

Revision round #1

Decision for round #1 : **Revision needed**

Major revision

Dear authors,

Sincere apologies for the length review process. Both the reviewers and I have found your manuscript very interesting and important, well-written, referenced and illustrated. As pointed out by one reviewer, there unfortunately great overlap between your studie and that of Carsten Grupstra et al (doi:10.1038/s41559-023-02319-y). One reviewer suggested several ways to circumvent this problem: stressing more strongly the conclusions that are original to your study, reducing the parts that are redundant with Grupstra et al, adding any new references to your analysis. I would add it is implicit that your study (and Grupstra) focus on reef-building corals of the photic zone, while deep-water corals forming reefs and gardens likely present the same issues of confounding cryptic diversity. Widening the depth range and including deep-sea corals would therefore add significant value to your study. We would very much like to see a revised version of your paper. Beyond this important point on reducing the overlap with Grusprtra et al, please answer the other comments from both reviewers. Reviewer 2 noted that " the importance of the population level in conservation should be mentioned" ; to me this was well in your textboxes ; perhaps emphasizing that point in the main text could be useful as well. Please find attached my comments on the text, along with the reviewers.

Best regards, eric pante

Dear Dr. Pante –

We thank you and the two anonymous reviewers for your thoughtful comments and your patience with our long revision time. We have endeavoured to address the identified issues comprehensively. We have also received comments from MJH van Oppen and K Johannesson and thus some edits will reflect their suggestions. Prof Johannesson is well regarded as world expert on speciation and her suggestions on how to better integrate our work with speciation literature are reflected in the document, especially the revised introduction, section 2, and section 4.

The review by Grupstra et al. was published the same week that we posted our preprint and so any similarities indicate independent convergence. Nonetheless, we have taken reviewer 1's suggestions in stride and pruned away discussions of older coral literature to keep the focus on our new analyses of population genomic studies and to emphasize the components of our work that are unique, namely: (i) reproducible criteria for cryptic taxa delineation, (ii) consideration of hybridisation, (iii) discussion of how oversights affect conservation and restoration, (iv) concrete recommendations on how to advance coral studies, and finally (v) linkages to speciation and adaptation fields. There will, of course, be some areas of unavoidable

overlap with Grupstra et al., but we have tried to minimise these while keeping our narrative coherent. Because of this updated focus, there has been substantial reorganisation and rewriting of the text, including a new figure (Fig. 4) and a new Table (Table 1).

Our search of the literature included both shallow and deep-water corals; however, no deep-water coral study passed our criteria for inclusion. The fact that only shallow water corals have sufficient data for cryptic taxa assessment is interesting. To highlight these points, we have updated section 2.2 “Although we did not restrict our search by sampling depth, none of the recovered records included species beyond mesophotic depths (i.e., >150 m), and therefore the results that follow describe shallow water and mesophotic corals.” (lines 250-252) and the conclusions state that, “Although our assessments reflect findings for shallow-water corals, we would anticipate that deep-water corals also harbour substantial cryptic diversity. Our failure to locate population genomic studies of deep-water corals indicates that more genetic studies of deep-water corals are needed.” (lines 812-813).

We have addressed population conservation by adding a sentence to the conclusions as suggested by the reviewer and (823-826) highlighted differences between evolutionary and ecologically significant levels of gene flow (450-454).

by **Eric Pante**, 24 May 2024 15:04

Manuscript: <https://doi.org/10.32942/X2502X>

version: 1

Review by anonymous reviewer 1, 22 Apr 2024 14:32

Review for the PCI Manuscript “Cryptic species and hybridization in corals: challenges and opportunities for conservation and restoration” by C Riginos et al.

As this manuscript is a review article, some of the questions in the PCI checklist don't apply. Here below are my answers to ones I deemed relevant:

- Title and abstract
- Does the title clearly reflect the content of the article? Yes
- Does the abstract present the main findings of the study? Yes
- Introduction
- Are the research questions/hypotheses/predictions clearly presented? Yes
- Does the introduction build on relevant research in the field? Yes
- Materials and methods

- Are the methods and analyses sufficiently detailed to allow replication by other researchers? Yes
- Are the methods and statistical analyses appropriate and well described? Yes and No see below
- Discussion
- Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? Yes
- Are the conclusions adequately supported by the results (without overstating the implications of the findings)? Yes

General comments

The manuscript is really well written and addresses an important issue in coral reef studies. Through its analysis of the literature, it also stresses a point I strongly back, that corals are very nice models for the study of speciation processes.

Thank you for your positive comments.

However, the read would have been totally enjoyable and timely if another review on precisely the same topic had not been published very recently (“Integrating cryptic diversity into coral evolution, symbiosis and conservation” by Grupstra et al. published online in February 2024 in Nature Ecology & Evolution <https://www.nature.com/articles/s41559-023-02319-y>). Overall, the manuscript under evaluation shares more than a quarter of its references with the published review, and even if the authors of the present manuscript stress that they focused their analyses on NGS based studies, this proportion of shared studies rises to more than 40% for coral related citations. A good point for the present manuscript is that it could profit from the more recent publications that per force were not analyzed in the already published review (a strong signal of the current high activity in the domain).

As pointed out previously, our preprint was also posted the same week in February 2024 and so the overlapping references reflect the fact that two independent set of authors have reached similar conclusions. We think that this independence and convergence underscores the importance of the central messages in both papers. Rather than putting our efforts to updating surveyed studies, an exercise that can be never ending where the main messages are unlikely to change, we prioritised expanding discussion (and analyses) for the topics where our manuscript diverges from Grupstra and reducing the areas of overlap – see details in the next response below.

Unfortunately, this leads to very similar discussions and conclusions in the two articles on several topics, leaving involuntarily the somewhat false impression that NGS based approaches did not bring about new insights in coral crypticity. But, again, this feeling arises when reading the two articles in a row and is not due to any

fault of the authors of the present study. They just had the bad luck of publishing their analysis in second...

On the other hand, the present manuscript develops more issue around speciation processes, and goes back on previous thermotolerance literature in the light of the high occurrence of cryptic species, two original and valuable points.

There are some important differences between the manuscripts and in our response to handling editor Dr. Pante (above) we highlight five topics where our manuscript provides greater commentary (aligning to R1's comments). Additionally, we tried to capture all coral population genomic studies published at the time of our search (examining 1656 studies in total) followed by stringent and reproducible criteria for recognising cryptic taxa. In contrast, Grupstra non-exhaustively examined 100 papers (regardless of genetic markers) and synthesize findings from the original authors without new analyses. Thus, we can provide the first estimate for the prevalence of cryptic taxa. Additionally, in line with R1's comment, we integrate our discussion with speciation literature (as suggested), expand implications of cryptic species for thermal tolerance (and other conservation relevant issues) and align to speciation literature.

The Nature Ecol. Evol. Review being already published, I would recommend to the authors, with the objective to gain in added value for their manuscript, to slightly amend their text in stressing more strongly the conclusions that are original to their study (especially their focus on genetic data analysis), and in reducing the parts that are now redundant to the published review (see more detailed comments below).

We appreciate this suggestion, and the revised manuscript focuses more strongly on genomic studies only, and we removed passages and sections based on older literature (low marker number studies) where information overlaps with the published review.

Line by Line comments:

Lines 215-217: As stated above (and on line 190), this focus on NGS based approaches is original to this manuscript. I would therefore recommend that conclusions based on earlier techniques be reduced if not skipped, as they are developed in the published review.

These sentences have been removed.

Line 261: the statement that PCA and hierarchical genetic clustering methods are "unsupervised machine learning methods" seems to me a bit bold, and would have at least needed more justification...

The phrasing has been removed, although we disagree that this statement is controversial (see <https://www.kaggle.com/code/kashnitsky/topic-7-unsupervised-learning-pca-and-clustering> and <https://www.sciencedirect.com/science/article/pii/B9780128240540000125>).

Lines 296-314: If I understood correctly, these lines describe the way the literature survey was conducted. They therefore arrive late in the manuscript, in the sense that this part is included in section 2 whose title is already a conclusion of the survey. This part would have gained to be presented in its own section, as it describes the data mining protocol.

Thank you for this suggestion. The manuscript has been substantially reorganised and therefore this “methods” section now appears much earlier in the manuscript and has been given its own subsection (2.2) to call attention to the data mining procedures.

Line 299: The authors restricted their review to publications using Structure and ADMIXTURE as model-based clustering analysis. I wonder why they excluded snmf analyses (Frichot & François 2015) from their choice, especially when focusing on NGS based approaches (considering that snmf clustering is particularly adapted to large datasets).

This was an oversight on our part. Results from sNMF were included. Thank you for pointing this out.

Line 312: The authors also restricted their survey of model-based clustering analyses to outcomes when individuals were assigned to only two groups ($K=2$). Isn't this threshold too stringent, as the number of cryptic species found in a given dataset is strongly dependent on the sampling scheme (i.e. it can be relatively easy in some places to sample more than two cryptic species even in few individuals)?

We agree with the reviewer that in some cases there might be more than two cryptic species. However, we wanted to devise tests that were conservative to the hypothesis that cryptic species exist. This is why we feel confident that the results presented in Fig 2 (and our associated statistic of 68%; line 254) represents a minimum threshold of cryptic taxa.

Lines 357-408: This whole section, through based on recent publications, is quite redundant in its conclusions to the corresponding section in Grupstra et al. (which also included some of these publications). It could maybe therefore be reduced to develop more its last part (lines 402-408) that stress the need to go beyond single marker approaches for the characterization of the symbiont population.

This section (now 2.3) has been substantially shortened and reorganised. We stress the need to go beyond single marker approaches as suggested (318-330).

Lines 384-387 A verb seems to be missing.

Fixed

Lines 410-478: The discussion on depth structuration, mostly based on less recent papers, is also well developed in Grupstra et al. and would gain by differentiating itself from the published review. In that prospect, the Figure 4 is quite interesting and welcome.

This section (now 2.4) has been substantially reduced and the focus put on the genomic studies reviewed, along with Fig. 3.

Lines 524-540: This whole section is totally redundant to its counterpart in Grupstra et al.

This section has been removed.

Lines 542-547: This section, and Textbox 2, on the other hand, are totally original and definitely interesting (through disturbing!).

Thank you for supporting this analysis. Because the section was removed, we have relocated relevant text discussing Textbox 3 (previously TB2) to section 3.2.

Lines 578-615: Same comment, these sections are original and interesting and would therefore gain in being more developed.

In line with this suggestion, we have substantially expanded this section (now 2.5) and added a new figure (Figure 4) to support the text.

Lines 762-804 Textbox 1 relies heavily on the conclusions of Pante et al. 2015 (and not 2014, the online publication date), cited elsewhere but not here, and Carstens et al. 2013, not cited at all)

Thank you for pointing out our citation error with Pante et al 2015, which is now fixed throughout.

In reviewing the text in question, however, we disagree that our interpretations rely on Carstens' study (and indeed we had not previously read Carstens et al 2013). Here, we are focusing on weakly differentiated groups that are discerned by allele frequency differences, allele to genotype ratios (i.e., methods like STRUCTURE that place individuals in groupings to minimise Hardy-Weinberg disequilibria), and covariance and linkage disequilibria among loci, whereas the situations that Carstens et al. describe involve greater levels of differentiation, supporting their choice of "lineage" as a biological unit. In the present case, however, because gene trees of individual loci are unlikely to align with weakly differentiated groups, the term of lineage can be confusing as it implies monophyly and implicitly suggests non reticulate evolution. Therefore, we avoid the term lineage (lines 121-123). Additionally, our criteria focus on the situation where genetic groups are found in sympatry, a scenario not explicitly discussed by Carstens et al. Thus, this citation is not relevant to the present study.

We do, however, find much overlap with Pante et al (2015), and therefore now refer readers to that review in several places in the document (111, 625, 630, 891).

Also –

We also thank R1 for their annotated comments in a marked-up version of the pdf. We have endeavoured to make changes as appropriate. For Fig 1, the reviewer suggests including pictures of corallite structures or other taxonomic characters – this would be a great addition but unfortunately, we do not have such photographs.

Review by anonymous reviewer 2, 04 May 2024 13:07

This manuscript provides an interesting review on why and how cryptic species and hybridisation should be taken into account in the conservation of corals. As well demonstrated by the authors, cryptic species and hybrids are observed in different coral genera, and the development of genomic approaches expanded the scope of these observations. Nevertheless this is not always well used in conservation, or even in experimental biology. The article convincingly shows that such lack of knowledge regarding species limits has important consequences for the design of restoration approaches or the study of the response to climate change for example. The article is well written, and well argued, with pertinent references and a meta-analysis of the identification of cryptic taxa in corals. Though dedicated to a specific group of Metazoans, this review has a more general interest, as the questions raised here could be applied to other eukaryote groups. The article may be shortened, but I acknowledge that several of my comments would add to the length of the manuscript.

Thank you for your kind comments regarding our manuscript.

The article, from the title, discusses cryptic species and hybridisation. But hybridisation can also be observed between well defined, non-cryptic taxa. Conversely, some cryptic species can be observed without hybridisation, and do not correspond to the grey zone of speciation. Maybe this could be clarified in the text (see specific comments below).

Thank you for these comments. We have restructured the introduction substantially in response to comments from both reviewers and believe that the definitions are now more explicit (118-123, 168-170). Mentions of hybridisation between non cryptic species are also more prominent.

Regarding the identification of cryptic species, the authors mainly discuss multivariate or structure-like analyses. There are other approaches which could be mentioned as well, such as methods of species delimitations based on single locus or genomic data (see for example Oury et al., 2023; Puillandre et al. 2021).

The scenarios that we focus on in this manuscript are those of subtle genetic differentiation that will primarily be reflected in covariances of allele frequency differences across loci rather than fixed differences of select loci – see also response to R1 for not citing Carstens et al (2013). Single locus delimitation methods rely upon first recognising distinct groups and subsequently identifying loci with fixed differences (should they exist). Thus, our focus here is on the initial step of recognising distinct groups – these issues are described in detail in 2.1 (especially 179-197) along with our motivation for relying on multivariate analyses.

Additionally, demographic inferences now provide a powerful way to estimate gene flow among populations or species (e.g. Fraïsse et al., 2021), and to test evolutionary scenarios. I understand that this is not a methodological article, so I let the authors decide if they extend textbox 1 with such methods.

This is a good point. We have added a sentence to the end of Textbox 1 that points towards these ideas: “Once taxa are delineated, investigators can look for recent hybridisation (e.g., Anderson & Thompson, 2002) and test scenarios of gene flow and divergence history (as in, Roux *et al.*, 2016; De Jode *et al.*, 2023).” In addition, we have greatly expanded our review of studies using demographic inference in section 2.5 and have added a new figure (Fig. 4) summarising results from studies that used demographic inference.

The conclusion shows well the importance, and maybe the limits, of these studies in a context of global change. At that point I think the importance of the population level in conservation should be mentioned. Even in the absence of cryptic species, a precautionary approach would involve the identification and conservation of populations of a given species in different environments and different genetic backgrounds.

This is an excellent suggestion, and we used the reviewer’s phrasing of “precautionary” and have taken the spirit of this suggestion to form new sentence in the conclusions “Without genomic and/or experimental data on hand, a precautionary principle may be to assume that populations inhabiting distinct environments (especially depth) are likely to be evolutionarily distinct and ecologically independent.” (823-826) Because we have not attempted to capture population structure within taxa, it would not be appropriate for us to comment on within-taxon dispersal (a very interesting topic for another paper). Aligned to this comment, however, we have also highlighted differences between evolutionary and ecologically significant levels of gene flow (450-454).

I also have specific comments below.

Specific comments

Line 59-65: I totally agree. But as a personal note, I would add that corals per se are wonderful model species to study for several reasons: symbiotic interactions, adaptive abilities, and of course as developed here, speciation and hybridization.

Certainly, we all agree on these points!

Line 76: “observations” of what?

This sentence was removed with rewriting.

Line 80: morphology can also lead to overestimate diversity in case of morphological plasticity for example? This could be mentioned. But underestimation is probably more frequent.

Good point. Text modified somewhat: “Phenotypic plasticity could sometimes upwardly species counts, but under estimation is likely more prevalent.” (569-570)

Line 87: so this may also point to well differentiated populations inside species? (Which I find interesting to consider as well)

We agree that well differentiated populations within species would be interesting to consider. For this manuscript, however, we are focusing solely on groups where there is circumstantial evidence for reproductive isolation due to the groups being sympatric. When there is a spatial component to differentiation, both extrinsic and intrinsic barriers to gene flow need to be considered. By focusing solely on sympatric groups, the emphasis is on intrinsic barriers to reproduction, aligning to speciation theory. This logic is fully explained in lines 170-177.

Lines 89-90: you could also consider the definitions discussed by Cahill et al. (2024)

Thank you for pointing out this reference. The distinction of pseudo and strict cryptic species is useful, and we mention this and cite the reference (112).

Lines 119-122: you could develop this discussion to explain the link with the previous sentences: the first article relied on morphological identifications.

We have added text linking these ideas (namely that hybrids may have unusual morphologies):

“Conversely, some rare species may in fact be hybrids (Richards *et al.*, 2008) and thus the number of rare species might be reduced.” (567-569)

Lines 124-137: this is partly said here, but from an experimental point of view inadequate species delimitation or identification could lead to erroneous estimates on thermotolerance, and then this can have important consequences on species distribution models forecasting the impact of climate change for example.

Excellent point. We have added the following sentence to this paragraph: “Such erroneous estimates of species niches and phenotypes would, in turn, undermine the accuracy of species distribution models that might be used to predict future locations with suitable environments under climate change.” (595-597)

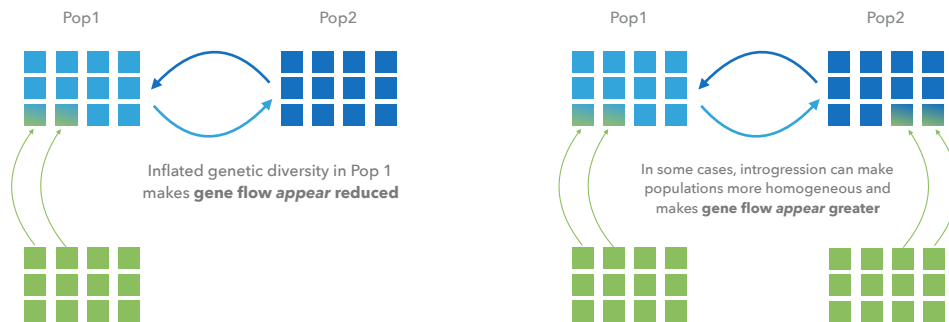
Lines 135-137: this is not only about agglomeration, but also misidentification: one can erroneously assign a trait range to a species if it's not properly recognised

Fixed. The sentence now reads:

“Current evidence suggests that conclusions drawn from incorrectly identified taxa are likely to be overly optimistic in terms of species ranges and niche breadth, and therefore will likely overestimate coral resilience to environmental change.” (599-602)

Line 153: hybridisation can indeed increase genetic diversity. But is it really a bias?

We do think this increase in diversity can bias summary statistics such as FIS and FST. Below we show two hypothetical scenarios comparing the effects of admixture (from an unsampled ghost population, in green) into one or both focal populations (in blue shades). We have modified the sentence in question but if the reviewer disagrees, we can focus on the first case that we think is more likely.



“For example, introgression may inflate the measured diversity for populations that include individuals of mixed ancestry, while population structure (F_{ST} and other similar measures that use both between and within population variation) can be biased in either direction depending on admixture proportions in populations being compared.” (635-638)

Figure 2: do the different levels of grey have a particular meaning?

No, but we can see how this could be construed! The figure legend has been amended: “Gray shading of lines is to aid visualising connections but does not convey specific meaning.” (649-651)

Regarding reproductive isolation: if the objective is to transplant colonies with particular adaptations, reproductive isolation could be seen as beneficial by limiting the breakdown of co-adaptations among loci. Regarding gene-manipulation, can you be more specific about the conclusions? If the edited genes are then restricted to the “manipulated” taxon, it can be viewed as a benefit by limiting the escape of this gene? Or is the diffusion of the edited gene among taxa an objective?

These are great points and highlight how differing objectives may have different requirements. We have modified the figure based on the reviewer’s insights and also updated text (now in section 3.4) to reflect these ideas.

Line 192: rather divergence than “delineation”?

Fixed.

Line 203: “photosynthetic symbionts”: only for species which host such symbionts

Sentence has been removed with reorganisation and rewriting.

Line 213: be more specific about the type of inferences you want to do?

Sentence has been removed with reorganisation and rewriting. This section in question (first paragraph of section 2) is more specific, keeping with the spirit of the reviewer's comment,

Lines 220-221: I don't think that these two references alone allow to state that many coral inhabit the grey zone of speciation. Your results may rather support this.

Have softened the language – the sentence now reads: "It is possible that many closely related coral taxa inhabit the "grey zone" of the speciation continuum" (125)

Line 229: some particular type of selection can favour homogenisation for alleles which are adaptive in both species

True. We have modified the sentence "When reproductive barriers are not complete, the outcome of interbreeding between groups is controlled by the relative strength of divergent selection (when different alleles are advantageous for different groups) and the genomic extent of gene exchange (which promotes homogenisation)." (128-131)

Lines 230-231: one important point here is that there are often heterogeneous levels of interspecific gene flow (see for example de Jode et al. 2023). This should be taken into account in the next paragraph as well, even if you develop this point later

The first section of the paper is now significantly reorganised, and the concept of variable gene flow across genomes is mentioned ("...where taxa are linked by continuing gene flow that may be variable in strength across the genome (Seehausen *et al.*, 2014; Roux *et al.*, 2016; De Jode *et al.*, 2023)" 126-127) with the full explanation developed in section 4.2.

Thank you for bringing the reference of de Jode et al 2023 to our attention.

Line 259: the original STRUCTURE software is not very well suited for such high-throughput data

It is true that STRUCTURE is not well suited to high-throughput data but many studies using reduced representation continue to use STRUCTURE. Additionally, since this is the most familiar of the admixture detection softwares to many readers, we prefer to mention it first. The phrasing "typified by" implies that the criterion is not strict.

Lines 253-267: of interest here are demographic inferences which allow to go from patterns (genetic structure) to evolutionary scenarios (see for example Fraïsse et al., 2021)

We completely agree that demographic inferences are exceptionally useful, and this is why section 2.5 reviews outcomes of such analyses in corals. However, before undertaking an analysis of demographic inference, individuals have to be placed in

groups and PCA and admixture analyses are the first steps for recognising groupings among genotyped individuals. Also, because we are undertaking a review, we are limited by the analyses that the original authors have conducted. To signpost this important limitation, we have added new text within this section:

“Focusing on reported results from principal components analyses and model-based clustering allowed us to evaluate *patterns* across a broad cross section of published studies. Ideally, the *processes* responsible for creating such patterns should be further evaluated, where demographic inference can be used to estimate gene flow and thereby provide greater insights on reproductive isolation (see for example Fraïsse et al., 2021, and section 2.5). (275-280)

Lines 284-285: here demographic inferences can be used to test for current gene flow.

Yes – agreeing, but not feasible to do within the scope of the present review. However, we have now created a new figure (Fig 4) to summarise the results of studies that have undertaken demographic inference and highlight the findings of ubiquitous gene flow in a much-expanded section 2.5.

Figure 3: this figure is very interesting. Just a detail, it would be helpful to use the same vocabulary and order here and in the presentation of the criteria (lines 286-294)

Thank you for pointing out the inconsistencies. We have endeavoured to improve alignment between the figure, the figure legend, and in text criteria (This is now Fig 2).

Lines 378-379: what do you mean by “summarizing symbiont genomes”?

Rephrased to: “characterising symbiont genomic diversity with *k*-mer analyses”

Line 387: “symbiont types”: maybe precise the level of discrimination?

Changed to “symbiont strains”.

Line 408: it seems clear that species delineation can not rely on a single marker, especially when this marker has a very particular mode of evolution such as ITS

We could not agree more! (Indeed, co-authors of this paper are developing alternative approaches to characterise symbiont diversity based on genome scale information.) Most work on symbionts to date, however, is based on ITS and therefore our discussion is constrained by available information, and we don't want to add a large digression to an already long manuscript. Nonetheless, an expanded paragraph (318-333) discusses multi marker studies of symbionts.

Line 414: this very interesting article of Bierne et al. 2011 underlines the phenomenon of coupling between endogenous and exogenous barriers to gene flow

Yes, we agree. It is unclear if the reviewer wanted us to modify anything here?

Line 436: “damicornis”

Fixed. Thank you.

Line 440: “undata” is not completely in italics

Fixed. Thank you.

Figure 4: can you indicate something about differentiation along depth here when in the same location? maybe this is not easy to add

(Now Fig. 3) We tried to make a figure summarising differentiation by depth but because different studies use different criteria, there was no easy way to apply consistent criteria. Moreover, many studies have depth and geography confounded (a particular depth sampled at only one geographic location) and therefore ascribing differentiation by depth cannot be distinguished from geographic differentiation. For this reason, we would prefer the figure to remain as is, and textually emphasising the sampling issues pervasive in coral genetics (386-398).

Lines 556-557: there is an example of inference of gene flow using transcriptome data and tests of speciation scenarios in *Eunicella* octocorals in Roux et al. (2016)

Thank you for pointing that out. It looks like this comparison is between two species with different names (nominal species) and *Da* places it towards the high end of the grey zone (Roux et al., Fig 3). Given that the species are taxonomically recognised, they are probably not morphologically cryptic, so the situation is a little different from that we are seeking to highlight.

Line 578: what do you mean by historical gene flow? Is it past gene flow without current gene flow? Or is it on-going gene flow. See for example the scenarios in Roux et al., 2016

Apologies for the vague phrasing. Section 2.5 has been almost entirely rewritten and that sentence is no longer relevant. More to the point, we have endeavoured to be clearer in time scale and model scenarios and include a new Fig 4 showing results from studies with demographic inference.

Line 594: similar question: current “genetic exchange”?

As with previous comment – the phrase is no longer relevant.

Line 598: “geographically widespread”: what do you mean? Long distance gene flow?

This is now clarified – we were trying to point out that none of these examples match the scenario of a single secondary contact tension zone.

The text now reads:

“Divergence dates between cryptic taxa often pre-date Holocene reef configurations (Fig. 4), implying that old standing genetic diversity is spread across contemporary reefs that are characterised by spatially complex yet replicated microhabitats and environmental gradients.” (769-771)

Line 633: note that the question of hybridization is not only linked to cryptic species

We fully agree. With rewriting the sentence in question has been eliminated.

Line 663: “selection”: be more specific

Text now reads:

“Furthermore, the presence of distinct cryptic taxa in close geographic proximity suggests that selection for microhabitat matching (such as depth) may be very strong...” (741-742)

Lines 674-676: this would require a reference

The new Fig 4 includes dates and references.

Line 687: limit rather than suppress?

Changed.

Lines 707-710: but this would rely on the aforementioned hypothesis that hybrids could have higher fitness than parental individuals or could contribute to adaptive introgression?

The sentence in question is now best reflected by lines 793-797 that outlines the sorts of investigations required to test for differences in fitness between hybrids and parentals. We also have now included more review of relevant theory regarding hybrid fitness (701-705).

Lines 723-743: this part could be shortened, as this is partly a summary of the results

Shortened substantially. The paragraph in question was removed aside from its first sentence.

Lines 756: “attributes”: give some examples?

With reorganisation, the sentence in question has been removed.

Textbox 1: is this example from the authors or from another article? If from the authors, then it would require a full development about the sampling, genotyping,

data availability, etc. In both cases a link towards assembled data (e.g. vcf) would be welcome.

We omitted to cite ourselves and have corrected this situation including pointing to data files. Thanks for pointing this out.

Textbox 2: lines 835-836: and in these cases, did the cryptic taxa show different responses?

We reviewed the papers in question and revised our summarizing text. For most studies, it was impossible to make inferences about the presence or absence of multiple taxa given the very small sample sizes of genotyped individuals. Some studies pre-screened for cryptic taxa and then focused on a single taxon, and we highlight those studies. This is now textbox 3 and the most relevant lines are 1030-1034.

References (only suggestions):

Thank you for suggesting these references. We have incorporated them as appropriate.

Cahill, A. E., Megléczy, E., & Chenuil, A. (2024). Scientific history, biogeography, and biological traits predict presence of cryptic or overlooked species. *Biological Reviews*, 99(2), 546-561.

De Jode, A., Le Moan, A., Johannesson, K., Faria, R., Stankowski, S., Westram, A. M., ... & Fraïsse, C. (2023). Ten years of demographic modelling of divergence and speciation in the sea. *Evolutionary Applications*, 16(2), 542-559.

Fraïsse, C., Popovic, I., Mazoyer, C., Spataro, B., Delmotte, S., Romiguier, J., ... & Roux, C. (2021). DILS: Demographic inferences with linked selection by using ABC. *Molecular Ecology Resources*, 21(8), 2629-2644.

Oury, N., Noël, C., Mona, S., Aurelle, D., & Magalon, H. (2023). From genomics to integrative species delimitation? The case study of the Indo-Pacific *Pocillopora* corals. *Molecular Phylogenetics and Evolution*, 184, 107803.

Puillandre, N., Brouillet, S., & Achaz, G. (2021). ASAP: assemble species by automatic partitioning. *Molecular Ecology Resources*, 21(2), 609-620.