berumen, M. L., Stolarski, J., Terraneo, T. I. & Benzoni, F. Uncovering hidden coral diversity: a new cryptic lobophylliid scleractinian from the Indian Ocean. *Cladistics* **35**, 301–328 (2019).
31. Miller, K. J. & Benzie, J. A. H. No clear genetic distinction between morphological species within the coral genus *Platygyra*. *Bull. Mar. Sci.* **6**, 907–917 (1997).
32. Fukami, H. et al. 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 (2008).
33. Huang, D., Licuanan, W. Y., Baird, A. H. & Fukami, H. Cleaning up the 'Bigmessidae': molecular phylogeny of scleractinian corals from Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae. *BMC Evol. Biol.* **11**, 37 (2011).
34. Van Oppen, M. J. H., Koolmees, E. M. & Veron, J. E. N. Patterns of evolution in the scleractinian coral genus *Montipora* (Acroporidae). *Mar. Biol.* **144**, 9–18 (2004).
35. Cunha, R. L. et al. Rare coral under the genomic microscope: timing and relationships among Hawaiian *Montipora*. *BMC Evol. Biol.* **19**, 153 (2019).
36. Forsman, Z. H. et al. Ecomorph or endangered coral? DNA and microstructure reveal Hawaiian species complexes: *Montipora dilatata/flabellata/turgescens* & *M. patula/verrilli*. *PLoS ONE* **5**, e15021 (2010).
37. Matias, A. M. A. et al. Cryptic diversity and spatial genetic variation in the coral *Acropora tenuis* and its endosymbionts across the Great Barrier Reef. *Evol. Appl.* **16**, 293–310 (2023).
38. Ladner, J. T. & Palumbi, S. R. Extensive sympatry, cryptic diversity and introgression throughout the geographic distribution of two coral species complexes. *Mol. Ecol.* **21**, 2224–2238 (2012).
39. Boulay, J. N., Hellberg, M. E., Cortés, J. & Baums, I. B. Unrecognized coral species diversity masks differences in functional ecology. *Proc. R. Soc. B.* **281**, 20131580 (2014).
40. Prada, C., Schizas, N. V. & Yoshioka, P. M. Phenotypic plasticity or speciation? A case from a clonal marine organism. *BMC Evol. Biol.* **8**, 47 (2008).
41. Fifer, J. E., Yasuda, N., Yamakita, T., Bove, C. B. & Davies, S. W. Genetic divergence and range expansion in a western North Pacific coral. *Sci. Total Environ.* **813**, 152423 (2022).
42. Frade, P. R. et al. Semi-permeable species boundaries in the coral genus *Madracis*: introgression in a brooding coral system. *Mol. Phylogenet. Evol.* **57**, 1072–1090 (2010).
43. Bongaerts, P. et al. Genetic divergence across habitats in the widespread coral *Seriatopora hystrix* and its associated *Symbiodinium*. *PLoS ONE* **5**, e10871 (2010).
44. Prada, C. & Hellberg, M. E. Long prereproductive selection and divergence by depth in a Caribbean candelabrum coral. *Proc. Natl Acad. Sci. USA* **110**, 3961–3966 (2013).
45. Prada, C. & Hellberg, M. E. Strong natural selection on juveniles maintains a narrow adult hybrid zone in a broadcast spawner. *Am. Nat.* **184**, 702–713 (2014).
46. Bongaerts, P. et al. Adaptive divergence in a scleractinian coral: physiological adaptation of *Seriatopora hystrix* to shallow and deep reef habitats. *BMC Evol. Biol.* **11**, 303 (2011).
47. Serrano, X. et al. Geographic differences in vertical connectivity in the Caribbean coral *Montastraea cavernosa* despite high levels of horizontal connectivity at shallow depths. *Mol. Ecol.* **23**, 4226–4240 (2014).
48. Suzuki, G. et al. Genetic evidence of peripheral isolation and low diversity in marginal populations of the *Acropora hyacinthus* complex. *Coral Reefs* **35**, 1419–1432 (2016).
49. Nakabayashi, A. et al. The potential role of temperate Japanese regions as refugia for the coral *Acropora hyacinthus* in the face of climate change. *Sci. Rep.* **9**, 1892 (2019).
50. Schoepf, V. et al. Corals at the edge of environmental limits: a new conceptual framework to re-define marginal and extreme coral communities. *Sci. Total Environ.* **884**, 163688 (2023).
51. Gold, Z. & Palumbi, S. R. Long-term growth rates and effects of bleaching in *Acropora hyacinthus*. *Coral Reefs* **37**, 267–277 (2018).

52. Knowlton, N., Weil, E., Weigt, L. A. & Guzmán, H. M. Sibling species in *Montastraea annularis*, coral bleaching, and the coral climate record. *Science* **255**, 330–333 (1992).
53. Scucchia, F. et al. The role and risks of selective adaptation in extreme coral habitats. *Nat. Commun.* **14**, 4475 (2023).
54. Van Oppen, M. J. et al. Adaptation to reef habitats through selection on the coral animal and its associated microbiome. *Mol. Ecol.* **27**, 2956–2971 (2018).
55. Iguchi, A. et al. RADseq population genomics confirms divergence across closely related species in blue coral (*Heliopora coerulea*). *BMC Evol. Biol.* **19**, 187 (2019).
56. Smith, H., Epstein, H. & Torda, G. The molecular basis of differential morphology and bleaching thresholds in two morphs of the coral *Pocillopora acuta*. *Sci. Rep.* **7**, 10066 (2017).
57. Starko, S. et al. Marine heatwaves threaten cryptic coral diversity and erode associations amongst coevolving partners. *Sci. Adv.* **9**, eadf0954 (2023).
58. Forsman, Z. H., Ritson-Williams, R., Tisthammer, K. H., Knapp, I. S. S. & Toonen, R. J. Host–symbiont coevolution, cryptic structure, and bleaching susceptibility, in a coral species complex (Scleractinia; Poritidae). *Sci. Rep.* **10**, 16995 (2020).
59. Schoepf, V. et al. Thermally variable, macrotidal reef habitats promote rapid recovery from mass coral bleaching. *Front. Mar. Sci.* **7**, 245 (2020).
60. Dziedzic, K. E., Elder, H., Tavalire, H. & Meyer, E. Heritable variation in bleaching responses and its functional genomic basis in reef-building corals (*Orbicella faveolata*). *Mol. Ecol.* **28**, 2238–2253 (2019).
61. Traylor-Knowles, N., Rose, N. H., Sheets, E. A. & Palumbi, S. R. Early transcriptional responses during heat stress in the coral *Acropora hyacinthus*. *Biol. Bull.* **232**, 91–100 (2017).
62. Conti-Jerpe, I. E. et al. Trophic strategy and bleaching resistance in reef-building corals. *Sci. Adv.* **6**, eaaz5443 (2020).
63. Grottoli, A. G., Rodrigues, L. J. & Palardy, J. E. Heterotrophic plasticity and resilience in bleached corals. *Nature* **440**, 1186–1189 (2006).
64. Loya, Y. et al. Coral bleaching: the winners and the losers. *Ecol. Lett.* **4**, 122–131 (2001).
65. Darling, E. S., Alvarez-Filip, L., Oliver, T. A., McClanahan, T. R. & Côté, I. M. Evaluating life-history strategies of reef corals from species traits. *Ecol. Lett.* **15**, 1378–1386 (2012).
66. Anthony, K. R. N., Hoogenboom, M. O., Maynard, J. A., Grottoli, A. G. & Middlebrook, R. Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. *Funct. Ecol.* **23**, 539–550 (2009).
67. Scheufen, T., Krämer, W. E., Iglesias-Prieto, R. & Enríquez, S. Seasonal variation modulates coral sensibility to heat-stress and explains annual changes in coral productivity. *Sci. Rep.* **7**, 4937 (2017).
68. Enríquez, S., Méndez, E. R., Hoegh-Guldberg, O. & Iglesias-Prieto, R. Key functional role of the optical properties of coral skeletons in coral ecology and evolution. *Proc. R. Soc. B.* **284**, 20161667 (2017).
69. Budd, A. F. & Pandolfi, J. M. Evolutionary novelty is concentrated at the edge of coral species distributions. *Science* **328**, 1558–1561 (2010).
70. Huang, D. et al. Taxonomic classification of the reef coral families Merulinidae, Montastraeidae, and Diploastraeidae (Cnidaria: Anthozoa: Scleractinia): taxonomy of reef corals. *Zool. J. Linn. Soc.* **171**, 277–355 (2014).
71. Ramírez-Portilla, C. et al. Quantitative three-dimensional morphological analysis supports species discrimination in complex-shaped and taxonomically challenging corals. *Front. Mar. Sci.* **9**, 955582 (2022).
72. Ramírez-Portilla, C. et al. Solving the coral species delimitation conundrum. *Syst. Biol.* **71**, 461–475 (2022).
73. Lachs, L. et al. No apparent trade-offs associated with heat tolerance in a reef-building coral. *Commun. Biol.* **6**, 400 (2023).
74. Grupstra, C. G. B. et al. Thermal stress triggers productive viral infection of a key coral reef symbiont. *ISME J.* **16**, 1430–1441 (2022).
75. Van Oppen, M. J. H. & Medina, M. Coral evolutionary responses to microbial symbioses. *Phil. Trans. R. Soc. B* **375**, 20190591 (2020).
76. Voolstra, C. R. et al. Extending the natural adaptive capacity of coral holobionts. *Nat. Rev. Earth Environ.* **2**, 747–762 (2021).
77. Howe-Kerr, L. I. et al. Viruses of a key coral symbiont exhibit temperature-driven productivity across a reefscape. *ISME Commun.* **3**, 27 (2023).
78. Kwong, W. K., Del Campo, J., Mathur, V., Vermeij, M. J. A. & Keeling, P. J. A widespread coral-infecting apicomplexan with chlorophyll biosynthesis genes. *Nature* **568**, 103–107 (2019).
79. Silverstein, R. N., Cunning, R. & Baker, A. C. Change in algal symbiont communities after bleaching, not prior heat exposure, increases heat tolerance of reef corals. *Glob. Change Biol.* **21**, 236–249 (2015).
80. Manzello, D. P. et al. Role of host genetics and heat-tolerant algal symbionts in sustaining populations of the endangered coral *Orbicella faveolata* in the Florida Keys with ocean warming. *Glob. Change Biol.* **25**, 1016–1031 (2019).
81. Jones, A. & Berkelmans, R. Potential costs of acclimatization to a warmer climate: growth of a reef coral with heat tolerant vs. sensitive symbiont types. *PLoS ONE* **5**, e10437 (2010).
82. Shore-Maggio, A., Callahan, S. M. & Aeby, G. S. Trade-offs in disease and bleaching susceptibility among two color morphs of the Hawaiian reef coral, *Montipora capitata*. *Coral Reefs* **37**, 507–517 (2018).
83. Rouzé, H., Lecellier, G., Saulnier, D. & Berteaux-Lecellier, V. Symbiodinium clades A and D differentially predispose *Acropora cytherea* to disease and *Vibrio* spp. colonization. *Ecol. Evol.* **6**, 560–572 (2016).
84. Ziegler, M. et al. Coral bacterial community structure responds to environmental change in a host-specific manner. *Nat. Commun.* **10**, 3092 (2019).
85. Ziegler, M., Seneca, F. O., Yum, L. K., Palumbi, S. R. & Voolstra, C. R. Bacterial community dynamics are linked to patterns of coral heat tolerance. *Nat. Commun.* **8**, 14213 (2017).
86. Peixoto, R. S. et al. Coral probiotics: premise, promise, prospects. *Annu. Rev. Anim. Biosci.* **9**, 265–288 (2021).
87. Peixoto, R., Rosado, P., Leite, D., Rosado, A. S. & Bourne, D. Beneficial microorganisms for corals (BMC): proposed mechanisms for coral health and resilience. *Front. Microbiol.* **8**, 341 (2017).
88. Davies, S. W. et al. Building consensus around the assessment and interpretation of Symbiodiniaceae diversity. *PeerJ* **11**, e15023 (2023).
89. Fujise, L. et al. Unlocking the phylogenetic diversity, primary habitats, and abundances of free-living Symbiodiniaceae on a coral reef. *Mol. Ecol.* **30**, 343–360 (2021).
90. Grupstra, C. G. B., Rabbitt, K. M., Howe-Kerr, L. I. & Correa, A. M. S. Fish predation on corals promotes the dispersal of coral symbionts. *Anim. Microbiome* **3**, 25 (2021).
91. Quigley, K. M., Bay, L. K. & Willis, B. L. Temperature and water quality-related patterns in sediment-associated Symbiodinium communities impact symbiont uptake and fitness of juveniles in the genus *Acropora*. *Front. Mar. Sci.* **4**, 401 (2017).
92. Davies, S. W., Moreland, K. N., Wham, D. C., Kanke, M. R. & Matz, M. V. *Cladocopium* community divergence in two *Acropora* coral hosts across multiple spatial scales. *Mol. Ecol.* **29**, 4559–4572 (2020).
93. Pollock, F. J. et al. Coral-associated bacteria demonstrate phylosymbiosis and cophylogeny. *Nat. Commun.* **9**, 4921 (2018).

94. Buitrago-López, C. et al. Disparate population and holobiont structure of pocilloporid corals across the Red Sea gradient demonstrate species-specific evolutionary trajectories. *Mol. Ecol.* **32**, 2151–2173 (2023).
95. Pogoreutz, C. et al. Coral holobiont cues prime *Endozoicomonas* for a symbiotic lifestyle. *ISME J.* **16**, 1883–1895 (2022).
96. Maire, J. et al. Colocalization and potential interactions of *Endozoicomonas* and chlamydiae in microbial aggregates of the coral *Pocillopora acuta*. *Sci. Adv.* **9**, eadg0773 (2023).
97. Bove, C. B., Ingersoll, M. V. & Davies, S. W. Help me, symbionts, you're my only hope: approaches to accelerate our understanding of coral holobiont interactions. *Integr. Comp. Biol.* **62**, 1756–1769 (2022).
98. Prata, K. E. et al. Deep connections: divergence histories with gene flow in mesophotic *Agaricia* corals. *Mol. Ecol.* **31**, 2511–2527 (2022).
99. Richards, E. J., Servedio, M. R. & Martin, C. H. Searching for sympatric speciation in the genomic era. *BioEssays* **41**, 1900047 (2019).
100. Pinho, C. & Hey, J. Divergence with gene flow: models and data. *Annu. Rev. Ecol. Evol. Syst.* **41**, 215–230 (2010).
101. Schluter, D. Ecological character displacement in adaptive radiation. *Am. Nat.* **156**, S4–S16 (2000).
102. Kulmuni, J. & Westram, A. M. Intrinsic incompatibilities evolving as a by-product of divergent ecological selection: considering them in empirical studies on divergence with gene flow. *Mol. Ecol.* **26**, 3093–3103 (2017).
103. Veron, J. E. N. et al. Delineating the coral triangle. *Galaxea J. Coral Reef. Stud.* **11**, 91–100 (2009).
104. Richmond, R. H. in *Life and Death of Coral Reefs* (ed. Birkeland, C.) 175–197 (Chapman & Hall, 1997).
105. Golbuu, Y., Gouezo, M., Kurihara, H., Rehm, L. & Wolanski, E. Long-term isolation and local adaptation in Palau's Nikko Bay help corals thrive in acidic waters. *Coral Reefs* **35**, 909–918 (2016).
106. Chan, W. Y., Peplow, L. M. & Van Oppen, M. J. H. Interspecific gamete compatibility and hybrid larval fitness in reef-building corals: implications for coral reef restoration. *Sci. Rep.* **9**, 4757 (2019).
107. Fogarty, N. D., Vollmer, S. V. & Levitan, D. R. Weak prezygotic isolating mechanisms in threatened caribbean *Acropora* corals. *PLoS ONE* **7**, e30486 (2012).
108. Swanson, W. J. & Vacquier, V. D. The abalone egg vitelline envelope receptor for sperm lysin is a giant multivalent molecule. *Proc. Natl Acad. Sci. USA* **94**, 6724–6729 (1997).
109. Vacquier, V. D. & Moy, G. W. Isolation of bindin: the protein responsible for adhesion of sperm to sea urchin eggs. *Proc. Natl Acad. Sci. USA* **74**, 2456–2460 (1977).
110. Rosser, N. L. Asynchronous spawning in sympatric populations of a hard coral reveals cryptic species and ancient genetic lineages. *Mol. Ecol.* **24**, 5006–5019 (2015).
111. Furukawa, M., Ohki, S., Kitanobo, S., Fukami, H. & Morita, M. Differences in spawning time drive cryptic speciation in the coral *Acropora divaricata*. *Mar. Biol.* **167**, 163 (2020).
112. Ohki, S., Kowalski, R. K., Kitanobo, S. & Morita, M. Changes in spawning time led to the speciation of the broadcast spawning corals *Acropora digitifera* and the cryptic species *Acropora* sp. 1 with similar gamete recognition systems. *Coral Reefs* **34**, 1189–1198 (2015).
113. Abe, M., Watanabe, T., Hayakawa, H. & Hidaka, M. Breeding experiments of hermatypic coral *Galaxea fascicularis*: partial reproductive isolation between colonies of different nematocyst types and enhancement of fertilization success by presence of parental colonies. *Fish. Sci.* **74**, 1342–1344 (2008).
114. Watanabe, T., Nishida, M., Watanabe, K., Wewengkang, D. S. & Hidaka, M. Polymorphism in nucleotide sequence of mitochondrial intergenic region in scleractinian coral (*Galaxea fascicularis*). *Mar. Biotechnol.* **7**, 33–39 (2005).
115. Levitan, D. R. et al. Mechanisms of reproductive isolation among sympatric broadcast-spawning corals of the *Montastraea annularis* species complex. *Evolution* **58**, 308–323 (2004).
116. Levitan, D. R., Fogarty, N. D., Jara, J., Lotterhos, K. E. & Knowlton, N. Genetic, spatial, and temporal components of precise spawning synchrony in reef building corals of the *Montastraea annularis* species complex. *Evolution* **65**, 1254–1270 (2011).
117. Turelli, M. & Orr, H. A. Dominance, epistasis and the genetics of postzygotic isolation. *Genetics* **154**, 1663–1679 (2000).
118. Wu, C.-I. The genic view of the process of speciation. *J. Evol. Biol.* **14**, 851–865 (2001).
119. Wolf, J. B. W. & Ellegren, H. Making sense of genomic islands of differentiation in light of speciation. *Nat. Rev. Genet.* **18**, 87–100 (2017).
120. Guerrero, R. F. & Hahn, M. W. Speciation as a sieve for ancestral polymorphism. *Mol. Ecol.* **26**, 5362–5368 (2017).
121. Cruickshank, T. E. & Hahn, M. W. Reanalysis suggests that genomic islands of speciation are due to reduced diversity, not reduced gene flow. *Mol. Ecol.* **23**, 3133–3157 (2014).
122. Jouganous, J., Long, W., Ragsdale, A. P. & Gravel, S. Inferring the joint demographic history of multiple populations: beyond the diffusion approximation. *Genetics* **206**, 1549–1567 (2017).
123. Gutenkunst, R. N. dadi.CUDA: accelerating population genetics inference with graphics processing units. *Mol. Biol. Evol.* **38**, 2177–2178 (2021).
124. Van Woesik, R., Sakai, K., Ganase, A. & Loya, Y. Revisiting the winners and the losers a decade after coral bleaching. *Mar. Ecol. Prog. Ser.* **434**, 67–76 (2011).
125. Baum, J. K. et al. Transformation of coral communities subjected to an unprecedented heatwave is modulated by local disturbance. *Sci. Adv.* **9**, eabq5615 (2023).
126. Voolstra, C. R. et al. Consensus guidelines for advancing coral holobiont genome and specimen voucher deposition. *Front. Mar. Sci.* **8**, 701784 (2021).
127. Bridge, T. C. L. et al. A *tenuis* relationship: traditional taxonomy obscures systematics and biogeography of the '*Acropora tenuis*' (Scleractinia: Acroporidae) species complex. *Zool. J. Linn. Soc.*, https://doi.org/10.1093/zoolinnean/zlad062 (2023).
128. Scott, C. B. et al. Millennia-old coral holobiont DNA provides insight into future adaptive trajectories. *Mol. Ecol.* **31**, 4979–4990 (2022).
129. Donovan, M. K. et al. Local conditions magnify coral loss after marine heatwaves. *Science* **372**, 977–980 (2021).
130. Donovan, M. K. et al. Nitrogen pollution interacts with heat stress to increase coral bleaching across the seascape. *Proc. Natl Acad. Sci. USA* **117**, 5351–5357 (2020).
131. Thomas, L. et al. Mechanisms of thermal tolerance in reef-building corals across a fine-grained environmental mosaic: lessons from Ofu, American Samoa. *Front. Mar. Sci.* **4**, 434 (2018).
132. van Woesik, R. et al. Climate-change refugia in the sheltered bays of Palau: analogs of future reefs. *Ecol. Evol.* **2**, 2474–2484 (2012).
133. Baums, I. B. et al. Considerations for maximizing the adaptive potential of restored coral populations in the western Atlantic. *Ecol. Appl.* **29**, e01978 (2019).
134. Fogarty, N. Caribbean acroporid coral hybrids are viable across life history stages. *Mar. Ecol. Prog. Ser.* **446**, 145–159 (2012).
135. Aguilar-Perera, A. & Hernández-Landa, R. C. Occurrence of large thickets of *Acropora prolifera* (Scleractinia: Acroporidae) in the southern Gulf of Mexico. *Mar. Biodivers.* **48**, 2203–2205 (2018).
136. Japaud, A., Fauvelot, C. & Bouchon, C. Unexpected high densities of the hybrid coral *Acropora prolifera* (Lamarck 1816) in Guadeloupe Island, Lesser Antilles. *Coral Reefs* **33**, 593–593 (2014).
137. Kalla, S. E., Queller, D. C., Lasagni, A. & Strassmann, J. E. Kin discrimination and possible cryptic species in the social amoeba *Polysphondylium violaceum*. *BMC Evol. Biol.* **11**, 31 (2011).

138. Roca, A. L., Georgiadis, N., Pecon-Slattery, J. & O'Brien, S. J. Genetic evidence for two species of elephant in Africa. *Science* **293**, 1473–1477 (2001).
139. Pfenninger, M. & Schwenk, K. Cryptic animal species are homogeneously distributed among taxa and biogeographical regions. *BMC Evol. Biol.* **7**, 121 (2007).
140. Pipithkul, S. et al. High clonality and geographically separated cryptic lineages in the threatened temperate coral, *Acropora pruinosa*. *Front. Mar. Sci.* **8**, 668043 (2021).
141. Rosser, N. L. et al. Phylogenomics provides new insight into evolutionary relationships and genealogical discordance in the reef-building coral genus *Acropora*. *Proc. R. Soc. B* **284**, 20162182 (2017).
142. Rosser, N. L., Edyvane, K., Malina, A. C., Underwood, J. N. & Johnson, M. S. Geography and spawning season drive genetic divergence among populations of the hard coral *Acropora tenuis* from Indonesia and Western Australia. *Coral Reefs* **39**, 989–999 (2020).
143. Gilmour, J. P., Underwood, J. N., Howells, E. J., Gates, E. & Heyward, A. J. Biannual spawning and temporal reproductive isolation in *Acropora* corals. *PLoS ONE* **11**, e0150916 (2016).
144. Suzuki, G. & Fukami, H. Evidence of genetic and reproductive isolation between two morphs of subtropical-dominant coral *Acropora solitaryensis* in the non-reef region of Japan. *Zool. Sci.* **29**, 134–140 (2012).
145. Nakajima, Y., Nishikawa, A., Iguchi, A. & Sakai, K. Regional genetic differentiation among northern high-latitude island populations of a broadcast-spawning coral. *Coral Reefs* **31**, 1125–1133 (2012).
146. Richards, Z. T., Berry, O. & van Oppen, M. J. H. Cryptic genetic divergence within threatened species of *Acropora* coral from the Indian and Pacific Oceans. *Conserv. Genet.* **17**, 577–591 (2016).
147. Zayasu, Y. et al. Genome-wide SNP genotyping reveals hidden population structure of an acroporid species at a subtropical coral island: implications for coral restoration. *Aquat. Conserv.* **31**, 2429–2439 (2021).
148. Sheets, E. A., Warner, P. A. & Palumbi, S. R. Accurate population genetic measurements require cryptic species identification in corals. *Coral Reefs* **37**, 549–563 (2018).
149. Mitsuki, Y. et al. Distinct species hidden in the widely distributed coral *Coelastrea aspera*. *Invertebr. Syst.* **35**, 876–891 (2021).
150. Carlon, D. B. & Lippé, C. Estimation of mating systems in short and tall ecomorphs of the coral *Favia fragum*. *Mol. Ecol.* **20**, 812–828 (2011).
151. Carlon, D. B. & Budd, A. F. Incipient speciation across a depth gradient in a scleractinian coral? *Evolution* **56**, 2227–2242 (2002).
152. Teschima, M. M., Zilberberg, C. & Nunes, F. L. D. Strong genetic differentiation demarks populations of *Favia* across biogeographic regions of the Atlantic Ocean. *Coral Reefs* **41**, 523–534 (2022).
153. Grinblat, M. et al. Biogeography, reproductive biology and phylogenetic divergence within the Fungiidae (mushroom corals). *Mol. Phylogenet. Evol.* **164**, 107265 (2021).
154. Oku, Y. et al. *Fungia fungites* (Linnaeus, 1758) (Scleractinia, Fungiidae) is a species complex that conceals large phenotypic variation and a previously unrecognized genus. *Contrib. Zool.* **89**, 188–209 (2020).
155. Wepfer, P. H. et al. Evolutionary biogeography of the reef-building coral genus *Galaxea* across the Indo-Pacific Ocean. *Mol. Phylogenet. Evol.* **151**, 106905 (2020).
156. Nakajima, Y., Zayasu, Y., Shinzato, C., Satoh, N. & Mitarai, S. Genetic differentiation and connectivity of morphological types of the broadcast-spawning coral *Galaxea fascicularis* in the Nansei Islands, Japan. *Ecol. Evol.* **6**, 1457–1469 (2016).
157. Nakajima, Y., Shinzato, C., Satoh, N. & Mitarai, S. Novel polymorphic microsatellite markers reveal genetic differentiation between two sympatric types of *Galaxea fascicularis*. *PLoS ONE* **10**, e0130176 (2015).
158. Bongaerts, P. et al. Prevalent endosymbiont zonation shapes the depth distributions of scleractinian coral species. *R. Soc. Open Sci.* **2**, 140297 (2015).
159. Frade, P. R., Bongaerts, P., Winkelhagen, A. J. S., Tonk, L. & Bak, R. P. M. In situ photobiology of corals over large depth ranges: a multivariate analysis on the roles of environment, host, and algal symbiont. *Limnol. Oceanogr.* **53**, 2711–2723 (2008).
160. Weil, E. & Knowlton, N. A multi-character analysis of the Caribbean coral *Montastraea annularis* (Ellis and Solander, 1786) and its two sibling species, *M. faveolata* (Ellis and Solander, 1786) and *M. franksi* (Gregory, 1895). *Bull. Mar. Sci.* **55**, 151–175 (1994).
161. Feldman, B. et al. Distinct lineages and population genomic structure of the coral *Pachyseris speciosa* in the small equatorial reef system of Singapore. *Coral Reefs* **41**, 575–585 (2022).
162. Juszkiewicz, D. J. et al. Phylogeography of recent *Plesiastrea* (Scleractinia: Plesiastreidae) based on an integrated taxonomic approach. *Mol. Phylogenet. Evol.* **172**, 107469 (2022).
163. Voolstra, C. R. et al. Disparate genetic divergence patterns in three corals across a pan-Pacific environmental gradient highlight species-specific adaptation. *npj Biodivers.* **2**, 15 (2023).
164. Oury, N., Gélin, P. & Magalon, H. Cryptic species and genetic connectivity among populations of the coral *Pocillopora damicornis* (Scleractinia) in the tropical southwestern Pacific. *Mar. Biol.* **167**, 142 (2020).
165. Pinzón, J. H. & Lajeunesse, T. C. Species delimitation of common reef corals in the genus *Pocillopora* using nucleotide sequence phylogenies, population genetics and symbiosis ecology. *Mol. Ecol.* **20**, 311–325 (2011).
166. Pinzón, J. H. et al. Blind to morphology: genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). *J. Biogeogr.* **40**, 1595–1608 (2013).
167. Schmidt-Roach, S. et al. Assessing hidden species diversity in the coral *Pocillopora damicornis* from eastern Australia. *Coral Reefs* **32**, 161–172 (2013).
168. Gélin, P., Postaire, B., Fauvelot, C. & Magalon, H. 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 (2017).
169. Souter, P. Hidden genetic diversity in a key model species of coral. *Mar. Biol.* **157**, 875–885 (2010).
170. Gélin, P., Fauvelot, C., Bigot, L., Baly, J. & Magalon, H. From population connectivity to the art of striping Russian dolls: the lessons from *Pocillopora* corals. *Ecol. Evol.* **8**, 1411–1426 (2018).
171. Torda, G., Lundgren, P., Willis, B. L. & Van Oppen, M. J. H. Revisiting the connectivity puzzle of the common coral *Pocillopora damicornis*. *Mol. Ecol.* **22**, 5805–5820 (2013).
172. Thomas, L. et al. Population genetic structure of the *Pocillopora damicornis* morphospecies along Ningaloo Reef, Western Australia. *Mar. Ecol. Prog. Ser.* **513**, 111–119 (2014).
173. Serrano, X. M. et al. Long distance dispersal and vertical gene flow in the Caribbean brooding coral *Porites astreoides*. *Sci. Rep.* **6**, 21619 (2016).
174. Schweinsberg, M., Tollrian, R. & Lampert, K. P. Genetic variation in the massive coral *Porites lobata*. *Mar. Biol.* **163**, 242 (2016).
175. Tisthammer, K. H., Forsman, Z. H., Toonen, R. J. & Richmond, R. H. Genetic structure is stronger across human-impacted habitats than among islands in the coral *Porites lobata*. *PeerJ* **8**, e8550 (2020).
176. Afiq-Rosli, L. et al. Barriers and corridors of gene flow in an urbanized tropical reef system. *Evol. Appl.* **14**, 2502–2515 (2021).
177. Tisthammer, K. H. & Richmond, R. H. Corallite skeletal morphological variation in Hawaiian *Porites lobata*. *Coral Reefs* **37**, 445–456 (2018).

178. Camp, E. et al. Mangrove lagoons of the Great Barrier Reef support coral populations persisting under extreme environmental conditions. *Mar. Ecol. Prog. Ser.* **625**, 1–14 (2019).
179. Stefani, F., Benzoni, F., Pichon, M., Cancelliere, C. & Galli, P. A multidisciplinary approach to the definition of species boundaries in branching species of the coral genus *Psammocora* (Cnidaria, Scleractinia). *Zool. Scr.* **37**, 71–91 (2007).
180. Underwood, J. N., Richards, Z. T., Miller, K. J., Puotinen, M. L. & Gilmour, J. P. Genetic signatures through space, time and multiple disturbances in a ubiquitous brooding coral. *Mol. Ecol.* **27**, 1586–1602 (2018).
181. Warner, P. A., van Oppen, M. J. H. & Willis, B. L. Unexpected cryptic species diversity in the widespread coral *Seriatopora hystrix* masks spatial-genetic patterns of connectivity. *Mol. Ecol.* **24**, 2993–3008 (2015).
182. Sinniger, F., Prasetia, R., Yorifuji, M., Bongaerts, P. & Harii, S. *Seriatopora* diversity preserved in upper mesophotic coral ecosystems in southern Japan. *Front. Mar. Sci.* **4**, 155 (2017).
183. Nakajima, Y. et al. Elucidating the multiple genetic lineages and population genetic structure of the brooding coral *Seriatopora* (Scleractinia: Pocilloporidae) in the Ryukyu Archipelago. *Coral Reefs* **36**, 415–426 (2017).
184. Stefani, F. et al. Comparison of morphological and genetic analyses reveals cryptic divergence and morphological plasticity in *Stylophora* (Cnidaria, Scleractinia). *Coral Reefs* **30**, 1033–1049 (2011).
185. Keshavmurthy, S. et al. DNA barcoding reveals the coral 'laboratory-rat', *Stylophora pistillata* encompasses multiple identities. *Sci. Rep.* **3**, 1520 (2013).
186. Flot, J.-F. et al. Incongruence between morphotypes and genetically delimited species in the coral genus *Stylophora*: phenotypic plasticity, morphological convergence, morphological stasis or interspecific hybridization? *BMC Ecol.* **11**, 22 (2011).
187. Taninaka, H. et al. Phylogeography of blue corals (genus *Heliopora*) across the Indo-West Pacific. *Front. Mar. Sci.* **8**, 714662 (2021).
188. Yasuda, N. et al. Genetic diversity, paraphyly and incomplete lineage sorting of mtDNA, ITS2 and microsatellite flanking region in closely related *Heliopora* species (Octocorallia). *Mol. Phylogenet. Evol.* **93**, 161–171 (2015).
189. Taninaka, H. et al. Limited fine-scale larval dispersal of the threatened brooding corals *Heliopora* spp. as evidenced by population genetics and numerical simulation. *Conserv. Genet.* **20**, 1449–1463 (2019).
190. Villanueva, R. D. Cryptic speciation in the stony octocoral *Heliopora coerulea*: temporal reproductive isolation between two growth forms. *Mar. Biodivers.* **46**, 503–507 (2016).
191. Yasuda, N. et al. Genetic structure and cryptic speciation in the threatened reef-building coral *Heliopora coerulea* along Kuroshio Current. *Bull. Mar. Sci.* **90**, 233–255 (2014).
192. Ruiz-Ramos, D. V., Saunders, M., Fisher, C. R. & Baums, I. B. Home bodies and wanderers: sympatric lineages of the deep-sea black coral *Leiopathes glaberrima*. *PLoS ONE* **10**, e0138989 (2015).
193. Quattrini, A. M. et al. Phylogeography of *Paramuricea*: the role of depth and water mass in the evolution and distribution of deep-sea corals. *Front. Mar. Sci.* **9**, 849402 (2022).
194. Mokhtar-Jamaï, K. et al. From global to local genetic structuring in the red gorgonian *Paramuricea clavata*: the interplay between oceanographic conditions and limited larval dispersal. *Mol. Ecol.* **20**, 3291–3305 (2011).
195. Coelho, M. A. G. et al. Not out of the Mediterranean: Atlantic populations of the gorgonian *Paramuricea clavata* are a separate sister species under further lineage diversification. *Ecol. Evol.* **13**, e9740 (2023).
196. Pelosi, J. A. et al. Fine-scale morphological, genomic, reproductive, and symbiont differences delimit the Caribbean octocorals *Plexaura homomalla* and *P. kükenthali*. *Coral Reefs* **41**, 635–653 (2022).
197. Fišer, C., Robinson, C. T. & Malard, F. Cryptic species as a window into the paradigm shift of the species concept. *Mol. Ecol.* **27**, 613–635 (2018).
198. Swift, H. F., Gómez Daglio, L. & Dawson, M. N. Three routes to crypsis: stasis, convergence, and parallelism in the *Mastigias* species complex (Scyphozoa, Rhizostomeae). *Mol. Phylogenet. Evol.* **99**, 103–115 (2016).
199. Huang, S., Roy, K., Valentine, J. W. & Jablonski, D. Convergence, divergence, and parallelism in marine biodiversity trends: integrating present-day and fossil data. *Proc. Natl Acad. Sci. USA* **112**, 4903–4908 (2015).
200. Todd, P. A. Morphological plasticity in scleractinian corals. *Biol. Rev.* **83**, 315–337 (2008).
201. Gault, J. A., Bentlage, B., Huang, D. & Kerr, A. M. Lineage-specific variation in the evolutionary stability of coral photosymbiosis. *Sci. Adv.* **7**, eabh4243 (2021).
202. Kayal, E. et al. Phylogenomics provides a robust topology of the major cnidarian lineages and insights on the origins of key organismal traits. *BMC Evol. Biol.* **18**, 68 (2018).
203. Budd, A. F., Romano, S. L., Smith, N. D. & Barbeitos, M. S. Rethinking the phylogeny of scleractinian corals: a review of morphological and molecular data. *Integr. Comp. Biol.* **50**, 411–427 (2010).
204. Hellberg, M. E. No variation and low synonymous substitution rates in coral mtDNA despite high nuclear variation. *BMC Evol. Biol.* **6**, 24 (2006).
205. Veron, J. E. N. *Corals of the World*, vol 1 (Australian Institute of Marine Science & CRR Qld. Pty. Ltd., 2000).
206. Johnston, E. C., Forsman, Z. H. & Toonen, R. J. A simple molecular technique for distinguishing species reveals frequent misidentification of Hawaiian corals in the genus *Pocillopora*. *PeerJ* **6**, e4355 (2018).
207. Knowlton, N. Thresholds and multiple stable states in coral reef community dynamics. *Am. Zool.* **32**, 674–682 (1992).
208. Leray, M. & Knowlton, N. DNA barcoding and metabarcoding of standardized samples reveal patterns of marine benthic diversity. *Proc. Natl Acad. Sci. USA* **112**, 2076–2081 (2015).
209. Quek, Z. B. R. & Huang, D. Application of phylogenomic tools to unravel anthozoan evolution. *Coral Reefs* **41**, 475–495 (2022).
210. Vollmer, S. V. & Palumbi, S. R. Testing the utility of internally transcribed spacer sequences in coral phylogenetics. *Mol. Ecol.* **13**, 2763–2772 (2004).
211. Arrigoni, R. et al. A new sequence data set of SSU rRNA gene for Scleractinia and its phylogenetic and ecological applications. *Mol. Ecol. Resour.* **17**, 1054–1071 (2017).
212. Matz, M. V. Fantastic beasts and how to sequence them: ecological genomics for obscure model organisms. *Trends Genet.* **34**, 121–132 (2018).
213. Alexander, D. H. & Lange, K. Enhancements to the ADMIXTURE algorithm for individual ancestry estimation. *BMC Bioinform.* **12**, 246 (2011).
214. Jombart, T. adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics* **24**, 1403–1405 (2008).
215. Pickrell, J. K. & Pritchard, J. K. Inference of population splits and mixtures from genome-wide allele frequency data. *PloS Genet.* **8**, e1002967 (2012).
216. Pritchard, J. K., Stephens, M. & Donnelly, P. Inference of population structure using multilocus genotype data. *Genetics* **155**, 945–959 (2000).
217. Knowlton, N. & Leray, M. in *Coral Reefs in the Anthropocene* (ed. Birkeland, C.) 117–132 (Springer, 2015).

218. Li, Z., Löytynoja, A., Fraimout, A. & Merilä, J. Effects of marker type and filtering criteria on Q_{ST}–F_{ST} comparisons. *R. Soc. Open Sci.* **6**, 190666 (2019).
219. Truett, G. E. et al. Preparation of PCR-hotquality mouse genomic DNA with hot sodium hydroxide and tris (HotSHOT). *BioTechniques* **29**, 52–54 (2000).
220. Leliaert, F. et al. DNA-based species delimitation in algae. *Eur. J. Phycol.* **49**, 179–196 (2014).
221. De Queiroz, K. Species concepts and species delimitation. *Syst. Biol.* **56**, 879–886 (2007).

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Author contributions

C.G.B.G. and S.W.D. conceptualized the manuscript. C.G.B.G. and H.E.A conducted the literature analysis with help from all authors. C.G.B.G., M.G.-C., J.E.F., H.E.A., K.S.M.-K., C.P. and S.W.D. all contributed to writing and editing.

Competing interests

The authors declare no competing interests.

Additional information

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