



Peer Community In Evolutionary Biology

How common cryptic coral diversity can blur biodiversity metrics and challenge management

Eric Pante  based on peer reviews by 2 anonymous reviewers

Cynthia Riginos, Iva Popovic, Zoe Meziere, Vhon Garcia, Ilha Byrne, Samantha Howitt, Hisatake Ishida, Kevin Bairos-Novak, Adriana Humanes, Hugo Scharfenstein, Thomas Richards, Ethan Briggs, Vanessa Clark, Chuan Lei, Mariam Khan, Katharine Prata (2024) Cryptic species and hybridisation in corals: challenges and opportunities for conservation and restoration. *EcoEvoRxiv*, ver. 2, peer-reviewed and recommended by Peer Community in Evolutionary Biology. <https://doi.org/10.32942/X2502X>

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Biological conservation aims at protecting the genetic diversity generated by evolutionary processes over the course of life's history on earth (Allendorf and Luikart 2007), and to be effective, it requires that its fundamental units (among which populations and species) be delimited as precisely as possible. This exercise is particularly important for corals because hybridisation and introgression have played a fundamental role in shaping their contemporary diversity (eg Veron 1995).

In their review paper, Riginos et al (2024) show that 68% of nominal taxa investigated for genomic population structure bear the molecular signature of partial reproductive isolation, and can be considered as cryptic genetic groups. Another review study (published a day before the preprint of Riginos et al), converges in the finding that cryptic diversity is rampant in nominal coral species (Grupstra et al 2024). This result has strong bearing on the study of coral biology; as Riginos et al state, "any coral investigation that does not genotype the corals under study risks treating a heterogeneous mix of partially reproductively isolated taxa as a single species." The stakes are therefore high, given the ecological importance of corals and the ecosystem services they provide.

While Grupstra et al (2024) discusses the impact of cryptic coral diversity in the context of functional differences in thermal adaptation and the processes that lead to cryptic lineages, Riginos et al (2024) provide a quantitative review of cryptic lineages within nominal species, providing reproducible criteria for delineation, details the importance of detecting hybrids, summarises how biodiversity metrics and conservation efforts can

be biased by unrecognised cryptic lineages, offer recommendations on how to recognise and deal with cryptic diversity, and discuss how corals can be regarded as highly valuable model systems to study adaptation and speciation. The study of Riginos et al (2024) is therefore a must-read to all coral biologists, especially those involved in biological conservation.

References:

Fred W. Allendorf and Gordon Luikart (2007) Conservation and Genetics of Populations. Blackwell Publishing, Malden MA, USA.

Carsten G. B. Grupstra, Matías Gómez-Corrales, James E. Fifer, Hannah E. Aichelman, Kirstin S. Meyer-Kaiser, Carlos Prada, Sarah W. Davies (2024) Integrating cryptic diversity into coral evolution, symbiosis and conservation. Nat Ecol Evol 8, 622–636 (2024).

<https://doi.org/10.1038/s41559-023-02319-y>

Cynthia Riginos, Iva Popovic, Zoe Meziere, Vhon Garcia, Ilha Byrne, Samantha Howitt, Hisatake Ishida, Kevin Bairos-Novak, Adriana Humanes, Hugo Scharfenstein, Thomas Richards, Ethan Briggs, Vanessa Clark, Chuan Lei, Mariam Khan, Katharine Prata (2024) Cryptic species and hybridisation in corals: challenges and opportunities for conservation and restoration. EcoEvoRxiv, ver.2 peer-reviewed and recommended by PCI Evol Biol <https://doi.org/10.32942/X2502X>

J. E. N. Veron (1995) Corals in Space and Time: The Biogeography and Evolution of the Scleractinia. Cornell University Press

Reviews

Evaluation round #1

DOI or URL of the preprint: <https://doi.org/10.32942/X2502X>

Version of the preprint: 1

Authors' reply, 12 September 2024

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Decision by [Eric Pante](#) , posted 24 May 2024, validated 26 May 2024

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 study 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 Grupstra 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

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Reviewed by anonymous reviewer 2, 04 May 2024

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.

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).

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). 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.

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.

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.

Line 76: "observations" of what?

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.

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

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

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

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.

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

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

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

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?

Line 192: rather divergence than "delineation"?

Line 203: "photosynthetic symbionts": only for species which host such symbionts

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

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.

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

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

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

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)

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

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)

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

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

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

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

Line 436: "damicornis"

Line 440: "undata" is not completely in italics

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

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)

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

Line 594: similar question: current "genetic exchange"?

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

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

Line 663: "selection": be more specific

Lines 674-676: this would require a reference

Line 687: limit rather than suppress?

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?

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

Lines 756: "attributes": give some examples?

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.

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

References (only suggestions):

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.