

PERSPECTIVE

Mammals and meaningful taxonomic units: the debate about species concepts and conservation

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Keywords

conservation, meaningful taxonomic units, population-level lineages, species concepts, species delimitation

Submitted: 14 December 2017

Returned for revision: 17 January 2018

Revision accepted: 18 January 2018

Editor: DR

doi: 10.1111/mam.12121

ABSTRACT

Mammalian taxonomy based on the diagnosability version of the Phylogenetic Species Concept has recently been declared the only sound approach to mammalian classification. In this article, based on the underlying evolutionary ontology of species taxa, I explain the fallacy of these arguments and hold that in a 'grey area' after lineage sundering, completely objective species delimitation is impossible, making both lumping and splitting equally correct or incorrect. As a consequence, we may have to get used to the idea that described species are often a poor guide to the delineation of meaningful taxonomic units for conservation.

INTRODUCTION

The species problem is still one of the most pressing issues in biology, and a consensual solution seems as far away as ever (Zachos 2016). Mammalian taxonomy has recently been centre-stage in the discussion due to the application of the diagnosability version of the Phylogenetic Species Concept (dPSC, see Appendix S1 for species concept definitions) to a number of mammalian taxa, most notably ungulates (Groves & Grubb 2011). This triggered a lively debate on the theoretical foundations of taxonomy and its impact on conservation. Roughly (and not accounting for differences within the two groups), the divide runs between authors more prone to lumping (e.g. Frankham et al. 2012, Heller et al. 2013, Zachos & Lovari 2013, Zachos et al. 2013) and the adherents of the dPSC who are more prone to splitting (e.g. Gippoliti et al. 2013, Groves 2013, Cotterill et al. 2014, Groves 2014, for a very good and balanced empirical analysis, see Mouton et al. 2017). 'Splitters' have been accused of taxonomic inflation, 'lumpers' of taxonomic inertia. Most recently, two new articles were published, making strong claims about how taxonomic inertia has had detrimental impacts on African ungulate conservation and how the dPSC, as the allegedly single theoretically sound species concept, can and should be used as a remedy (Groves et al. 2017, Gippoliti et al.

2018). Mammals are special in that they get more attention from the general public than other groups, and nowhere is coverage by the media more guaranteed (with the exception of new fossil human taxa) than when new iconic mammal species are described, such as elephants, rhinos or, most recently, great apes (Nater et al. 2017). The issue at stake transcends taxonomy and even biology, being relevant for conservation, management, and environmental policy. At the same time, the debate is not only of practical relevance, but also reflects diverging views on the foundations of taxonomy and the ontology of species. In the present commentary, I will briefly outline the fundamental difference between ontological and identification concepts, argue that taxonomic inflation and taxonomic inertia are extreme positions along a continuum of taxonomic tastes and traditions, and that the fact that both extremes are still around is due to a 'grey area' of lineage sundering where there is no scientifically objective way of deciding whether two populations are conspecific or not. Finally, I will discuss the consequences of these insights for the relationship between taxonomy and conservation.

SPECIES AS LINEAGES AND THE DPSC

Groves et al. (2017) and Gippoliti et al. (2018; abbreviated as G&G hereafter) are elaborate reviews, by renowned

experts in the field, on the biodiversity of African ungulates and their neglected protection due to, in their view, taxonomic inertia grounded in a longstanding application of the Biological Species Concept, which considers populations as conspecific if they actually or potentially produce fertile hybrids. I will not discuss their views in detail, which would be beyond the scope of this article. I agree with them that lumping (just like splitting) can have detrimental consequences, for example, when distantly related individual animals are crossed in captive breeding programmes and the offspring suffers outbreeding depression (one example they give is the dikdik *Madoqua kirkii*). Also, there can be little doubt that taxonomic acknowledgement or the lack thereof (having a name or not) can tip the scales towards survival or extinction ('taxonomy as destiny', May 1990). Again, splitting can be as detrimental as lumping, through decreasing population sizes of acknowledged species or legal obstacles for genetic rescue (Frankham et al. 2012, Zachos et al. 2013). Probably the best conclusion from this is to mistrust names more, and rather rely on the underlying data. That may be challenging, but the translation of diversity into taxonomy is necessarily imprecise.

G&G, however, interpret their findings in a way that is more fundamental – but in my view also fundamentally flawed. They claim nothing less than that their preferred approach to the species problem (the dPSC) not only provides a remedy to correct mistakes made in more inclusive species concepts like the Biological Species Concept, but is also the only correct or most appropriate species concept. In other words, they claim to have solved large parts of the species problem. As is usually the case when dealing with species, things are complicated, though. Their taxonomic philosophy is grounded in the very useful insights of Mayden (1997) and de Queiroz (1998, 2007) that not all species concepts are the same, but that there is one ontological concept that tells us what species really are, while all the others function as identification concepts or criteria, telling us when the conditions of the ontological concept are met. The ontological concept is the Evolutionary Species Concept according to Mayden, or the General Lineage Species Concept or Unified Species Concept according to de Queiroz. Although they are not completely identical, all three define the species category essentially as separately evolving population or meta-population lineages, i.e. as distinct evolutionary entities at the level of populations.

All the other 30 or so concepts, rather than defining the species category ontologically, help us identify the distinct evolutionary entities at the level of populations that we are looking for. They are operational concepts or criteria, because once two populations diverge, sooner or later (and in no specific order) the criteria of these

concepts will be met, such as reciprocal monophyly, lack of fertile hybrids, diagnosability etc. Thus, if two populations are considered different species under the Ecological Species Concept, they are not separate species by virtue of having distinct ecological niches, but because the very existence of different niches is evidence that there are two separately evolving population-level entities. G&G (see also Cotterill et al. 2014) explicitly embrace this ontology, and they claim to use the dPSC (which aims at diagnosably distinct populations) as an operational concept to detect lineages under the ontological Evolutionary Species Concept. That is not what they are doing, though. They consider the dPSC as the identification criterion that trumps all others, presenting this as the only sound option. This is a violation of the ontology introduced by Mayden (1997) and de Queiroz (1998, 2007). Particularly de Queiroz was very clear that the various operational concepts complement each other and that they all function as identification criteria – there is no *primus inter pares* to be found here. This is directly related to the second flaw in G&G's argument: they claim to use the dPSC as an identification criterion, i.e. as something that is not part of what makes a species. If it is clear that two populations are evolving separately, then diagnosability should not be necessary for species status, because what diagnosability is supposed to identify has been established by other means. Yet, G&G only assign species status if both their conditions are met: (1) separately evolving population lineages that (2) must be diagnosably distinct. This is why Groves and Grubb (2011) assign species status to the isolated red deer on the Tyrrhenian islands Corsica and Sardinia (*Cervus corsicanus*) but not to the equally isolated red deer in, for example, the British Isles (*Cervus elaphus*; see also Zachos 2015). That it is not about lineages alone can also be seen from the fact that *Cervus corsicanus* comprises not only the Tyrrhenian island deer but also the North African Barbary red deer which have been isolated from the former for millennia. On the other hand, de Queiroz (1998, 2007) is very clear that species status is only dependent on being a separately evolving population or meta-population lineage. His General Lineage Species Concept just identifies the element common to all species concepts, whereas the Unified Species Concept makes it explicit that all separately evolving population-level lineages in fact are species. No further, contingent property of these lineages is necessary for species status – not a distinct ecological niche, not the lack of fertile hybrids, and not diagnosability either. This means that, if species are really to be objective entities without arbitrary delimitation criteria as to their inclusiveness, then any two allopatric populations cannot be conspecific. This is neither feasible nor desirable in practice, and so lineage status is usually viewed only as the necessary condition, while something else is added as

the sufficient condition (see Freudenstein et al. 2017). As all taxonomists probably agree, this is indispensable to avoid ephemeral entities. In line with this, de Queiroz also characterised the operational identification concepts as describing a certain stage that the species is in after populations get separated (reproductively isolated stage, monophyly stage etc., de Queiroz 1998, p. 71) – a view reminiscent of Dobzhansky's (1937, p. 312) dictum that "Species is a stage in a process, not a static unit".

In order for species to be fully objective, no condition other than separate lineage status can exist. At one stage there may be a panmictic population, which is clearly a single species, and at some distant later point in time there are two very distinct populations that differ in a variety of biologically relevant features, i.e. they are clearly two different species. However, where along the trajectory of these two diverging populations the line is to be drawn between one and two species is necessarily a grey area (see Figures 5.4 in de Queiroz 1998 and 5.2 in Zachos 2016). There is no completely objective way of deciding this, and this is why species delimitation is only ever unequivocal retrospectively, when the two populations have left the grey area. Any claims to the contrary are misleading or even wrong, and that includes G&G's presentation of the dPSC. Diagnosability is just one of the many contingent properties mentioned above. Essentially, what G&G are advocating is simply to reject the arbitrary thresholds or criteria of reproductive isolation, reciprocal monophyly etc. and accept another, equally arbitrary, threshold (diagnosability). It is also untrue that delimiting species in a more inclusive way ('taxonomic inertia') means that morphology-based taxonomy is dismissed and superseded by phylogeographical molecular studies (Gippoliti et al. 2018, p. 123). The only real difference is that G&G's arbitrary threshold delimits population lineages in a less inclusive way. Within the hierarchical pattern of population lineages that make up the Tree of Life, they delimit species within the grey area in such a way that there are more species taxa than under the other criteria.

To claim that only this is a lineage-based approach, while all others are not, is clearly wrong. All these contingent arbiters are based on biological phenomena, and it is important to realise that there is no right or wrong identification criterion. All operational species concepts identify real lineages, but their inclusiveness varies, and there is no such thing as a scientifically correct (or incorrect) level of inclusiveness within the grey area of diverging lineages. Within this grey area, delimiting species is like delimiting one's own family in a pedigree; you may or may not include fourth cousins, but either way the grouping is real, only more or less inclusive. G&G and Cotterill et al. (2014) do not seem to be aware of this, and it is perhaps a symptomatic Freudian slip that at one point

Gippoliti et al. (2018) call their own taxonomy "ESC (=PSC) derived" (p. 124), falsely equating the two ontologically very different concepts. G&G also accuse adherents of more inclusive species concepts of pheneticism. Allegations of pheneticism, typology, essentialism and the like are not helpful, and the practical procedure G&G recommend to identify species (finding non-overlapping groups of individuals in morphospace based on discriminant analysis or similar approaches) produces clouds of taxa that are quite reminiscent of the phenetic operational taxonomic units in numerical taxonomy. However, if we do not want to call every single allopatric population a species, we have to settle for some kind of distinctness, and that will always be based on similarity in one way or another. Why else are tigers in India naturally considered a different species from African lions, while lions in India, although equally separately evolving, are considered conspecific with African lions? One can choose a different example, but the honest answer will be: because African and Indian lions are much more similar than tigers and lions, i.e. they are still in or at least closer to the grey area after lineage sundering. In this light, terms like pheneticism and taxonomic inflation and inertia might be counterproductive. We may differ in our predilections as to how inclusive species taxa should be, and accordingly which delimitation criterion should be applied, but 'inflation' and 'inertia' carry negative connotations that may foster disputes between parties on both sides of what is perceived as a trench, but in reality is a continuum. They also contribute to the blurring of a fundamental truth: boundaries in nature are fuzzy, and taxonomy as a discrete, binary classification system (the same or different species?) that is imposed on a continuous process (evolution) will never yield a perfect match with reality. When alternative taxonomies are called 'imprecise' (Gippoliti et al. 2018, p. 124), the authors perhaps do not realise that imprecision is inherent to taxonomy in principle. It is worth noting that ever more sophisticated statistical approaches to species delimitation, for example based on coalescent theory, do not change that conclusion: the Tree of Life will be uncovered with higher and higher resolution but the grey area remains (see Sites & Marshall 2004 and Sukumaran & Knowles 2017).

The Biological Species Concept is perhaps the best-known of the identification concepts, but unfortunately it is only really applicable to extant sexual populations in synchrony and sympatry (Zachos 2016, Chapter 5.3) and therefore, it is of limited use for taxonomic practice. Reproductive isolation, just like ecological distinctness (the core of the Ecological Species Concept), is difficult to test because it is hard to measure and quantify. The dPSC seems attractive because its sufficient condition for species status is easily testable, but an objectively testable criterion is not

the same as an objective criterion! Also, diagnosability can only serve as a clear-cut criterion if any trait can be used. If not, an arbitrary choice has to be made about which traits are appropriate and which are not. But if any kind of trait that shows diagnosably different groups is accepted, the result will be ephemeral taxa diagnosed by trivial differences, e.g. single-nucleotide polymorphisms of non-coding DNA, and the rank of species will ultimately converge on what is now considered a population. Every isolated population that, through genetic drift, reaches a level of divergence that makes it diagnosable would have to be given its own species name (Zachos & Lovari 2013). Anthropogenic habitat fragmentation would thus function as a (purely taxonomic) speciation pump. This is not meant as a cynical comment. These diverging populations are a biological reality, and calling them species is not wrong in a biological or logical sense. It is just not what the term species has usually been used for, and, just like over-lumping, it would cause serious conservation issues (Agapow et al. 2004, Frankham et al. 2012, Zachos et al. 2013).

TAXONOMY AND CONSERVATION

Where does all this leave us with respect to the role of taxonomy in conservation? It is becoming obvious that the inherent fuzziness of species boundaries and the concomitant inconsistency in species delimitation cause an ‘apples and oranges’ problem when using species taxa and species counts as the unquestioned currency in ecology and evolutionary biology (Riddle & Hafner 1999, Fairby et al. 2016, Chapter 7 in Zachos 2016). This is why abolishing the species rank altogether has been suggested; just like with the higher Linnaean ranks, the mere fact that two taxa are ranked at species level and given a binomial does not make them the same kind of thing (for references and a discussion of taxonomic or T species vs. evolutionary or E species and species category nominalism, see Chapters 1.3.2, 1.5 and 3.6 in Zachos 2016). This dilemma is also the reason for somewhat less radical attempts to standardise the assignment of species status (e.g. by the ‘Tobias criteria’ in ornithology, Tobias et al. 2010). This standardisation would not make the species rank fully objective, but at least taxonomic conclusions would be consistent, and, given the same raw data, the same species taxa would be delimited by different taxonomists, which at present is clearly not the case.

Since conservation has not only a biological, but also a societal and, importantly, a legal dimension, the fuzziness of nature (and hence taxonomy) creates problems in legal practice (see, for example, a petition for legally unequivocal definitions of the species and subspecies categories in the framework of the US Endangered Species

Act: <https://pacificlegal.org/wp-content/uploads/2017/11/ESA-Taxonomy-Rulemaking-Petition.pdf>). It is this background against which Garnett and Christidis (2017) recently proposed the centralisation of taxonomic decisions, to make them compatible with societal and legal needs. Not surprisingly, the reactions from the taxonomic community have been very critical, but the problem remains very real, and simply defending the scientific freedom of taxonomists is not enough to solve it.

There are different ways to deal with the predicament of fuzzy boundaries. Since taxonomic classifications not only serve scientific purposes but are also necessary to enable communication about biodiversity, adopting two different classifications side by side has been suggested – one for convenience and communication, and one with scientifically more robust and less inclusive taxa. This goes back at least to de Vries and his systematic vs. elementary species (de Vries 1905, p. 12, see also Kunz 2012, p. 44). Since this is unlikely ever to be realised (and for good reasons), one is left with basically two options. First, one could standardise taxonomy to such a degree that the assignment of taxonomic rank (species, subspecies etc.) becomes more consistent, e.g. along the lines of the ‘Tobias criteria’. However, any such standardisation would suffer from limited applicability, because species delimitation would have to be based on very different characters or data in different branches of the Tree of Life. The ‘Tobias criteria’ are tailored for birds and will not work for nematodes or plants. The only remedy would be a very crude yardstick such as genetic similarity based on certain marker genes. Microbiologists have done this for a long time, but at least in eukaryotes this would neglect so many evolutionarily relevant features that the species rank would be in danger of becoming an empty name. And in any case it would only work for extant species, while for many diversification analyses or quantifications of biodiversity through time, fossils are indispensable.

The second option is to decouple conservation from taxonomy, at least partially. Because of the above-mentioned grey area and because of the nature of taxonomy, the match between taxonomy on the one hand and evolution or biodiversity on the other will never be a perfect one. Inherently fuzzy boundaries in nature are real, but they are further exacerbated by the intermediate step of having to press continuously variable biodiversity into discrete taxonomic names. So, instead of using these names as proxies for conservation, why not use the raw data (quantified biodiversity) themselves? This was already done when Evolutionarily Significant Units were introduced, and it is no coincidence that originally they were meant as a replacement for a taxonomic category (the subspecies, Ryder 1986). There are practical difficulties with the Evolutionarily Significant Unit approach, but it remains an important

point that biodiversity and knowledge thereof must not be conflated with the taxonomic conclusions that are based on those things. G&G are right in stating that much of earth's biodiversity is as yet unknown and unquantified (including that of African ungulates), but that holds irrespective of whether uncovered diversity is interpreted as intraspecific or as evidence of separate species. Discovery of diversity does not in itself necessitate taxonomic splitting, and the loss of diversity within what is classified as a single taxon is also not necessarily less bad than the loss of taxonomically acknowledged portions of biodiversity. From this it becomes clear that taxonomy alone is an incomplete and sometimes even a poor guide to conservation, and it should, as far as possible, be the underlying data on diversity themselves that matter for conservation – not a name that imprecisely captures this diversity one way ('splitting') or the other ('lumping'). Thus, Table 2 in Gippoliti et al. (2018) on extinct and near-extinct African ungulates loses nothing of its sadness, regardless of whether or not one accepts the taxonomy behind it. The fact remains that significant portions of ungulate diversity have vanished.

From a scientific point of view, the underlying diversity discovered in the case of the recently described orangutan species *Pongo tapanuliensis* (Nater et al. 2017) should not matter less than the new name attached to it. However, most of the attention in these cases is directed at the name, not the hitherto unknown diversity. If only the latter had been published, saying that this adds considerably to what is known about orangutan variability, it would not have made it into the headlines. Prioritising the name over the diversity may perhaps be acceptable for the media and the general public, but the scientific community should know better.

Scientists should care less about names and more about what could be dubbed, in analogy to operational taxonomic units (OTUs) in phylogenetics, meaningful taxonomic units (MTUs) in or for conservation. MTUs could be based on some measure of phylogenetic diversity (Faith 1992), which is a tree-based quantification of distinctiveness among OTUs using branch length as a distance measure. Although phylogenetic diversity can be used in combination with taxonomy-based information, for example as Evolutionarily Distinct and Globally Endangered species (the EDGE approach; Isaac et al. 2007), phylogenetic diversity is independent of *a priori* taxonomic classification. Branch lengths are usually quantified based on genetic (soon: genomic) data, but any kind of character could be used instead or in addition. An advantage of decoupling taxonomy from conservation is that MTUs could be chosen according to context: in captive breeding programmes where outbreeding depression might be an issue (see above), data on karyotype or the genetic load of populations, rather than overall branch length, could be chosen to define meaningful taxonomic units.

In conservation, the meaningful could and should be prioritised over the easily measurable. Rather than relying on a one-size-fits-all taxonomy, researchers could decide on a case-by-case basis which biological parameters are most relevant to the conservation of particular populations under study. Importantly, international conservation organisations (e.g. the International Union for Conservation of Nature and the World Wide Fund for Nature) would have to embrace this approach by focusing more on intraspecific conservation units and by allowing these units to be defined flexibly (as it stands now, even the subspecies category is not given full attention). This would acknowledge the inherent limitations of taxonomy (the grey area) and do justice to the essential aim of conservation – to protect as much variance among living beings as possible.

CONCLUSIONS

Most researchers agree that species are lineages, or, more specifically, separately evolving population-level lineages. For species delineation to be fully objective, this is the only (i.e. both necessary and sufficient) condition for species status. Since nobody wants to acknowledge every single allopatric population taxonomically, other sufficient conditions are considered important. During lineage sundering, there is a grey area in which the biological phenomena evolve, in no specific order, that are the content of the various species concepts (apomorphies, diagnosability, reciprocal monophyly, reproductive isolation etc.). All of them are equally contingent with regard to the status as a separate lineage, and different decisions for a particular one as the arbiter for when two separate species should be acknowledged delimit species at different levels of inclusiveness. Importantly, any such decision is in part arbitrary.

Accordingly, application of the dPSC in a lineage framework of species is not superior, in fact not even theoretically different, from other operational species concepts. Claiming objectivity where it does not exist does a disservice to both science (taxonomy) and practice (conservation). Within the grey area of lineage sundering, species delimitation is something like an executive decision, and both more inclusive ('lumping') and less inclusive ('splitting') decisions are neither right nor wrong.

This fuzziness of species boundaries is grounded in the fuzziness of nature, but it creates an 'apples and oranges' problem for disciplines in which species and their numbers are used as a currency (macroecology, evolutionary biology, conservation).

Particularly in conservation, rather than taking taxonomy ('names') at face value, perhaps the underlying biological data (such as genetic divergence, outbreeding depression,

occupied volume in ecospace or morphospace etc.) should be considered more informative and more relevant for delineating meaningful taxonomic units that are the target of practical decisions.

DEDICATION

While I was working on the manuscript of this article, Colin Groves (1942–2017) sadly passed away. Although we disagreed strongly on taxonomic principles, I admired his probably unparalleled taxonomic knowledge of mammals and his kind and humble personality. I would have loved to hear his critique of the views put forward in this article, which is dedicated to his memory.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. List and definitions of species concepts mentioned in the text.