Cryptic species and hybridisation in corals: challenges and opportunities for conservation and restoration

Cynthia Riginos[1,2,3] 0000-0002-5485-4197
Iva Popovic[1] 0000-0001-6582-4236
Zoe Meziere[1] 0000-0001-6874-8523
Vhon Oliver Garcia[1] 0000-0002-8933-452X
Ilha Byrne[1] 0000-0003-3909-2902
Samantha M Howitt[1] 0009-0002-6272-5261
Hisatake Ishida[1] 0000-0001-8401-8395
Kevin R Bairos-Novak[1] 0000-0002-0152-1452
Adriana Humanes[4] 0000-0001-7962-2635
Hugo Scharfenstein[3,5] 0000-0003-3408-2350
Thomas Richards[1] 0000-0001-5945-6545
Ethan J. Briggs[1] 0000-0002-3475-5669
Vanessa Clark[1] 0000-0001-6125-9399
Chuan Lei[1]
Mariam Khan[1]
Katharine E Prata[1] 0000-0001-6679-0066

Corresponding author: Riginos

[1] School of the Environment, The University of Queensland, St Lucia, QLD, Australia
[2] Department of Marine Sciences – Tjärnö Marine Laboratory, University of Gothenburg, Strömstad, Sweden
[3] Australian Institute of Marine Science, Townsville, QLD, Australia
[4] School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne, UK
[5] School of BioSciences, The University of Melbourne, Melbourne, VIC, Australia

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Abstract

Conservation and management of coral reef ecosystems will depend on accurate assessments of reef-building coral species diversity. However, the true diversity of corals may be obfuscated by the presence of cryptic species, which are likely much more pervasive than is currently recognised. Additionally, cryptic species may sometimes hybridize, resulting in gene introgression between species. Here, we investigate the prevalence of cryptic coral species via a structured literature review and find that over 50% of population genomic studies show evidence for divisions within taxonomically recognised species and that such closely-related taxa are often linked by gene flow. We find that cryptic taxa frequently segregate by environment, especially depth, and may differ by phenotypic characteristics including resilience to heat stress. This hidden biodiversity creates challenges for coral conservation and restoration planning that are not well appreciated, including hiding true population declines, biasing estimates for species' phenotypic breadth, overestimating the resilience of species to stressors, yielding uncertainty in evolutionary dynamics inferred from past studies, and creating reproductive barriers that may limit mating between local and translocated corals. Increasing awareness that coral cryptic species with incomplete species boundaries are common and building this expectation into conservation and restoration plans is an important pathway forward. Rich opportunities for interdisciplinary collaboration among coral and speciation biologists could fill key knowledge gaps relevant to conservation. We detail recommendations for best practice and strategies for identifying cryptic taxa and hybrids and urge their consideration in all future studies on corals.

1 Introduction: Hidden dimensions of coral biodiversity pose conservation challenges

Coral reefs are highly biodiverse and productive ecosystems (Reaka-Kudla, 1997; Fisher *et al.*, 2015) that substantially contribute to human well-being (Moberg & Folke, 1999; Adey, 2000). Yet, reef-building corals are imperilled by rising temperatures and other anthropogenic stressors worldwide (Hughes *et al.*, 2017; Knowlton *et al.*, 2021; Souter *et al.*, 2021). Thus, there is great urgency to inventory coral biodiversity and to deepen knowledge regarding the processes that create and maintain this diversity to guide conservation and restoration actions.

For corals it has long been recognised that morphological variation is unlikely to align well with genetic variation. Molecular based phylogenetic investigations are uncovering unexpected relationships and unanticipated numbers of distinct taxa (reviewed by Kitahara *et al.*, 2016; Cowman *et al.*, 2020), and similarly, multilocus population genetic surveys routinely find distinct genetic taxa within morphologically defined taxonomic species. These so-called *cryptic species* (recent reported genomic examples include: Gomez-Corrales &

Prada, 2020; Underwood *et al.*, 2020; Wepfer *et al.*, 2020; Afiq-Rosli *et al.*, 2021; Bongaerts *et al.*, 2021a; Feldman *et al.*, 2021; Fifer *et al.*, 2021; Rippe *et al.*, 2021; Zayasu *et al.*, 2021; Adam *et al.*, 2022; Prata *et al.*, 2022; Rivera *et al.*, 2022; Matias *et al.*, 2023; Voolstra *et al.*, 2023; Meziere *et al.*, 2024) reinforce observations previously made with microsatellites and few nuclear markers (such as Bongaerts *et al.*, 2010; Souter, 2010; Ladner & Palumbi, 2012; Schmidt-Roach *et al.*, 2012; Prada & Hellberg, 2013; Boulay *et al.*, 2014; Prada *et al.*, 2014; Warner, van Oppen & Willis, 2015; Gélin *et al.*, 2017) and demonstrate how species designations based on morphology alone can underestimate true community diversity (Fig 1). Indeed, most conservation management and restoration plans implicitly assume that coral species are recognisable and biologically valid entities (Baums, 2008; Anthony *et al.*, 2017; National Academies of Sciences, 2018; Colton *et al.*, 2022). These assumptions may unintentionally bias conservation and restoration efforts when such biodiversity is not acknowledged. Yet, detecting and delineating distinct genetic groups presents a substantial challenge (which we discuss in more detail in Section 2.1). Rather than adopting a specific criterion for species status, we use the terms *genetic groups* or *taxa* to signify their genetic distinctiveness. We avoid terms such as clade or lineage, as monophyly across all or many gene trees is unlikely when divergence is recent. We use *cryptic* to signify that taxa appear morphologically similar to the "untrained human eye", at least under field conditions.

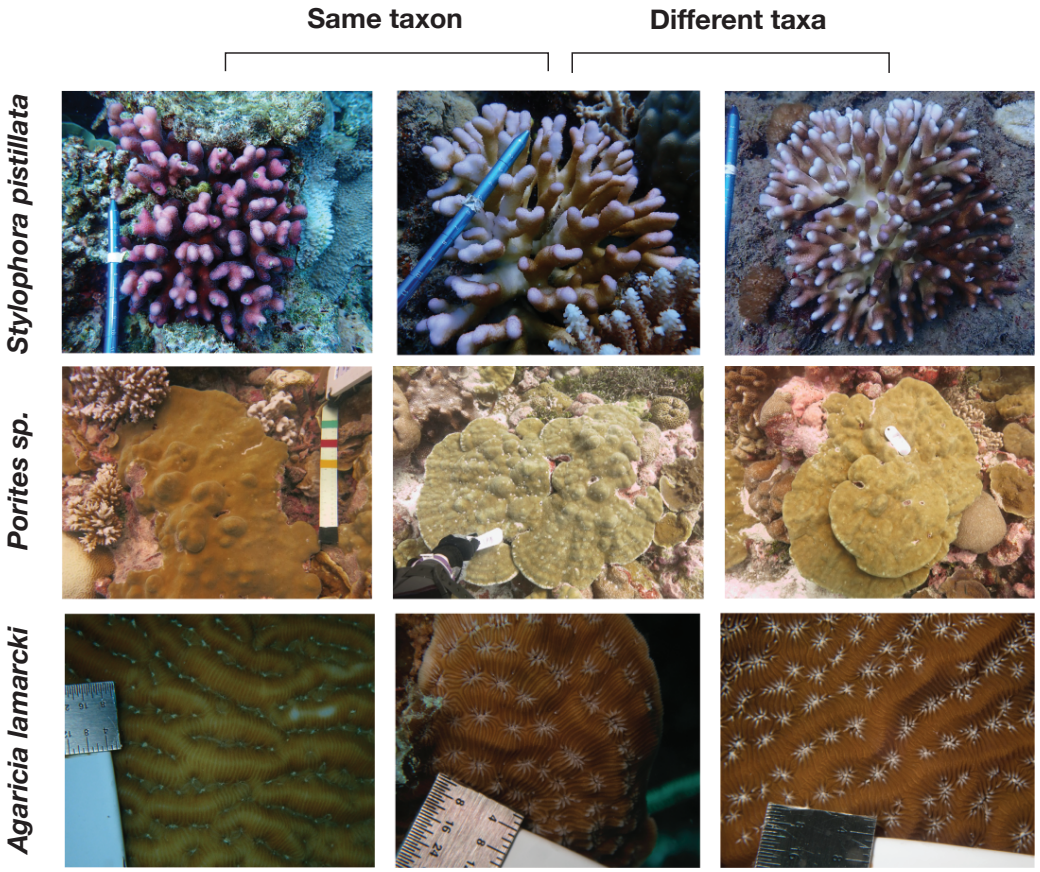

Figure 1 – Examples of closely related cryptic species. Details can be found in the original studies: *Stylophora pistillata* (Meziere *et al.*, 2024), *Porites sp*. (Starko *et al.*, 2023), and *Agaricia lamarcki* (Prata *et al.*, 2022).

Further complicating taxonomic delineations, cryptic coral taxa may be linked by occasional gene flow, or *hybridisation*. Morphologically intermediate individuals are often encountered in the field (Veron, 1995; Richards *et al.*, 2008), and many species can be crossed at least under experimental conditions (Isomura *et al.*, 2016; Chan, Peplow & van Oppen, 2019; Kitanobo *et al.*, 2022). Genomic studies confirm that hybridisation is common in corals, where gene flow has been documented between distinct taxa (Cooke *et al.*, 2020; Fifer *et al.*, 2021; Prada & Hellberg, 2021; Rippe *et al.*, 2021; Prata *et al.*, 2022; Matias *et al.*, 2023; Starko *et al.*, 2023; Zhang *et al.*, 2023; Meziere *et al.*, 2024), including historical gene flow between taxa separated by over 15 million years (reviewed by van Oppen & Gates, 2006; Willis *et al.*, 2006; Mao & Satoh, 2019; González, Rivera-Vicéns & Schizas, 2021; Hobbs *et al.*, 2021; Pinsky, Clark & Bos, 2023). Cryptic genetic groups or taxa, potentially connected by limited gene flow, present distinct challenges for understanding coral biodiversity. Failing to recognize cryptic coral taxa and appropriately adjust interpretations can result in misleading conclusions about fundamentally important aspects of biodiversity measurement, including: i) underestimating species diversity, ii) overestimating within-species variances for various traits and tolerances,

iii) biasing inferences regarding within-species patterns of genetic diversity and population structure, and iv) invalidating assumptions about reproductive compatibility.

First, biodiversity inventories typically determine the count and abundances of distinct species. Common methods, such as field surveys, are usually based on morphological identification of live organisms. If distinct taxa are not appropriately recognised and delineated, then total species counts will be greatly underestimated, presenting an unstable base from which to draw conclusions about coral population sizes, species extinction vulnerabilities, and biodiversity valuations. For example, estimates of census population sizes for present-day corals have been recently debated (Dietzel *et al.*, 2021; Muir *et al.*, 2022), as smaller population sizes would imply greater vulnerability to extinction (Dietzel *et al.*, 2021; Muir *et al.*, 2022).

Second, assessment of trait diversity is compromised if cryptic taxa are not identified, and trait measurement occurs on an amalgamation of distinct taxa. The agglomerate will contain more variation than the distinct groups, which will inflate estimates of both genetic and phenotypic variance. This phenomenon can affect interpretation for a diverse array of traits. For example, species range estimates would be upwardly biased if cryptic species are geographically restricted within the broader range of a morphospecies. Environmental niche breadth can also be overestimated: for instance, many coral species that were previously considered depth generalists could resolve into taxa with more restricted depth distributions when cryptic species are considered (e.g., Bongaerts *et al.*, 2021a). Similarly, a presumed species may appear to have a generalist phenotype but actually comprise multiple taxa that are more specialized, as appears to be the case for bleaching responses among *Orbicella faveolata* taxa (Gomez-Corrales & Prada, 2020). In summary, single-species conclusions drawn from agglomerated data from multiple cryptic taxa are likely to be overly optimistic in terms of coral resilience.

Third, common measures of population genetics and gene flow may be inherently biased and incorrect when cryptic taxa are examined as one. For example, using allele frequencies to make inferences about microevolutionary dynamics without delineating separate gene pools can yield incorrect results and interpretations. Lumping genetically distinct groups will inflate apparent within-population diversity (based on measures of allelic diversity or expected heterozygosity) and will therefore cause inbreeding to be overestimated – known as the Wahlund effect (as discussed in Schmidt, Thia & Hoffmann, 2023). When comparing across geographic locations, measures of population structure (notably F_{ST}) can be biased either upwards or downwards, depending on the particular mix of cryptic taxa sampled. These phenomena are neatly illustrated and discussed by Sheets et al. (2018) for *Acropora hyacinthus* in the western Pacific (see also Pante *et al.*, 2014; Warner *et al.*, 2015). Additionally, common metrics of population genetics such as genetic diversity, differentiation, inbreeding and effective population size may be biased when hybridization

between differentiated taxa is not taken into account (Hoban *et al.*, 2022). For example, hybridisation may inflate the measured diversity for populations that include individuals of mixed ancestry, while gene flow or dispersal inferences may be biased in either direction. Together, cryptic taxa and hybridisation are likely to greatly affect the accuracy of studies aiming to assess and monitor genetic diversity.

Finally, the existence of cryptic taxa implies that there is some form of reproductive isolation between taxa. Intrinsic barriers such as incompatible loci are likely to reduce gene flow among taxa in nature, so populations of a morphospecies may not be as strongly linked by gene flow as is often assumed. In restoration contexts, intrinsic barriers could lead to translocated individuals being unable to mate with local individuals and could prevent crossing in captivity and/or reduce hybrid fitness (outbreeding depression). Extrinsic barriers to reproduction arise when survival or fertility differs between taxa based on their surrounding environments, and as a result, they inhabit different niches. This means that cryptic taxa may not be ecologically or functionally equivalent. Restoration actions that involve coral outplanting (i.e., fragments or sexually propagated colonies) risk mis-matching the source taxon's niche with their new destination's environmental conditions. Conversely, hybridisation between taxa could enhance fitness or phenotypic breadth of resultant offspring (Chan *et al.*, 2018).

Figure 2 outlines some possible consequences of cryptic coral taxa to current restoration actions such as direct transplantation and coral gardening, as well as actions that are being actively researched for potential use in coral restoration (National Academies of Sciences, 2018; Anthony *et al.*, 2020; Hein *et al.*, 2020; Bay *et al.*, 2023).

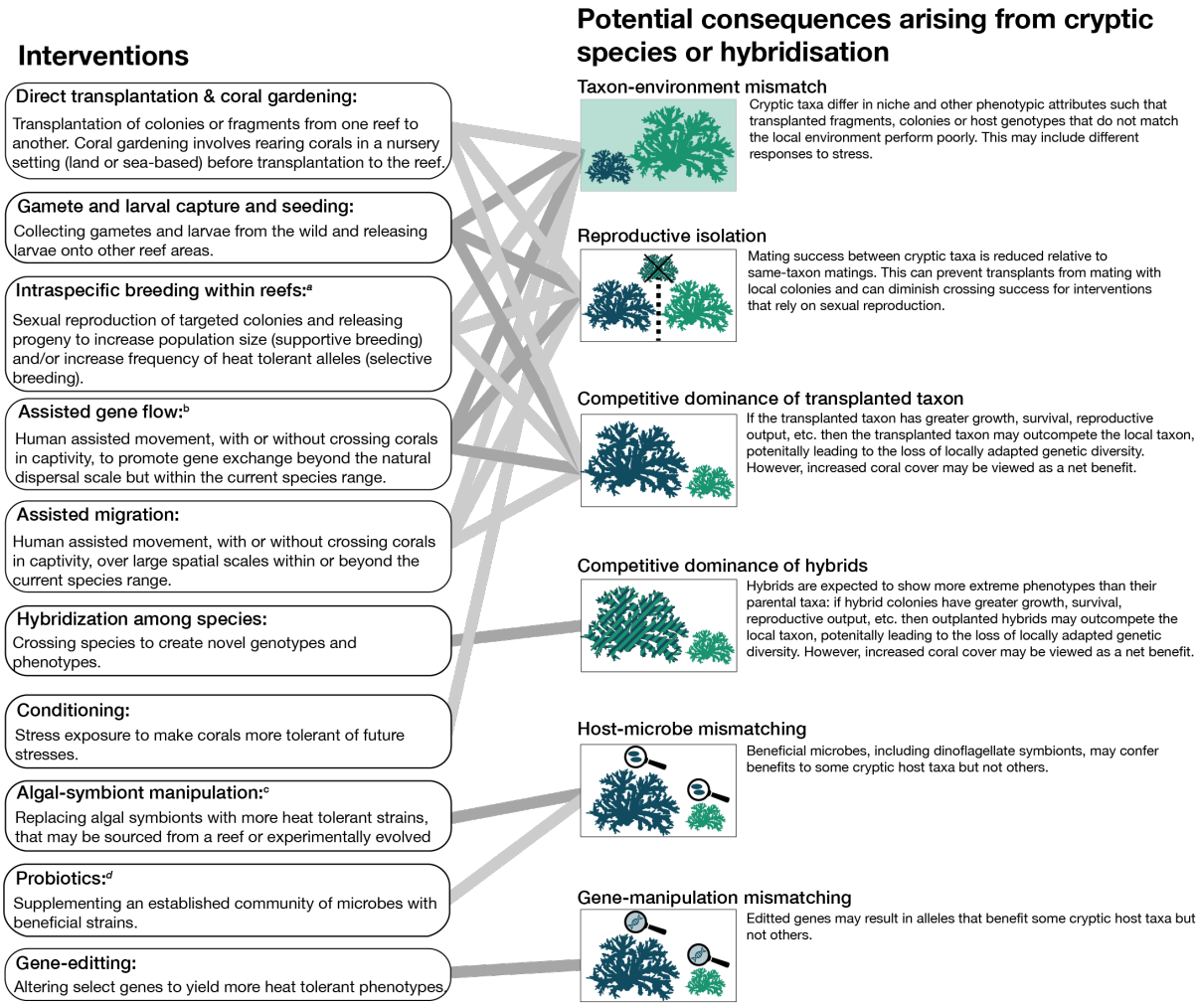

Figure 2 - How cryptic coral taxa and hybridisation could affect coral reef restoration actions that aim to preserve biological diversity, counter population declines, and promote resilience to climate change through biological adaptation. Terminologies follow (van Oppen *et al.*, 2015; National Academies of Sciences, 2018; Hein *et al.*, 2020; Bay *et al.*, 2023) and are not necessarily mutually exclusive. For example, assisted migration could be undertaken on fragments (direct transplantation), larvae, or via the progeny of captive, sexually propagated corals. In all graphics, the coral colony shown as a larger size indicates greater fitness (survival, reproductive output, thermal tolerance, etc) leading to competitive dominance.

As outlined above, cryptic taxa and hybridisation have substantial implications for understanding and predicting the ecological and evolutionary dynamics of corals, and thus will be essential for making informed conservation and restoration decisions into the future. In this review, we critically assess the prevalence of hidden biodiversity among corals. By corals, we refer to benthic Anthozoans including Scleractinians (hard corals) as well as Octocorallians (soft corals). We focus primarily on population *genomic* studies (supported by whole genome or reduced representation sequencing of genome-wide variation) because thousands of loci are often required to detect recent evolutionary delineations between taxa. This paper builds upon important earlier reviews and syntheses of cryptic taxa (Richards, Berry & van Oppen, 2016) and hybridisation in corals (van Oppen & Gates, 2006; Willis *et al.*,

2006; Hobbs *et al.*, 2021; Pinsky *et al.*, 2023) that primarily focused on studies with few markers (microsatellites, few sequenced loci, or allozymes).

Here we explore how evolutionary processes in corals can and should shape conservation and restoration priorities and actions. Specifically, we: 1) develop criteria for recognising cryptic taxa from population genetic data, 2) describe and evaluate surveyed genomic literature against these guidelines to show that cryptic taxa frequently exist in sympatry, 3) determine whether cryptic divergence in cnidarian hosts is accompanied by divergence in their photosynthetic symbionts, 4) explore the environmental factors segregating cryptic taxa, 5) review examples of hybridisation and/or gene flow between taxa, and 6) discuss how corals could be exciting model systems for speciation and adaptation studies. The main text is supported by text boxes that, A) provide a worked example of delineating coral taxa, B) demonstrate how cryptic taxa are commonly overlooked in coral experiments, and C) outline best practices for designing studies when cryptic taxa are likely to be encountered.

2 Closely related coral taxa are common in sympatry and frequently connected by gene flow

To gauge the prevalence and impacts of cryptic coral taxa and hybridisation, we evaluate findings from a structured literature search alongside a broader literature review. Although our primary intent is to draw inferences from more informative genome-based studies, population genomic studies for corals are limited both in their number and in scope. Thus, we also include some discussion of noteworthy results based on microsatellite surveys and also review microbial symbiont diversity because of their relation to cryptic host taxa (under Sections 2.2 and 2.3).

2.1 Detecting cryptic coral species using criteria based on reproductive isolation

Many coral taxa potentially inhabit the “grey zone” of the speciation continuum (de Queiroz, 2005; Roux *et al.*, 2016). That is, genetically distinct groups may coexist within dispersal range, yet these groups may not have all the contingent properties of distinct ‘species’ (sensu de Queiroz, 2005), including complete reproductive isolation. However, for groups with overlapping ranges to remain genetically distinct, reproductive barriers of some form must be present. Reproductive barriers between groups may occur due to differences in microhabitats or spawning times resulting in infrequent fertilisation, producing offspring with phenotypes that do not match microhabitats, or other intrinsic genetic incompatibilities. When reproductive barriers are not complete, the outcome of interbreeding between groups is controlled by the relative strength of selection (which promotes divergence), and the scale of gene exchange (which promotes homogenisation). Even low levels of gene exchange between otherwise distinct groups will cause alleles to be shared. Allele sharing will also be prevalent if divergence time between groups is recent whereby groups share ancestral

variation. Thus, allele sharing is expected to be common between cryptic coral taxa that are recently diverged (with or without ongoing gene flow).

Population genomic surveys have the power to detect subtly differentiated genetic groups where allele frequency differences between groups are small. The statistical power of common methods is determined by the number of loci examined as well as the extent of genetic covariance among loci, where distinct populations exhibit non-random associations of alleles at various loci across the genome (i.e., *linkage disequilibria*). While physical linkage on a chromosome alone will cause covariance among loci, genome-wide covariance also arises as a direct consequence of population structure (reflecting distinct gene pools subject to independent outcomes of genetic drift and selection). For example, reproductively isolated taxa or geographically separated populations will be differentiated across loci due to genetic drift and selection. In contrast, gene flow among them will erode both their allele frequency differences and linkage disequilibria. Statistical power for identifying small allele frequency differences and linkage disequilibria in empirical surveys is increased by sampling many individuals and many loci, where subtle differences between groups can be missed when few individuals or few loci are sampled. For example, two co-occurring genetic groups of *Montastraea cavernosa* were clearly delineated using thousands of loci and yet ambiguous with 9 microsatellite loci (Sturm *et al.*, 2020).

We focus on two general approaches for detecting subtle differentiation between genetic groups: ordination-based analyses and model-based clustering. Ordination-based analyses, such as principal components analyses (PCA), principal coordinates analysis, multidimensional scaling, etc., describe multidimensional relationships among entities and are based on (and visually represent) the genetic covariance matrix (Patterson, Price & Reich, 2006). Model-based clustering analyses – typified by admixture detection analyses such as STRUCTURE (Pritchard, Stephens & Donnelly, 2000) and ADMIXTURE (Alexander, Novembre & Lange, 2009) – partition groups (K) based on associations among alleles and loci. Ordination and model-based clustering approaches are unsupervised machine learning methods that are valuable for exploring relationships between individuals (that is, without pre-assigning individuals to “populations”, as is required by F-statistics and other population-level metrics). These methods are some of the most common and routinely employed methods in genomic surveys and provide complementary insights into spatial patterns of genetic diversity. We omit results from supervised methods, such as discriminant analysis, that maximize variance using user-assigned groupings (see Thia, 2022 for extended discussion).

We define taxa as distinct groups of individuals (genotypic clusters) within named species that maintain their distinctiveness even when their ranges overlap, therefore they have the

opportunity to mate (in line with Mallet, 1995). This definition aligns to many species concepts (de Queiroz, 2005), under the assumption that some form of reproductive isolation must be occurring. Instances where distinct genetic groups are found together (i.e., sympatric within the scale of dispersal distance) provide the strongest circumstantial evidence for some degree of reproductive isolation between groups, as reduced gene flow due to dispersal restrictions cannot be the primary cause of genetic divergence in these cases. These "taxa" might be considered species, depending on the definition of species employed (de Queiroz, 2005); as our focus is not taxonomy but evolutionary processes and their implications, the term "taxon" is more flexible. Thus, we focus on evidence for *sympatric* cryptic coral *taxa*. When distinct genetic groups are geographically separated (*i.e.*, allopatric), then divergence may solely reflect dispersal barriers to gene exchange and therefore are not informative for inferring reproductive isolation.

We propose three requirements for identifying and delineating taxa using ordination and model-based clustering:

1) Distinct genetic groups occur in sympatry relative to their dispersal ability.
2) Ordination (e.g., PCA) clusters these distinct genetic groups based on genotypes of individuals and/or model-based clustering indicates that individuals belong to separate groups.
3) When genetic distance between sympatric individuals is greater than the genetic distance between allopatric individuals. This is evidenced by divergence between groups across the primary ordination axis and/or at low hypothesized group numbers (K values) as compared to axes or groups that describe geographic structure.

To determine if published genomic surveys of corals typically test for and find evidence for cryptic taxa following the above criteria (see Textbox 1 for worked example), we searched the Web of Science for published papers displaying graphical results from ordination (PCA, primarily) and/or model-based clustering analyses (Structure and ADMIXTURE). We focus on studies that genotyped individual cnidarian genomes for 1000s of loci or more and sampled from two or more geographic locations (see Appendix for details of literature search). We additionally collected information on depth ranges and symbiont composition where reported. The literature search uncovered 41 papers describing results for 31 species, where some papers included multiple species and some species were studied across multiple papers, yielding a total of 51 unique records (available as supplemental data). Although we did not restrict the search by sampling depth, none of the recovered records included species deeper than mesophotic depths.

In our review of published studies, we apply the above criteria (1-3) conservatively by only looking for sympatric differentiation i) along the first principal component axis (referred to as 'PC1') in ordination analyses, and ii) for model-based clustering examining outcomes when individuals were assigned to only two groups (K=2). We consider individuals sampled ≤10 km apart as being broadly sympatric since dispersal distances for many coral species are unknown.

As shown in Fig. 3, over half of the coral population genomic studies (23 records out of 39 that could be evaluated against all three criteria) showed evidence for distinct cryptic taxa. While we might expect genetic differentiation to be greater among brooding corals that have less innate dispersal ability relative to broadcast spawning corals (Knowlton, 2001), the relative proportions of sympatric versus non-sympatric groups did not differ between brooding and broadcast spawning corals ($P > 0.2$ with Fisher's exact test using either ordination or clustering). Criterion 3 is based on genetically distinct groups co-occurring. This evidence is stronger when this groups co-occur across many geographic locations. Thus, we investigated whether pairs of genetically distinct coral groups were repeated across multiple sites using model-based clustering results based on author-selected K values. Across studies, it was common for cryptic groups to be sympatric at multiple sampled sites (Fig. 3). This observation strengthens the conclusion that closely-related, but distinct taxa, can co-occur over extensive geographic areas and implicates some degree of reproductive isolation maintaining the distinctiveness of each group. In summary, cryptic taxa are common features in population genetic studies of corals.

Our literature review shows that cryptic taxa are prevalent, implying that many conclusions related to biodiversity, species traits, and population genetic structure based at the morphospecies level are likely to be inaccurate based on the reasons discussed previously (see Section 1). Even when genomic data to evaluate cryptic taxa are presented, five studies that we assessed failed to include any mention of cryptic species or taxa, despite their results showing evidence for genetically distinct groups. Additionally, some of the studies reviewed here computed summary statistics such as heterozygosity, or F-statistics using all individuals from the sampling locations, despite evidence for cryptic taxa co-occurring within locations. We surmise that inferences regarding the absence of potential cryptic taxa based on analyses using few loci (including microsatellite studies) are likely lacking in terms of the power to detect recently differentiated taxa, and therefore many published studies – including studies published by authors of this review – may inadvertently base conclusions on heterogeneous mixes of cryptic taxa.

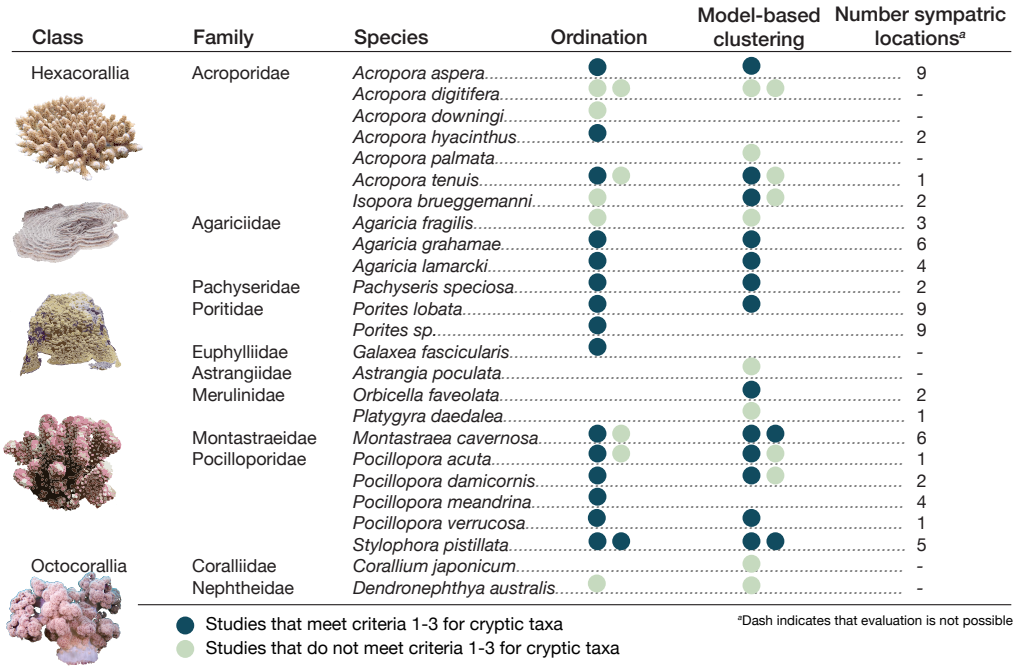

Figure 3 - For many genomic studies of corals, the greatest axis of genetic differentiation defines groups that are sympatric. Results by species are summarized as either meeting or not meeting the three criteria for cryptic taxa under the strictest definition where sympatric differentiation is aligned to the first axis (ordination) or K = 2 (model-based clustering). Some studies had both ordination and model-based clustering, and some species were included in more than one study, thus multiple points can appear against each species. Studies that did not present ordination or model-based clustering are not shown. The number of locations where distinct groups were sympatric was based on K clustering, using the K value preferred by the authors, where a dash indicates that this value could not be inferred. From the 51 studies examined, 39 presented results that could be evaluated against criteria 1-3.

2.2 No clear patterns for symbionts associated with cryptic coral host taxa

An important aspect of coral biodiversity is the diverse microbial community living within the cnidarian host, where mutualistic relationships with endosymbiotic dinoflagellates from the family Symbiodiniaceae are known to affect whole organism physiology (LaJeunesse *et al.*, 2018). The specificity of coral-symbiont pairings is influenced by host-symbiont genetic interactions, host reproduction, symbiont transfer mode, and environment (see Baker, 2003; Davies *et al.*, 2023; Turnham *et al.*, 2023 for further readings). While symbiont evolution is not the focus of this review, joint consideration of coral hosts and their microbes is relevant in understanding the specificity of associations that can affect traits, local adaptation, and restoration actions.

Among the population genomic studies that we surveyed, 43% genotyped dinoflagellate symbionts alongside the coral hosts. Several studies (e.g., Howells *et al.*, 2016; van Oppen *et al.*, 2018; Gomez-Corrales & Prada, 2020; Bongaerts *et al.*, 2021a; Prata *et al.*, 2022; Buitrago-Lopez *et al.*, 2023; Starko *et al.*, 2023) used internal transcribed spacer (*ITS*) sequences to characterize the community of symbiont lineages living within a colony, aligning with traditional marker-based methods (Davies *et al.*, 2023) for symbiont characterisation. Some

studies also used incidentally recorded symbiont sequences retrieved from whole-colony sequencing (either reduced representation or shotgun whole genome sequencing) to make inferences about symbionts, including reconstructing organelle diversity (Bongaerts *et al.*, 2017; Forsman *et al.*, 2017; Gonzalez-Zapata *et al.*, 2018; Cooke *et al.*, 2020; Bongaerts *et al.*, 2021a; Matias *et al.*, 2023; Zhang *et al.*, 2023) or summarizing symbiont genomes with *k*-mer analyses (Zhang *et al.*, 2023).

A central issue for coral adaptation and diversification is the extent to which symbiotic associations are flexible. Brooding corals are expected to have less flexible symbiont associations because they often exhibit vertical symbiont transmission from the maternal colony (Knowlton, 2001; Johnston, Cunning & Burgess, 2022; Turnham *et al.*, 2023). However, in our review, only one brooding coral (*Stylophora pistillata*) that was genotyped for both symbionts and hosts (Buitrago-Lopez *et al.*, 2023) preventing adequate comparisons among reproductive modes. Symbiont types were commonly found to be shared across cryptic host lineages for *S. pistillata* (Buitrago-Lopez *et al.*, 2023), for broadcast spawners (*O. faveolata*: Gomez-Corrales & Prada, 2020; *Pachyseris speciosa*: Bongaerts et al., 2021a; *Pocillopora verrucosa*: Buitrago-Lopez et al., 2023; *Porites lobata*: Rivera et al., 2022; *Porites sp.*: Starko et al., 2023) for mixed mode *Pocillopora damicornis* (van Oppen *et al.*, 2018), and for taxa with unknown modes of reproduction (*Agaricia fragilis*: Bongaerts et al., 2017; *Agaricia lamarcki*: Prata et al., 2022). Some symbiont types appeared specific to cryptic taxa (*O. faveolata*: Gomez-Corrales & Prada, 2020; *P. speciosa*: Bongaerts et al., 2021a; *P. verrucosa*: Buitrago-Lopez et al., 2023; massive *Porites sp*.: Starko et al., 2023; *P. damicornis:* van Oppen et al., 2018), whereas other sets of cryptic taxa were not associated with specific symbiont types (*Agaricia fragilis*: Bongaerts et al., 2017; *Agaricia lamarcki*: Prata et al., 2022; *S. pistillata*: Buitrago-Lopez et al., 2023). Thus, some symbiont strains may be specialized, as evidenced by symbiont lineages only associating with one host group; however, this pattern is not always a characteristic accompanying cryptic cnidarian taxa.

Moving beyond single marker genotyping of symbionts (Davies *et al.*, 2023; Ishida *et al.*, 2023; Zhang *et al.*, 2023) may provide better resolution of host-symbiont associations. For example, Rivera et al. (2022) found that symbiont identities among *P. lobata* did not align to host taxa using ITS genotyping but were concordant when using higher resolution SNP-based analyses. Additional studies are needed, however, to determine whether alternative methods harnessing whole-genome data to summarize symbiont diversity will reveal more nuanced patterns than ITS based results.

2.3 Depth and microhabitats can segregate cryptic taxa

For coral hosts, the existence of distinct genetic groups in sympatry implies that differentiation may be maintained by strong natural selection arising from local environments (Richardson *et al.*, 2014). Such strong selection and genotype-by-environment associations may merely reflect pre-existing reproductive isolation (Bierne *et al.*, 2011), although

divergent natural selection can also contribute to reproductive isolation (Schluter, 2001; Rundle & Nosil, 2005). For marine species, including corals, depth often delineates closely-related species (Knowlton, 1993) and could drive ecological speciation in corals (González *et al.*, 2020). In coral reef communities, depth is a predominant structuring aspect, with distinct species turnover between shallow (approximately < 30 m) and mesophotic (approximately 30-150 m) depth zones Importantly, these transitions exist across communities because many environmental factors covary with depth, such as light intensity and spectrum (Lesser, Slattery & Leichter, 2009), temperature (Kahng *et al.*, 2019), nutrients (Leichter, Stokes & Genovese, 2008), water flow (Muir *et al.*, 2015), as well as disturbance frequency and severity (Bongaerts & Smith, 2019), creating highly contrasted habitats often only meters apart. The strongest environmental differences are within the first few meters due to the exponential decay of light in the aquatic environment – the most important environmental factor for light-dependent scleractinians. Thus, it is highly likely that recently diverged taxa will also be partitioned by depth, matching patterns of species turnover.

Among the population genomic studies surveyed, cryptic taxa differed in abundance by depth-associated habitats. Eleven studies to date undertook extensive sampling over replicated depth-associated habitat contrasts (i.e., more than one site >10 km apart with two depth habitats sampled within each site). Replicated differentiation by depth was found for *Agaricia fragilis* (i.e., shallow vs. mesophotic, Bongaerts *et al.*, 2017), *Agaricia lamarcki* (i.e., shallow vs. mesophotic, Prata *et al.,* 2022), *Isopora brueggemanni* (*i.e.*, lagoon vs. slope; Thomas *et al.*, 2019), *Pocillopora damnicornis* (*i.e.*, flat vs. slope, van Oppen *et al.*, 2018) and *Montastraea cavernosa* (*i.e.*, shallow vs. mesophotic, Sturm *et al.*, 2022) but not for *Agaricia grahamae* (i.e., upper vs. lower mesophotic, Prata *et al.*, 2022), *Stephanocoenia intersepta* (i.e., shallow vs. mesophotic, Bongaerts *et al.*, 2017), *Acropora digitifera* (i.e., lagoon vs. slope, Thomas *et al.*, 2019), *Agaricia u*ndata (i.e, shallow vs. upper mesophotic and upper vs. lower mesophotic, Gonzalez-Zapata et al., 2018). Thus, differentiation by depth frequently discriminates cryptic coral taxa.

The most extensive investigations of differentiation by depth have been for *Seriatopora hystrix* (brooder) on the Great Barrier Reef, Australia and *Eunicea flexuosa* (broadcast spawner) in the Caribbean. Although most of the studies discussed below pre-date genomic-scale genotyping and thus rely on small numbers of microsatellite loci for making genetic inferences, they are noteworthy because they meticulously documented small scale depth and habitat segregation of host genotypes and also used reciprocal transplantation experiments to further support evidence for depth-associated adaptive differentiation. Bongaerts et al. (2010) showed that genetically distinct groups of *S. hystrix* were associated with reef zone and depth position (backreef at 2 m, shallow reef at 6 m, deep reef at ~27 m; locations within 200 m distant horizontally). For the gorgonian *E. flexuosa,* Prada & Hellberg (2013) demonstrated that individuals from <5 m and >20 m depths were distinct and joined by a narrow hybrid zone (< 200 m horizontally). This depth separation was likely maintained

by selection against juveniles (Prada & Hellberg, 2014). Reciprocal transplantation supported evidence for local adaptation in both cases (Bongaerts *et al.*, 2011; Prada & Hellberg, 2013). Together, these two examples (*S. hystrix* and *E. flexuosa*) show that cryptic coral taxa could comprise distinct depth-specific ecotypes maintained by selection and furthermore illustrate the utility and feasibility of using experiments to strengthen evidence for local adaptation across small spatial scales. There is an unrealised opportunity to combine future genomic investigations with manipulative experiments to advance the understanding of speciation and adaptation (discussed further in Section 3).

While depth has been one of the most investigated environmental axes of local genetic differentiation in corals, cryptic taxa can be associated with other habitat differences (and sometimes are evident with few markers (Warner *et al.*, 2015)). In one example, broad physiological differences between *A. hyacinthus* taken from two reef pools less than 500m apart but varying in natural thermal variability (coined "highly" and "moderately" variable pools (reviewed by Thomas *et al.*, 2018); were partially explained by the relative abundance of four cryptic species (identified using ordination of SNP-based genotypes) that differed in abundance between the two pools (Rose *et al.*, 2017). Similarly, substantial differences in skeletal morphologies and gene expression were found between *P. lutea* colonies sampled from a mangrove lagoon versus colonies from a reef approximately 500 m away (Scucchia *et al.*, 2023); however, these phenotypic differences also aligned with genome-wide differentiation measured by transcriptome-derived SNPs, suggesting that mangrove and reef populations could simply be different taxa (applying the criteria in Section 2.1).

It is important to note that the structure and composition of coral-associated microbial communities also often vary along environmental gradients, including those associated with depth and disturbance (Klaus *et al.*, 2007; Bongaerts *et al.*, 2013; Howells *et al.*, 2013; Quigley *et al.*, 2022), and likely help mediate coral holobiont adaptation to environmental stress. Endosymbiotic dinoflagellates (LaJeunesse *et al.*, 2018) enable certain coral species to reside within specific light environments, where mesophotic and shallow depth coral hosts often harbour distinct symbiont strains, whereas depth-generalists appear to be able to host many symbiont strains (Bongaerts *et al.*, 2013). Consistent with these previous findings, several of the studies examined here reported greater spatial or environmental partitioning among symbionts as compared to hosts (e.g., *Astrangia poculata*: Aichelman & Barshis, 2020; *P. verrucosa*: Buitrago-Lopez et al., 2023; *S. pistillata*: Buitrago-Lopez et al., 2023; *Platygyra daedalea*: Howells et al., 2016; *Acropora tenuis*: Matias et al., 2023; *A. lamarcki*: Prata et al., 2022; but not so for *A. digitifera*: Zhang et al., 2023). Intriguingly, Starko et al. (2023) demonstrated that a distinct symbiont community associated with one cryptic taxon of massive *Porites sp.* changed following a heatwave, such that the post heatwave composition better matched the symbiont communities living in the other two cryptic taxa. Thus, symbionts may change to track local environments (Baker, 2003), although this flexibility may differ among host taxa (Quigley *et al.*, 2022).

Whereas differentiation by depth and habitat appear to be fairly common in corals (and their associated microbes), sampling strategies for many coral genomic studies are surprisingly underpowered in their ability to detect genetic differentiation by depth or habitat. Among the population genomic studies examined here, 25% failed to report sampling depth (or any other relevant habitat, including our own work, e.g. Matias *et al.*, 2023). Presumably, most of the genotyped corals across the studies reviewed here were sampled on SCUBA from < 30 m and were sampled from a similar depth range across all sites. Among studies that did report depth, many sampling regimes had depth confounded with geography where each location was sampled at a single depth. A minority of studies (21%), however, implemented a structured sampling design where the same depth was sampled at more than one location (Fig. 4). More complete reporting on depth and other microenvironmental attributes alongside sampling study designs that replicate environmental contrasts are needed to advance our understanding of how cryptic taxa, reproductive barriers, heterogeneous environments, and natural selection interact to shape coral biodiversity.

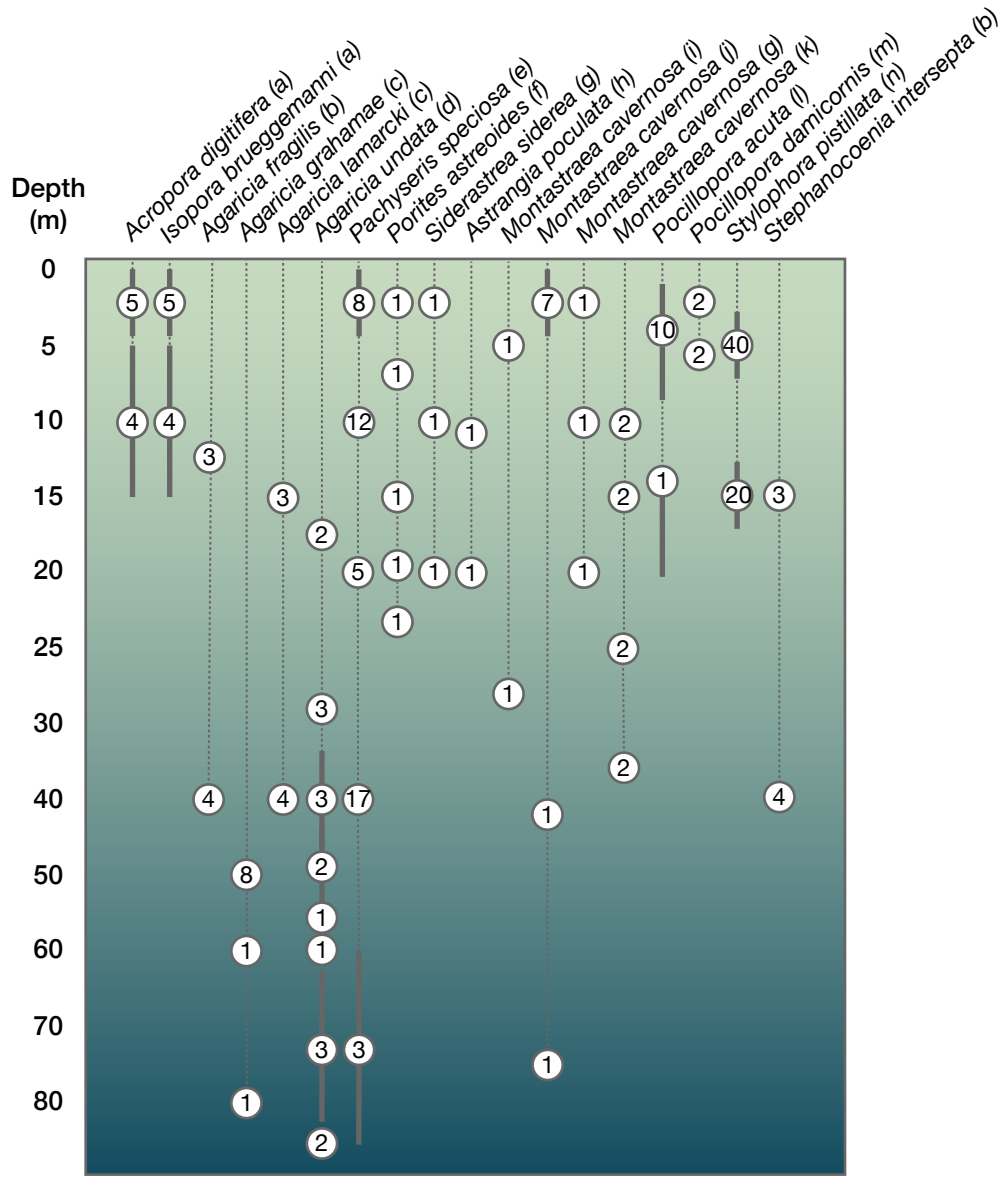

Figure 4 - Summary of depth sampling schemes for studies that reported depth and sampled at more than one depth. Numbers indicate the number of distinct locations that were sampled per depth. Locations were considered distinct if the nearest locations were depth contrasts (e.g., adjacent sites sampled at 5 and 15 m were considered as two locations); otherwise, same depth locations within 10 km were collapsed as a single location. Dotted lines connect locations from the same study and thick grey lines indicate the sampling range (as reported by authors). Citations are as follows: a) (Thomas *et al.*, 2019); b) (Bongaerts *et al.*, 2017); c) (Prata *et al.*, 2022); d) (Gonzalez-Zapata *et al.*, 2018); e) (Bongaerts *et al.*, 2021a); f) (Shilling *et al.*, 2023); g) (Rippe *et al.*, 2021); h) (Aichelman & Barshis, 2020); i) (Drury *et al.*, 2020); j) (Sturm *et al.*, 2020); k) (Sturm *et al.*, 2022); l) (Aurelle *et al.*, 2022); m) (van Oppen *et al.*, 2018); n) (Meziere *et al.*, 2024).

2.4 Cryptic taxa can differ in their susceptibility to thermal stress

Limited but growing evidence shows that phenotypes of closely related cryptic coral taxa can differ with respect to environmental tolerances, which may affect where they can live (i.e., their niche, including depth) and how they might respond to climate change and other anthropogenic stressors. For example, under experimental conditions, one genetic group of *A. hyacinthus* showed greater resistance to bleaching conditions under experimental trials compared to the three other groups, matching within reef microhabitat distributions of these taxa in American Samoa (Rose *et al.*, 2021). Likewise, heat resilience and survival may differ between cryptic taxa in the wild. By monitoring tagged colonies during an extreme heatwave, Starko et al. (2023) found that mortality was significantly higher for one of three massive *Porites* taxa on Kiritimati. In Palau, cores from *P. lobata* showed differences in past growth rates and stress banding between four cryptic taxa – indicative of taxa-specific differences over long time periods (1970-2014), with the two most heat tolerant taxa predominating at the warmest location (Rivera *et al.*, 2022). Similarly, survival through a heatwave differed among *Pocillopora* taxa distributed across Moorean reefs (Burgess *et al.*, 2021). These studies illustrate that cryptic taxa are not necessarily interchangeable, especially with respect to heat stress responses and survival over both short and long-time frames.

In Textbox 2, we investigate whether thermal biology studies are attuned to the coral cryptic taxon "problem". If cryptic coral taxa consistently differ in their phenotypes, including response to thermal stress, then experimental outcomes need to be evaluated with respect to taxonomic identity. Yet, we find that only 8% of such studies included genotyping that could identify cryptic taxa, suggesting that many studies could be inadvertently evaluating multiple taxa and thereby supporting incorrect or biased conclusions.

2.5 Gene flow and introgression link taxa across divergence histories

Interbreeding between genetically distinct groups of corals could elevate genetic diversity and contribute to adaptation. Hybridisation in corals has long been suspected (van Oppen & Gates, 2006; Willis *et al.*, 2006), but studies using few genetic markers often lack the resolution to appropriately investigate hybridisation in the context of recently diverged taxa, where genetic similarities can result from either shared ancestral diversity or gene flow. If hybrids interbreed with parental species (backcrossing), interspecific recombination leads to introgression of genetic material from one lineage into the other. Thus, by analysing thousands of genomic SNPs, genomic studies can often resolve whether genetic similarities are due to gene flow and sometimes identify genomic regions that have experienced high or low levels of gene flow as well as identify where selection may have shaped introgression patterns (Taylor & Larson, 2019).

Coral population genomic studies often find individuals with possible hybrid ancestries, but only two studies included explicit tests for recent hybridisation (such as tests implemented in NewHybrids (Anderson & Thompson, 2002)) that probabilistically assign individuals as

putative first-generation and early backcrosses. Hybrid individuals were found among *Agaricia* taxa (Prata *et al.*, 2022) but not among S. *pistillata* taxa (Meziere *et al.*, 2024). Other studies have identified likely hybrid individuals based on the proportion of assignment to different groups from model-based clustering outputs (e.g. Cooke *et al.*, 2020; Kitchen *et al.*, 2020; Bongaerts *et al.*, 2021a; Fifer *et al.*, 2021; Rippe *et al.*, 2021; Rivera *et al.*, 2022; Matias *et al.*, 2023). Using a majority background group assignment score of < 0.75 for distinct sympatric genetic groups as an indication of possible recent hybridisation, we identified potential hybrid individuals for 21 of the 34 species surveyed; however, these mixed ancestry individuals are based on original author preferred K groups and therefore do not necessarily reflect admixture between partially reproductively isolated groups (see Textbox 3 for further discussion). Nonetheless, the prevalence of individuals with mixed ancestry suggests that hybridisation could be ongoing for many taxa.

Historical gene flow between divergent species can be an important aspect of their evolutionary history (Shinzato *et al.*, 2015; Voolstra *et al.*, 2023) even without early generation hybrid individuals being frequent. Unique signatures of historical ("ancient") gene flow between taxa have been demonstrated by contrasting population genetic demographic models using alternative speciation scenarios (e.g., no gene flow versus periodic or ongoing gene flow) (Gutenkunst *et al.*, 2009; Beaumont, 2010; Sousa & Hey, 2013; Fraïsse *et al.*, 2021) thereby resolving the contributions of shared ancestral polymorphisms and introgression to shared genetic variation among taxa. Where demographic modeling has been applied to corals, divergence time estimates among cryptic taxa ranged between a few thousand years (e.g., ~10k between *A. digitifera*: Zhang *et al.*, 2023) and up to 9 million years (i.e., *Galaxea fascicularis*: Wepfer *et al.*, 2020). However, most studies reported recent divergence times ((~0.2-1 million years: Cooke *et al.*, 2020; Bongaerts *et al.*, 2021a; Fifer *et al.*, 2021; Matias *et al.*, 2023; Meziere *et al.*, 2024) that predate Holocene reef configurations. This suggests that divergence began before species shifted into their present-day ranges. Additionally, several studies found strong support for models of speciation with ongoing or episodic gene flow between genetically differentiated and sympatric and/or depth associated cryptic coral taxa with low-to-moderate levels of genetic exchange (e.g., Wepfer *et al.*, 2020; Fifer *et al.*, 2021; Rippe *et al.*, 2021; Prata *et al.*, 2022; Tsuchiya *et al.*, 2022; Matias *et al.*, 2023; Starko *et al.*, 2023; Zhang *et al.*, 2023; Meziere *et al.*, 2024) (Prada & Hellberg, 2021). These findings suggest that recent divergence with gene flow is common across a range of phylogenetic and functional coral diversity and is geographically widespread.

An emerging observation among diverse metazoans is that gene flow between closely-related species is variable across genomes (Ravinet *et al.*, 2017) due to local adaptation or reproductive incompatibilities that reduce gene flow for selected regions (Bay & Ruegg, 2017; Martin & Jiggins, 2017). In cases where variable introgression rates were tested explicitly using demographic modeling of coral divergence, models including heterogeneous gene flow rates received the highest support (Fifer *et al.*, 2021; Rippe *et al.*, 2021; Starko *et al.*, 2023;

Meziere *et al.*, 2024), providing evidence for genomic barriers to gene flow in the sympatric taxa studied and supporting the contention that some degree of reproductive isolation helps maintain genetic cohesion of these interbreeding taxa. For example, in *S. pistillata,* more divergent taxa had a higher proportion of their genomes experiencing reduced gene flow compared to the less divergent taxa, implying that islands of differentiation become wider as speciation proceeds (Meziere et al., 2023). These findings are consistent with morphologically similar taxa being at various stages of the divergence process (Roux *et al.*, 2016).

Low levels of gene flow can contribute to adaptation via introgression (Martin & Jiggins, 2017), where alleles derived from a different species can affect a specific beneficial trait (e.g. resistance to hypoxia at high altitude in humans: Huerta-Sánchez *et al.*, 2015; and winter coat colour in hares Giska *et al.*, 2019). In corals, a genomic region (approximately 220 kb) that appear to contribute to increased bleaching-tolerance for one *A. hyacinthus* taxon relative to other cryptic *A. hyacinthus* taxa was likely acquired through hybridisation with *A. millepora* (Rose *et al.*, 2021). This finding is consistent with some evidence suggesting that historical introgression events may have coincided with *Acropora* range expansions, with possible links to ecological opportunities associated with their diversification (Mao, Economo & Satoh, 2018). While these studies implicate a role for hybridisation in adaptive evolution, and the possibility that large chromosomal variants may be important for adaptation in the context of gene flow, there have been no comprehensive investigations of adaptive introgression in corals to date.

2.6 Implications: investigations that do not test for cryptic taxa risk biased estimates of ecologically important traits

The preceding review of population genomic studies shows that cryptic coral taxa are common (Section 2.1) and may be adapted to and associated with different microenvironments – especially depth (2.3). These cryptic taxa, however, are often linked by sharing symbiont strains (2.2) and via some gene exchange (2.5). Therefore, cryptic taxa may be distinct in terms of ecology, physiology, and evolution, but how to describe and delineate taxa is not obvious, as there may not be complete divisions or obvious diagnostic characteristics. Even with access to genomic-scale genotyping, taxonomic resolution is affected by sampling and open to interpretation. It is clear, however, that gross morphology assessed by humans under field conditions is unreliable for recognising closely related taxa, as over 50% of studies in our literature search show genetic evidence for cryptic taxa (Fig. 3). Simply put, any coral investigation that does not include genotyping, risks treating a heterogeneous mix of partially reproductively isolated taxa as a single species. To get a sense of how extensive this issue could be for other fields in coral biology, in Textbox 2 we show that only 8% of coral experiments on thermal tolerance include genotyping that could identify cryptic taxa. Although it is outside the scope of this paper to examine the thousands of papers in coral biology that examine phenotypes including niches and geographic distributions, we would expect that most experimental and ecological studies are not combined with

genotyping in a way that can detect cryptic taxa, if they are present. Given that unaccounted cryptic taxa can bias estimates of species' traits (alongside estimates of biodiversity and evolutionary dynamics - Section 1), inferences from many studies need to be viewed with scepticism.

3 Corals as untapped systems for studying speciation and adaptation in a changing world

Although cryptic species and gene flow (hybridisation) between closely related coral taxa are more common than previously thought, corals present largely overlooked systems for studying speciation and adaptation. Such studies could bring new insights to processes generating coral biodiversity and would also clarify biological attributes of corals that may sway conservation management decisions and strategies.

The emerging consensus that closely-related coral taxa are frequently sympatric at coarse spatial scales yet segregate by depth or other micro environmental characteristics aligns well with models of ecological speciation (Rundle & Nosil, 2005). Furthermore, the presence of distinct cryptic taxa in close geographic proximity suggests that selection may be very strong (a high selection to migration ratio: Richardson *et al.*, 2014)). To what extent cryptic taxa differ phenotypically or in terms of competitive ability is largely unknown, although differences in bleaching susceptibility among some cryptic taxa suggest differing vulnerabilities to climate change (Section 2.4). As sessile organisms, corals are well-suited to manipulative experiments such as common garden or reciprocal translocation designs. Additionally, their clonal nature means that genetically identical fragments from the same colony can be exposed to differing treatments, offering rich opportunities to combine experiments with genomic analyses to holistically investigate the interactions between taxon identity, phenotype, and environment (Pinsky *et al.*, 2023; Richards *et al.*, 2023).

Divergence dates between cryptic taxa often pre-date Holocene reef configurations, implying that old standing genetic diversity is spread across contemporary reefs that are characterized by spatially complex yet replicated microhabitats and environmental gradients. Thus, corals would be ideal for investigations that explore the genetic mechanisms of parallel divergence (e.g. analogous to fishes that have colonized post-glacial lakes: Rougeux, Bernatchez & Gagnaire, 2017; De-Kayne *et al.*, 2022). Such investigations would also provide insights on the geographic distribution of standing genetic variation, which may be under increasing selective pressure due to pervasive environmental changes. For example, knowing whether geographically distant populations do or do not share alleles for advantageous traits can guide decisions regarding the utility of assisted migration. This is because evolutionary rescue is only worth considering if donor and recipient populations differ in functional standing genetic diversity.

It is likely that endogenous barriers to reproduction suppress gene flow between taxa to some extent. Analyses to date support evolutionary genomic models that allow different genomic regions to be more or less permeable to gene flow, consistent with chromosomal inversions or other structural variants contributing to reproductive isolation (see section 2.5). Future studies that use chromosomal resolution genotyping will be critical to forming a deeper understanding of how species boundaries are maintained (e.g., Leitwein *et al.*, 2020) and can guide decisions on assisted migration or choosing broodstock for selective breeding (Fig. 2).

Individual colonies with genotypes consistent with recent hybrid ancestry have been noted (Section 2.5). To date, these individuals have largely been treated as curiosities and not subject to focused study. Studies of hybridization and hybrid zones also provide important insights on speciation and adaptation (Hewitt, 1988) and would yield key background information to evaluate suggestions that hybrid corals are viable in nature and could be used in restoration. Potential restoration interventions based on hybridisation rest on the supposition that hybrid corals differ in phenotypes from parental species through some combination of hybrid vigor or transgressive segregation. Promisingly, first generation (F1) crosses among *Acropora* species have showed that some crosses survived as well as or better than parentals in some conditions (Chan *et al.*, 2018). Aside from the transect studies of Prada & Hellberg (2014), we know of no systematic attempt to map the spatial and environmental distributions of hybrids relative to parental taxa, and yet this knowledge can yield important insights into natural selection and dispersal of cryptic taxa (Barton & Hewitt, 1985). Mapping hybrids would also allow restoration biologists to easily locate naturally-occurring hybrid corals with a wide diversity of genotypes that could be used as broodstock in restoration methods that rely on sexually-produced offspring (Table 1).

Throughout this review, we have focused primarily on the cnidarian component of coral genomes to document evidence for cryptic species and hybridization. However, in considering how future studies could build on these observations to better understand speciation and adaptation processes, it will also be important to integrate genetic analyses of microbes – especially symbiotic dinoflagellates – with those of the cnidarian host. An exciting line of investigation would be to try to understand the co-evolutionary dynamics of hosts and symbionts in reference to environmental adaptation and speciation, where environmental heterogeneity likely exerts direct selection on both corals and their symbionts (i.e. the coral holobiont) and indirect selection via host-symbiont genetic interactions.

4. Conclusions

In this review, we demonstrate that cryptic coral taxa are extremely common and are often connected by gene flow. Many previous studies have emphasized the importance of such

cryptic coral taxa (Gomez-Corrales & Prada, 2020; Bongaerts *et al.*, 2021a; Burgess *et al.*, 2021; Feldman *et al.*, 2021; Rippe *et al.*, 2021; Zayasu *et al.*, 2021; Prata *et al.*, 2022; Rivera *et al.*, 2022; Matias *et al.*, 2023; Pinsky *et al.*, 2023; Starko *et al.*, 2023; Voolstra *et al.*, 2023; Meziere *et al.*, 2024) and here we use a systematic examination of published population genomic studies to document that cryptic taxa are indeed widespread across coral families (Fig. 3).

The prevalence of cryptic coral taxa means that many accepted understandings and conclusions regarding coral biology could be incorrect. In this review, we argue that hidden taxonomic diversity can affect conservation thinking and, in the extreme, mislead possible management decisions if ignored. In Section 1, we highlight how ignoring cryptic taxa can: bias estimates of spatial biodiversity patterns; make species appear to have larger ranges, trait spaces, and niches; and can skew inferences regarding intraspecific population structure and gene flow in unpredictable ways. Thus, as a field, we are unable to confidently generalize species distributions, ranges, and phenotypes including resilience to heat stress without adequate study of potential cryptic taxa (Textbox 3). Identifying locations with high genetic diversity that may harbour greater adaptive potential or inferring sites with high gene flow and dispersal will crucially depend on analyses that are able to detect and account for distinct taxa.

Although observations of cryptic coral taxa are frequent, our collective knowledge regarding the evolutionary dynamics that enable closely-related taxa with incomplete species boundaries to persist in sympatry remains limited. There is a vast potential to unite coral studies with the insights and approaches into speciation and adaptation from other fields and organisms. For example, partnerships between coral ecologists, physiologists, and population geneticists may bridge insights into coral population microevolution to climate change, while collaborations with experts from other fields may broker novel analyses and genomic-based approaches to speciation and hybridisation in corals.

The reality, however, is that the future for corals and coral reefs is perilous (Knowlton *et al.*, 2021). Management decisions cannot wait for perfect information. Therefore, it is incumbent for evolutionary biologists to identify attributes that do or will affect coral health and evolutionary trajectories for the short-term future. An important next step will be to explore how conservation and management actions can best proceed with a newfound expectation that coral species boundaries are unlikely to be well defined – a conservation challenge that ultimately afflicts many other taxa apart from corals (Roux *et al.*, 2016).

Textbox 1: Applying taxonomic delineation with reproductive isolation criteria

We propose three requirements for identifying and delineating taxa using genomic-informed ordination and model-based clustering approaches. In the empirical example that follows, we detail how coral cryptic taxa were identified using three criteria (section 2.1) and highlight difficulties with interpretation.

Colonies of the brooding coral, *Agaricia agaricites*, were sampled at four sites ~10-15 km apart along southwest Curaçao, and collections were further subset to three depths (5, 10 and 20 m) at each site. Genotyping using reduced representation sequencing of 335 colonies and 1,629 SNP-loci revealed distinct genetic groups co-occurring within four sampled sites. This study provides a clear example of cryptic taxa identified according to criteria 1-3. Furthermore, taxa occupied unique depth ranges (AA1 occurs predominantly at 20 m, whereas AA2 occurred at all depth sampled) suggesting divergence of taxa by habitat (Fig. T1A & C).

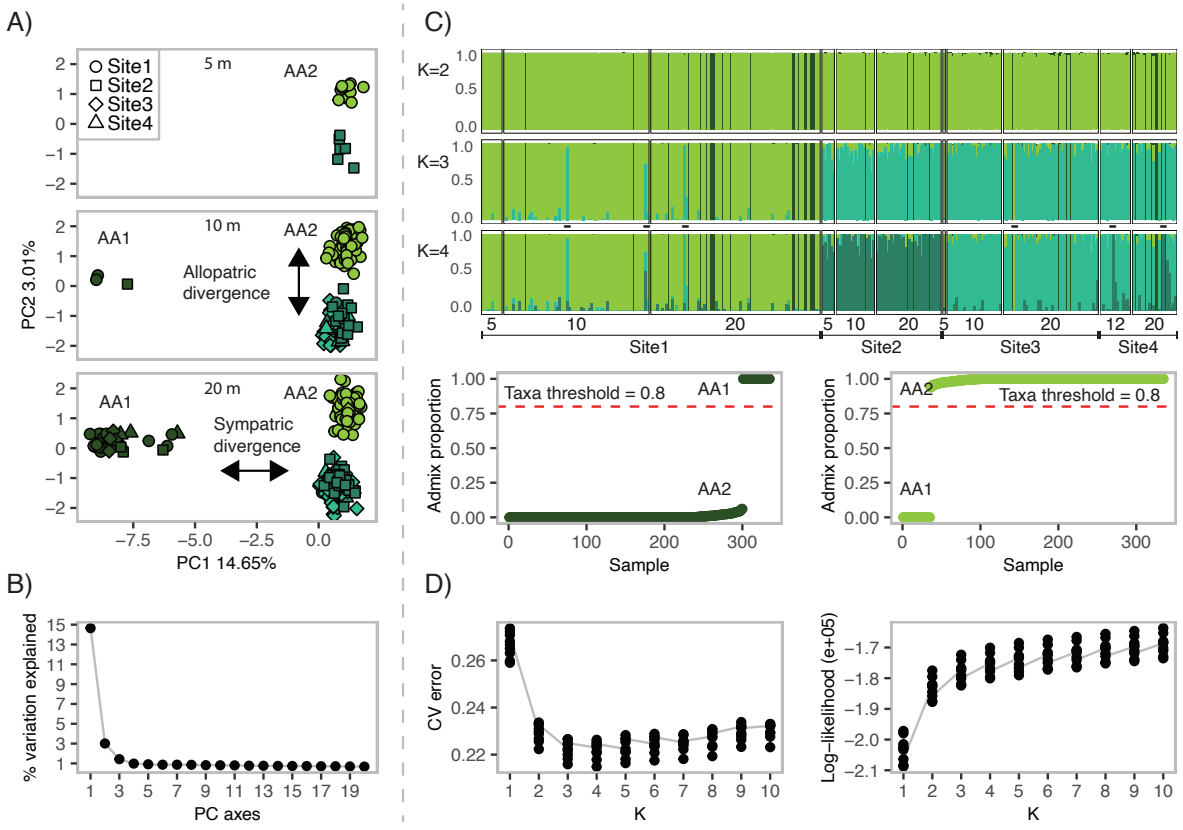

Figure T1 - *Agaricia agaricites* resolved into two distinct taxa and fulfil criteria 1, 2 and 3 for cryptic taxon delineation. A) PC1 resolves two sympatric groups at every sampling site. PC2 represents an example of geographic partitioning in AA2 (Site 1 vs Site 2 - 4) and therefore does not necessarily imply reproductive isolation. B) Shows that the percentage of variation explaining PC1 (14.65%) is ~5x more than PC2 (3.01%). C) Analyses using ADMIXTURE for K=2 assigned individuals to each group with high confidence (q > 0.9) and showed that AA1 and AA2 were sympatric at all sites. D) There is a significant drop in cross-validation error between K=1 and K=2, and greater log-likelihood, supporting

the selection of K = 2. All three criteria are met in delineating AA1 and AA2 cryptic taxa within *A. agaricites*.

This example also illustrates some complications for interpreting differentiation among putative taxa. The second PC axis (also mirrored in ADMIXTURE outcome for K=3 and K=4) shows partitioning that largely aligns with geographic separation and so would not be considered as delineating distinct taxa under our criterion of sympatry. If the variation captured by the second PC axis (and K=3 and K=4) reflects geographic differentiation, geographically mismatched genotypes likely reflect recent immigration (shown by dashes among K=3 and K=4 in Fig. T1C). Distinguishing migrants from distinct taxa may be especially difficult when sampling numbers are low. However, if immigration is high (> 1 migrant per generation) and there are no barriers to reproduction then the structure between populations is expected to dissipate over a few generations (Waples & Gaggiotti, 2006).

This example highlights the utility of PCA and cluster-based modeling methods for identifying cryptic coral taxa. However, additional subsetting and filtering steps are necessary to thoroughly scrutinize data for consistent patterns and reveal accurate groupings. To better understand the possible biases of both PCA and assignment methods, we refer readers to (Pritchard *et al.*, 2000; McVean, 2009; Puechmaille, 2016).

Textbox 2: Are coral experiments designed to detect cryptic taxa?

Overlooking cryptic taxa in experiments can bias interpretations of experimental results. To ascertain how substantial this issue might be for coral studies, we focus on experiments related to thermal tolerance as a subset of coral studies more generally. Marine heatwaves have caused extensive coral mortality and bleaching events globally (Leggat *et al.*, 2019), and thus numerous coral studies have aimed to ascertain intra- and inter-specific differences in phenotypic and physiological heat stress responses using experiments (e.g., common gardens, reciprocal transplants, etc.) and natural heating events. Mounting evidence suggests that cryptic species and hybrids display contrasting responses to heat stress (Section 2.4), and so experimental results may be more accurate when taking into account potential cryptic taxa – identified using genomic-scale genotyping .

The Coral Research and Development Accelerator Platform (CORDAP) database (Ortiz, Humanes & Scharfenstein, 2023) represents a curated search for papers that study thermal biology of corals. We screened the database to identify records which used genome-wide data of the coral host (i.e., coral SNP data) and those that conducted either ordination or model-based clustering (as in 2.1). We evaluated the database to determine:

1. The number of studies within the database undertaking marine heatwave experiments that genotyped corals for multiple unlinked markers (i.e., created data that could be used for ordination or model-based clustering).
2. The proportion of these studies that performed either an ordination or model-based clustering based on individual genotypes.
3. Whether there is evidence for cryptic taxa based on applying the criteria outlined in Section 2.1.

We found that very few experimental studies genotyped coral colonies - from 562 studies, 222 studies undertook marine heatwave experiments, of which 59 studies included any sort of host genotyping and only 17 used high-resolution genome-wide markers such as SNPs. Still fewer studies undertook either ordination or model-based clustering on their genomic data (n= 9; Fig. T2). Of those nine studies, three showed indications of cryptic taxa in line with proportions of cryptic taxa in population genomic surveys (Fig. 3). It is likely that many studies will have inadvertently sampled multiple taxa and therefore we would anticipate that reported variances among individuals within studies will be greater than true variances within cryptic taxa (see Section 1). This could manifest as a bias in overestimated thermal tolerance breadth and thus may also mask differences in measured tolerance in comparative tests between morphospecies. The CORDAP database focuses on one group of studies, but we would anticipate that similar issues arise across all coral experimental work that does not leverage genomic-level genotyping of individual colonies.

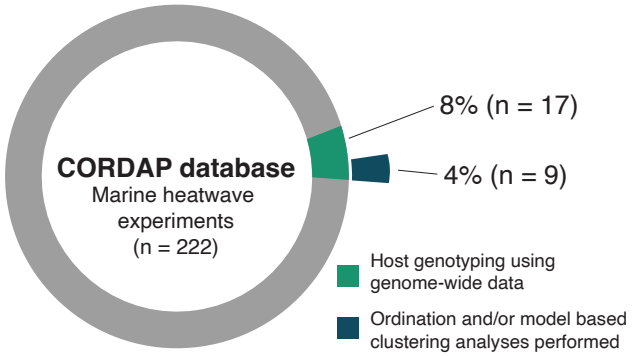

Figure T2 – Proportion of individual studies from the Coral Research and Development Accelerator Platform (CORDAP) thermal tolerance experiment database that: (1) record genotype data capable of identifying cryptic taxa via genome-wide data of hosts, and (2) test for cryptic taxa via ordination-based analyses or model-based clustering analyses.

Textbox 3: Best practice recommendations

Future genomic surveys of corals should be designed with the expectation that cryptic species could be encountered. This means undertaking structured and replicated sampling, reassessing field collection protocols, and testing for cryptic taxa as part of bioinformatic and

population genetic analyses. Ensuring that all data and metadata are thoroughly documented will create the best chances that future investigations can re-examine published data as novel methods emerge and thus bypassing the need for additional fieldwork and genotyping in some cases.

Spatial sampling at the colony level

The best evidence for discriminating cryptic taxa from population structure is when distinct taxa are observed in sympatry (or close geographic proximity) at multiple locations (Section 2.1). We acknowledge that there is an element of chance in co-sampling distinct taxa. Given that depth appears to be the most common axis of differentiation, however, researchers who are planning to sample across depth should ensure that the same depths are sampled at multiple distinct locations to enable the detection of repeated co-occurrences of distinct taxa.

Alongside structured sampling, investigators would greatly enhance their data's value (and scope for future inference) by transitioning from a population sampling mindset to focusing on individual sampling and seeking to capture as much environmental context as possible at the colony level. For instance, "cryptic" species may in fact be morphologically distinguishable based on subtle characteristics (for example, *S. pistillata*, Meziere *et al.*, 2024) and therefore taking comprehensive photographs that can be examined later (see, for example, Protocol for Coral Collection & Curation by Project Phoenix: https://coralprojectphoenix.org/resources/#protocols) may allow diagnostic characters to be identified post hoc. For a subset of samples, it would be useful to retain larger colony fragments that would be suitable as museum voucher specimens, if permits allow. Recording each colony's geoposition and depth can greatly support analyses based on depth (i.e. as a continuous rather than categorical predictor) and space, while simultaneously could provide insights on the microhabitat attributes of cryptic taxa and hybrid individuals (as in (Prada & Hellberg, 2014)). A particularly exciting technology that can greatly advance this colony-focussed perspective is photogrammetry (Bongaerts *et al.*, 2021b). We recognise that moving the focus from coral populations to colonies will require more time, effort, and expense, but the insights will be far richer.

Datasets that link genomic genotyping with ecological context at the colony level will be immensely valuable for gaining insights into ecological and evolutionary processes relevant to conservation. To maximise this value, investigators should strive to make all facets of their data open, which includes linking genotypes with all recorded metadata including metadata that might not be relevant to the original study (but that might be of value to others). Analytical pipelines also need to be fully reproducible by enabling consistency in bioinformatics and analytical decisions across studies such that outcomes can be confidently compared. No doubt, all this extra documentation is a substantial amount of work, and therefore should be incorporated into initial project planning. Coral biologists can take inspiration from plant population geneticists who have greatly advanced insights and impacts

by sharing highly curated data sets that have been re-used and supported a myriad of additional studies after their initial publication, for example, the IntraBioDiv (Meirmans *et al.*, 2011) dataset of 27 co-distributed alpine plant genotypes has supported numerous reanalyses and test cases. Additionally, the genomic (and phenotypic) datasets for lodgepole pine and spruce from the AdapTree group (https://adaptree.forestry.ubc.ca/about/scientific-summary/) have greatly advanced understandings of spatial adaptive diversity in trees.

Adjusting bioinformatic pipelines and analyses

Bioinformatics and population genetic analyses also need to be sensitive to the possibility of cryptic taxa (see also Section 2.1 and Textbox 1). Missing data thresholds and other data quality filters are employed as standard practice on individuals and loci. However, sensitivity of different missing data thresholds to test taxon assignment and hierarchy hypotheses are not often mentioned. The more divergent groups are, the fewer sites they will share and thus blanket missing data thresholds on heterogeneous samples may bias patterns. Applying different missing data filters and subsetting datasets by selecting an even representation of predetermined groups (from initial structure analyses) or isolating certain groups can help in determining if the assignment and hierarchy of groups is stable and robust to the filters selected (Pritchard *et al.*, 2000; McVean, 2009; Puechmaille, 2016). Intermediate or admixed individuals may appear as hybrid individuals, but the causes of these patterns are many, *e.g.*, unexplained variance due to geographic structure, under-sampled taxa, admixture with unsampled taxa, or higher levels of missing data for some individuals. Thus, we suggest formal hybrid tests are employed for clarification (e.g., NewHybrids). Investigators should be transparent regarding how biases or decisions were handled when reporting groupings. We suggest following advice from (Meirmans, 2015) by always reporting multiple K values when using assignment methods, as clustering analyses represent a heuristic approach that is open to interpretation for all biologically-sensible K values, even if an optimal K-value is selected by the user-defined summary statistic. Similarly, PCA results should present the percent of variation explained and include multiple axes. Ultimately, we hope that the guidelines presented here can be used as a framework to detect coral cryptic taxa in future population genomic investigations.

In the absence of genotypes….

While population geneticists are the target audience for our recommendations, any coral biologist whose data interpretations could be affected by cryptic species would do well to incorporate genotyping in their project planning. For instance, genotyping is largely overlooked in experiments (Textbox 2). For experimental work, we propose that future studies should: 1) where possible, include larger sample sizes (n > 30) to screen for cryptic genetic population structure (this will ensure downstream comparisons in individual phenotypic differences are not confounded by cryptic speciation); 2) follow guidelines from 2.1 to recognise cryptic species; 3) report initial data checking methods and results (e.g., screening population structure) in publications and reports (e.g., in supplementary items) to

assist the interpretation of individual- and population-level differences; and 4) clarify definitions and conventions for terms such as “cryptic species'' and establish common terminology.

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Data, scripts, code, and supplementary information availability

Data and supplementary information are available linked to this pdf at EcoEvoRxiv.

Conflict of interest disclosure

The authors declare that they have no financial conflicts of interest in relation to the content of the article.

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Appendix

Structured review for population genomic studies

An initial search of Web of Science on 21/10/2022, using the search terms "(TI=(coral) OR TI=(scleractinia*) NOT TI=(fish)) AND (AB=(rad*) OR ALL=(snp*)). The search returned 802 studies. Titles and abstracts were skimmed, and many irrelevant papers were excluded. Any manuscript that appeared to contain population genomic data of scleractinians or octocorallians was then retained for manual inspection.

Each manuscript was read and evaluated by two people to ensure that the genomic data: i) pertained to the cnidarian coral host, ii) used many loci on a genomic scale (i.e., not microsatellites, not metabarcoding), iii) surveyed two or more sites, and iv) presented results that included ordination based on individual genotypes (principal components analysis, principal coordinates analysis or multidimensional scaling) and/or unsupervised model based clustering test (such as ADMIXTURE or STRUCTURE). We did not consider papers that only reported discriminant analysis of principal components, as DAPC finds the eigenvectors that best differentiate prespecified groups, whereas PCA, PCOA and MDS find eigenvalues that best capture total diversity regardless of group membership (see (Thia, 2022) for further discussion). If these four criteria were not met, the paper was excluded. For each retained paper, the two evaluators independently extracted various attributes from the study (see raw data) and reconciled any discrepancies between their scoring through discussion. Despite attempting to undertake a rigorous and inclusive search, the authors noticed that several suitable manuscripts were missing and therefore on July 18, 2023 we ran an ad hoc search in WOS based on authors that are known to be publishing on population genomics of corals (namely Barshis, DJ; Baums, IB; Bay, LK; Bongaerts, P; Cooke, I; Matz, MV; Palumbi, SR; Richards, ZT, Underwood, JN, van Oppen, MJH) and also repeated the the above search with exactly the same criteria for articles published since 21/10/2022. These new papers were evaluated as above.

The initial search yielded 853 papers that were reduced to 27 after skimming titles and abstracts, and 25 were found to be suitable for data extraction. The ad hoc search (combining authors and new publications) initially identified 897 papers in WOS that were reduced to 16 papers once titles and abstracts were skimmed, and only 11 were suitable for data extraction.

Heat stress studies

The CORDAP database (Ortiz *et al.*, 2023) was downloaded and searched on 11/09/2023, searching for any records which used genome-wide data of the coral host (i.e., coral SNP data) and those which conducted clustering analyses (e.g., PCA, ADMIXTURE, or STRUCTURE). First,

records were filtered based on whether the database columns “Host_genotype”, “Symbiodiniaceae_genotype”, and “Microbiome_genotype” were listed as “TRUE”. Next, the columns “Symbiodiniaceae_genotyping_approach”, “Host_genotyping_approach” and “Microbiome_genotyping_approach” were interrogated and only records where the genotyping method was listed as RADseq, WGS or RNAseq were kept for further checks. The titles and abstracts of the remaining records were skimmed, and only records for which at least host genotyping was performed were included. The remaining records were read and evaluated to ensure that they i) pertained to the cnidarian coral host, ii) used many loci on a genomic scale (i.e., not microsatellites, not metabarcoding, but single nucleotide polymorphisms), iii) presented results that included ordination based on individual genotypes (principal components analysis, principal coordinates analysis or multidimensional scaling) and/or an assignment test (such as ADMIXTURE or STRUCTURE). Additionally, the number of cryptic species assigned in each paper by the original authors was noted, as well as the evaluators’ interpretation of the number of cryptic species based on the plots and analyses included (where possible).

The original database consisted of 562 records, many of which did not include host, Symbiodiniacae or microbiome genotyping. The initial filtering of the database for records that included some aspect of host genotyping yielded 223 results. Applying criteria i & ii by skimming abstracts and methods reduced the studies to 17 records. Of these 17 studies, nine studies included either ordination or model-based clustering analyses (e.g., PCA, ADMIXTURE). Of these, three (Rose *et al.*, 2017; Ruiz-Jones & Palumbi, 2017; Rose *et al.*, 2021) the criteria in Section 2.1. The remaining six studies were either ambiguous or showed no clear evidence for cryptic taxa.