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George Sangster, Meritxell Genovart, Tim Guilford, Daniel Oro, Maite Louzao, M. de L. Brooke, José Manuel Arcos

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<https://doi.org/10.1016/j.ympev.2025.108470>

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Letter to the Editor

Phylogenomics and the falsification of shearwater species (*Puffinus mauretanicus*, *P. yelkouan*) hypotheses: a comment on Ferrer Obiol et al. (2023)

ARTICLE INFO

Keywords:

Genomic islands of differentiation
Taxonomy
Vocalizations
Hybrid zone
Procellariiformes

ABSTRACT

Ferrer Obiol et al. (2023) applied double digest restriction-site associated sequencing (ddRAD-seq) data to delimit species in North Atlantic and Mediterranean *Puffinus* shearwaters. These authors concluded that the Balearic/Yelkouan shearwaters (*P. mauretanicus*/*P. yelkouan*) sister-species pair comprised a single species based on analyses of ddRAD-seq data and a very brief and deficient review of other evidence. While it is clear that reduced representation genomic data are often suitable for the discovery and documentation of species and their relationships, the issue of whether such data are sufficient to falsify hypotheses of species taxa has received only limited attention so far. Here, we note that detection of species in phylogenomic analyses based on reduced representation sequencing methods will be problematic if species differences are only found in a small portion of the genome (so-called ‘genomic islands of differentiation’), as has been documented in multiple case studies. This means that genomic differences between some species may only be detected if (i) entire genomes are sequenced, and (ii) a formal search for islands of differentiation is conducted. Valid species may be overlooked in reduced representation approaches, such as ddRAD sequencing. Consequently, an apparent lack of overall phylogenomic divergence (e.g. lack of reciprocal monophyly, low genome-wide F_{ST}) should not be used by taxonomists as evidence that such taxa are not valid species. We conclude that the apparent lack of divergence in the ddRAD-seq data of Ferrer Obiol et al. (2023) does not represent credible evidence that *P. mauretanicus* and *P. yelkouan* are conspecific. In addition, we show that the authors misrepresented other available taxonomic data, failing to properly follow an integrative approach.

1. Introduction

Ferrer Obiol et al. (2023) applied double digest restriction-site associated sequencing (ddRAD-seq) data to delimit species in several groups of North Atlantic and Mediterranean *Puffinus* shearwaters. Given the ubiquity of genomic data in modern systematics, it is important to establish the limits of what can and cannot be concluded from the various types of data and analyses. While it is clear that reduced representation genomic data are suitable for the discovery and documentation of species and their relationships, the issue of whether such data are sufficient to falsify hypotheses of species taxa has received only limited attention so far.

One of the groups studied by Ferrer Obiol et al. (2023) is the Balearic/Yelkouan shearwaters (*P. mauretanicus*/*P. yelkouan*) sister-species pair. The study included six samples of alleged *P. mauretanicus* from Ibiza, Mallorca and Menorca, and six of *P. yelkouan* from France, Croatia and Tunisia. The authors reported that genetic clustering analyses and species delimitation analyses did not recover *P. mauretanicus* and *P. yelkouan* as two distinct groups; phylogenetic analyses failed to recover reciprocal monophyly between the two taxa; coalescent-based divergence time estimation of *P. mauretanicus* and *P. yelkouan* included the present time in the 95 % highest posterior density (HPD) intervals; pairwise F_{ST} was extremely low ($F_{ST} = 0.04$); and no fixed differences (species-diagnostic SNPs) between *P. mauretanicus* and *P. yelkouan* were found. These findings were cited as evidence that *P. mauretanicus* and *P. yelkouan* should be considered as conspecific. The

authors also quoted a “gradient of phenotypes”, “partially overlapping non-breeding distributions”, “nearly indistinguishable vocalisations”, and “lack of correspondence at the individual level between phenotypic characters, stable isotope analyses, microsatellites and mtDNA”, as additional evidence for the lumping of these two taxa.

Here, we argue that the authors overinterpreted the lack of divergence in their ddRAD sequence data. Moreover, in our view they misrepresented and did not properly discuss other available taxonomic data, failing to properly follow an integrative approach.

2. Phylogenomics may overlook valid species

Ferrer Obiol et al. (2023) used 5.65 Mbp of ddRAD sequence data for species delimitation (J. Ferrer Obiol in litt.). This represents a tiny portion (0.46 %) of the genome of *P. mauretanicus* (1.22 Gbp; Cuevas-Caballé et al., 2022). Such reduced representation sequencing methods are not problematic for phylogenetic inference if there are many genomic differences between species that are scattered across the genome (e.g. Ravinet et al., 2018). In such cases, there will be enough data to detect species differences and obtain sufficient phylogenetic signal to reconstruct reciprocally monophyletic groups. However, detection of species in phylogenomic analyses based on reduced representation sequencing methods will be problematic if species differences are few. There are many cases known where species differences are only found in a small portion of the genome (so-called ‘genomic islands of differentiation’) (Wolf & Ellegren, 2017, Bravo et al., 2021). Examples

<https://doi.org/10.1016/j.ympev.2025.108470>

Received 8 June 2025; Received in revised form 9 September 2025; Accepted 11 September 2025

Available online 13 September 2025

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in birds are the Palaearctic crows *Corvus corone* and *C. cornix* (Poelstra et al., 2014), the North American warblers *Vermivora cyanoptera* and *V. chrysoptera* (Toews et al., 2016), and the South American capuchinos *Sporophila iberaensis* and *S. hypoxantha* (Turbek et al., 2021) and *S. beltoni* and *S. plumbea* (Nguyen et al., 2024). For instance, in the crows there is a single 1.95 Mbp island of differentiation, representing approximately 0.2 % of the entire sequenced genome (1.04 Gbp; Poelstra et al., 2014). Not surprisingly, overall genomic divergence (pairwise F_{ST}) between such species is low.

The fact that some valid species show only a few genomic islands of differentiation has important consequences for species delimitation using genomic data. First, genomic differences between some species will only be detected if entire genomes are sequenced, and may be overlooked in reduced representation approaches, such as ddRAD sequencing (Wolf & Ellegren, 2017). If a phylogenetic analysis is based on a relatively small part of the genome, the divergent part may simply not have been sequenced. This is illustrated by two studies of the South American capuchinos *Sporophila*. A study based on ddRAD data failed to find differences between several species (Campagna et al., 2015), whereas a follow-up study based on whole genome sequencing did find that species are differentiated at genomic islands of differentiation (Campagna et al., 2017). Second, even if whole genome sequencing is used, the phylogenetic signal (evidence for two species taxa) contained in one or a few small islands of differentiation may be obscured by the ‘noise’ in the much larger less-divergent parts of the genome (e.g. Poelstra et al., 2014). Indeed, it has been shown that phenotypic diversification and reproductive isolation may unfold in the near-absence of phylogenetic signal (Helmkamp et al., 2025). Third, a low genome-wide F_{ST} does not falsify species rank.

Phylogenomic analysis is widely used, and a valid method, for documenting putative species, but the converse is not necessarily true. Islands of differentiation may represent only a tiny portion of the genome, and thus contain very little overall phylogenetic signal in a genome-wide study. In such cases, phylogenomic analysis may not be sensitive enough to detect species. This means that a lack of monophyly in a genome-wide phylogenetic study is not valid evidence against the existence of species if those species are supported by other lines of evidence. Consequently, an apparent lack of overall phylogenomic divergence (e.g. lack of reciprocal monophyly, low genome-wide F_{ST}) should not be used by taxonomists as evidence that such taxa are not valid species; a comparison of genomes may still reveal that the relevant taxa are characterized by multiple islands of differentiation.

The above observations lead to an important insight: there is a fundamental difference between (i) the data that are required to produce a robust (well-supported) phylogenetic reconstruction, and (ii) the data required to *reject* a hypothesis of species rank based on genomic data (i.e. aimed at showing that there really are no islands of differentiation). The first can be done with ultra-conserved elements or ddRADseq data, whereas the second requires whole genome sequencing data. The present case clearly requires data of the second type.

We conclude that whereas the sequence data obtained by Ferrer Obiol et al. (2023) are by far the most complete genomic evidence for evaluating the relationships and divergence of *P. mauretanicus* and *P. yelkouan*, the apparent lack of divergence in a tiny portion of the genomes does not represent credible evidence that the two taxa are conspecific, especially since other evidence points in the opposite direction.

3. Other taxonomic data

Ferrer Obiol et al. (2023) claimed to follow an integrative taxonomic approach. However, aside from their phylogenomic analysis, they only provided a list of barely-discussed features that presumably supported their proposal of lumping *P. yelkouan* and *P. mauretanicus*. In our view, they misinterpreted part of this evidence, and understated the existence of obvious differences between the two taxa in coloration,

morphometrics and vocalizations (see below). These differences should merit particular attention as clues for specific differentiation in a group, the Procellariiformes, where ‘obvious’ phenotypical variability is substantially constrained by the environment and ‘cryptic’ species are numerous (Welch et al. 2011, del Hoyo & Collar, 2014, Taylor et al., 2019). In addition, previous genetic data (nuclear and mitochondrial DNA) also showed differences between the two taxa (Heidrich et al., 1998; Genovart et al., 2012).

Ferrer Obiol et al. (2023) quoted a “gradient of phenotypes” in support of lumping the two taxa, referring to Genovart et al. (2012) and Militão et al. (2014) even though these two studies did not discredit the existence of recognizable differences between both taxa. We regard this as a misleading representation of morphological variation in *P. mauretanicus* and *P. yelkouan*, which may be particularly confounded by the existence of a small historical contact-area (likely hybrid zone) in Menorca, where a large proportion of birds show intermediate features between both taxa (Genovart et al., 2007). Genovart et al. (2012) classified plumage variation into ‘white’, ‘intermediate’, and ‘dark’ coloration patterns. Dark coloration was found only in *P. mauretanicus* and was found on all islands. The proportion of the three coloration patterns differed depending on the breeding colony of *P. mauretanicus*, with the majority (86–99 %) of individuals from Mallorca, Cabrera and the Pit-iüsses colonies being dark or intermediate and the majority from Menorca (64 %) being white. Variation in *P. yelkouan* was not examined. This pattern is consistent with (i) a species-level difference in plumage (polymorphic in *P. mauretanicus*, monomorphic in *P. yelkouan*), and (ii) the singularity of the Menorcan population, where historical contact of *P. mauretanicus* with *P. yelkouan* has contributed to a high proportion of ‘white’ phenotypes. Militão et al. (2014) did not document a gradient of phenotypes, as claimed by Ferrer Obiol et al. (2023). Their morphometric data showed two clusters which corresponded to *P. mauretanicus* and *P. yelkouan*. Moreover, they showed that *P. mauretanicus* is significantly larger than *P. yelkouan* and univariate measurements of tarsus, wing and bill segregated the two species in two different clusters. We consider that these two shearwaters show overall consistent and straightforward differences in color, size and morphometrics, which allow us to tell them apart readily (Altaba, 1993, Gil-Velasco et al., 2015, Flood & Fisher, 2020). *P. mauretanicus* is notably darker, less contrasted, and considerably larger and heavier, than *P. yelkouan*. For instance, weight ranges 349–416 g in *P. yelkouan* and 430–640 g in *P. mauretanicus* (Gil-Velasco et al., 2015), with birds from Menorca showing intermediate values (range 320–585 g, n = 157; IRBI & SEO/BirdLife, unpublished data).

Another line of evidence cited by Ferrer Obiol et al. (2023) in support of lumping *P. mauretanicus* with *P. yelkouan* was that these species have “partially overlapping non-breeding distributions”. We contend that this information is misleading (“cherry picking”), as both taxa exhibit well-documented differences in their at-sea distributions (Austin et al., 2019). The alleged overlap is rather small; and, in any case, it should not be surprising that highly vagile, pelagic species of birds breeding geographically close to each other have overlapping at-sea ranges. Therefore, this should not be considered a criterion to determine species limits (Quillfeldt et al., 2017).

Ferrer Obiol et al. (2023) also stated that the vocalizations of *P. mauretanicus* and *P. yelkouan* are “nearly indistinguishable”, quoting a bird identification paper that did not include any kind of analysis of vocalizations (Yésou et al., 1990). However, critically, they overlooked a detailed and more recent quantitative study showing that the vocalizations of these species differ significantly and show no overlap in multivariate analyses of both males and females. Birds from Menorca show intermediate songs (Curé et al., 2010). In addition, incubating *P. mauretanicus* give lower territorial responses to *P. yelkouan* than to conspecific calls (Curé et al., 2012). There are substantial differences between *P. mauretanicus* and *P. yelkouan* in the acoustic cues used for species recognition, with *P. mauretanicus* being more sensitive to frequency value modification than *P. yelkouan* (Curé et al., 2012). The

available evidence shows that *P. mauretanicus* and *P. yelkouan* have substantial differences in their species-specific recognition systems (Curé et al., 2012). Vocal differences and reduced response to playback of heterospecific recordings suggest that isolating mechanisms are in place (assortative mating) that likely reduce the level of interbreeding whenever the two taxa co-exist. The differences in vocalizations between *P. mauretanicus* and *P. yelkouan* are crucial for species level taxonomy because vocalizations are considered an important pre-mating isolation barrier in shearwaters and other tubenoses (Bretagnolle, 1996).

Finally, the authors cited Genovart et al. (2012) and Militão et al. (2014) in support of their claim that there is a “lack of correspondence at the individual level between phenotypic characters, stable isotope analyses, microsatellites and mtDNA”. We regard this as a misleading representation of variation within *P. mauretanicus* and *P. yelkouan*. Almost all mismatches between morphology, microsatellites and mtDNA in the study by Genovart et al. (2012) were found on Menorca and are very likely to be a result of historical interbreeding of *P. mauretanicus* with *P. yelkouan*. Militão et al. (2014) examined bycatch birds of unknown breeding origin collected in the north-east of Spain and found a perfect match between phenotypic characters, stable isotope analyses, microsatellites and mtDNA in nearly 80 % of birds. Taxonomic conclusions about the proportion of mismatches in that study are mere speculation, since the origin of the birds analyzed was unknown.

4. Conclusion

The sequencing strategy and type of analysis of a genomic study strongly affect which conclusions about the systematics of the group can and cannot be drawn. Phylogenetic analysis of reduced representation genomic data are clearly able to document divergent species (using the criterion of monophyly) but may overlook valid species with a shallow divergence. Case studies illustrate that detailed comparison of whole-genome sequence data, and documenting a lack of islands of differentiation, would be necessary to falsify species hypotheses.

We regard the proposal of Ferrer Obiol et al. (2023) to lump *P. mauretanicus* with *P. yelkouan* as precipitate and insufficiently critical, based on overinterpretation of genomic data, and misrepresentation of other taxonomic evidence. Continued treatment as two species under both the Biological (Mayr, 1963) and General Lineage (de Queiroz, 2007, Padial et al., 2010) species concepts is supported by several lines of evidence, including differences in plumage, size and morphometry (Altaba, 1993, Militão et al., 2014, Gil-Velasco et al., 2015); reciprocal monophyly of mitochondrial DNA sequences (Heidrich et al., 1998, 2000, Ramirez et al., 2010); differences in non-breeding range (Austin et al., 2019); differences in the timing of breeding (Austin et al., 2019); and differences in song, assortative mating, and mate recognition cues (Curé et al., 2012). The localised and isolated hybrid zone on Menorca merits detailed study but should not be overinterpreted as evidence for conspecificity of *P. mauretanicus* and *P. yelkouan* given the evidence for pre-mating isolating barriers between the two species. We recommend that future studies use whole genome sequencing of a sufficient number of specimens of both species to locate and characterize genomic islands of differentiation to further clarify the nature of speciation in this group.

Although our conclusion that these taxa are best treated as species is independent of conservation concerns, it is important to recall that both species are globally threatened, with *P. mauretanicus* being the most endangered seabird in Europe (Critically Endangered), and *P. yelkouan* catalogued as Vulnerable (IUCN, 2024). This makes their lumping of particular concern, from a precautionary point of view. Indeed, such a decision could reduce attention to their threats and population status, most critically in the case of *P. mauretanicus*, potentially leading to disastrous consequences given the already limited conservation measures and research resources (Oro & Guilford, 2017).

CRedit authorship contribution statement

George Sangster: Writing – original draft, Methodology, Conceptualization. **Meritxell Genovart:** Writing – review & editing, Validation. **Tim Guilford:** Writing – review & editing. **Daniel Oro:** Writing – review & editing. **Maite Louzao:** Writing – review & editing. **M. de L. Brooke:** Writing – review & editing. **José Manuel Arcos:** Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank David García (IRBI) for providing biometric data of birds from Menorca, and Joan Ferrer Obiol for providing data on the length of the ddRAD sequences used in his study. Thierry Micol, Susan Waugh, two anonymous reviewers, associate editor Haw Chuan Lim and editor Guillermo Orti provided valuable comments on an earlier version of this manuscript.

Data availability

No data was used for the research described in the article.

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- George Sangster^{a,*} , Meritxell Genovart^b, Tim Guilford^c, Daniel Oro^b, Maite Louzao^d, M. de L. Brooke^e, José Manuel Arcos^f
- ^a *Naturalis Biodiversity Center, Darwinweg 2, PO Box 9517, 2300 RA Leiden, the Netherlands*
- ^b *Centre d'Estudis Avançats de Blanes (CEAB - CSIC), Acces Cala Sant Francesc 14, 17300 Blanes, Girona, Spain*
- ^c *Department of Biology, University of Oxford, 11a Mansfield Road, Oxford OX1 3SZ, UK*
- ^d *Fundación AZTI, Herrera kaia, Portualdea z/g, 20110 Pasaia, Spain*
- ^e *Strickland Curator of Ornithology (Emeritus), Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK*
- ^f *SEO/BirdLife, Marine Programme, Barcelona, Spain*

* Corresponding author.

E-mail addresses: g.sangster@planet.nl (G. Sangster), m.genovart@csic.es (M. Genovart), tim.guilford@biology.ox.ac.uk (T. Guilford), d.oro@csic.es (D. Oro), mlouzao@azti.es (M. Louzao), mb10005@cam.ac.uk (M.L. Brooke), jmarcos@seo.org (J.M. Arcos).