

A coalescent perspective on delimiting and naming species: a reply to Bauer *et al.*

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Invited reply

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‘Our classifications will come to be, as far as they can be so made, genealogies . . . The rules for classifying will no doubt become simpler when we have a definite object in view.’ (Darwin [1], p. 486).

Our paper about species delimitation in African forest geckos (*Hemidactylus fasciatus*) used a novel coalescent-based Bayesian method that has generated a new level of scrutiny in species delimitation and taxonomy [2]. One critique was voiced by Bauer *et al.* [3] (hereafter referred to as BEA), who are concerned about species delimitation and the primacy of the International Code of Zoological Nomenclature (ICZN; [4]) for the description of new species. BEA argued that the names we proposed for *Hemidactylus* geckos are invalid because they did not follow the ICZN. Here, we agree with BEA, and formal morphological species descriptions that are in accordance with the Code are forthcoming for these taxa. However, BEA’s critique was not limited to this technical issue as they also expressed concern that our approach to species delimitation (i) will lead to taxonomic inflation and (ii) is inferior to character-based taxonomies regarding comparability between species. Herein, we reply to BEA regarding both of these issues and furthermore comment on the fundamental issue of whether strict adherence to character-based descriptions limits our ability to generate objective taxonomies that are consistent with the goals of contemporary evolutionary biology research.

1. OBJECTIVITY IN SPECIES DELIMITATION IS CRUCIAL FOR STABILIZING TAXONOMIC PRACTICES

Taxonomic inflation occurs when investigators raise subspecies or geographical variants to the species level by applying alternative species concepts. The opposite can occur as well, and this disparity not only profoundly affects conservation and ecological research [5], but also highlights the inherent subjectivity in current practices of species delimitation and taxonomy. This subjectivity undermines taxonomic stability. The phylogenetic species concept, for example, is particularly prone to taxonomic inflation because it can diagnose species based on single character states, regardless of their significance [5,6]. Avoiding these pitfalls requires methods of species delimitation and description that are *objective* and *robust*, which will enhance comparability between species and result in

more stable taxonomies. The desire for objectivity is not new to species studies, but it is essential as long as investigators consider species as real entities [7]. BEA argue that character-based taxonomy following the guidelines of the ICZN provides the basis for comparability, but it also *allows* divergent taxonomic practices to persist, resulting in taxonomic instability. In addition, characters evolve at different rates in different lineages, which further undermines a standardized character-based system. The idealism of comparability as envisioned by BEA has proved difficult to achieve under the present system.

2. MULTI-LOCUS, COALESCENT-BASED METHODS INCREASE OBJECTIVITY IN SPECIES DELIMITATION

We delimited species in the *H. fasciatus* species group using the statistical results from Bayesian phylogenetics and phylogeography (BPP; [8]), a novel multi-locus species delimitation method based on a multi-species coalescent model [9]. Multi-locus approaches for species delimitation that use the multi-species coalescent model are advantageous because they can model the probabilities associated with lineage formation, which is directly aligned with the principles of lineage-based species concepts [10]; this is not the case when requiring strict adherence to intrinsic characters for defining species. Multi-locus data also capture the stochasticity inherent in the coalescent, including gene tree incongruence stemming from incomplete lineage sorting, variation in molecular sequences and variation in demographic parameters [8,11–14], all of which must be modelled to achieve accurate species delimitation with molecular genetic data.

A shift towards multi-locus coalescent-based methods for species delimitation, and ultimately taxonomy, is important for several reasons. First, the methods are more objective, and allow the data—not the biases of individual investigators—to determine the outcome by providing explicit probabilities of speciation events. Second, they are grounded in evolutionary history and population genetic theory. BEA do not deny that the new species of *Hemidactylus* that we named represent valid taxa under any of several lineage-based species concepts [10], yet they cite our failure to incorporate intrinsic characteristics of the organisms into our descriptions as a means for delaying formal description of the new taxa. We posit that the coalescent history of alleles is one of the most salient attributes of a *species*, and that species delimitation based on this history will become more

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commonplace as genetic and genomic data accumulate, and this should be accommodated by the Code. We emphasize that by coalescent history we do not mean reciprocal monophyly of alleles between species (although this could occur), but rather a significant shift in gene trees away from the patterns expected under the null hypothesis of random mating. Third, the method embraces genetics and lineage-based arguments. Unlike morphological characters that are under environmental influences, genetic variation is 100 per cent heritable; this is particularly important for taxonomy to reflect genealogical relationships as envisioned by Darwin. Fourth, the method is universal for comparing diversity across the entire tree of life, and by extension, allows for much greater comparability among species.

Based on the above arguments, our species delimitations of the *H. fasciatus* group avoided taxonomic inflation and provided clear, practical and philosophically grounded comparability between species. We suspect that taxonomic inflation will become less of an issue as taxonomists adopt more objective species delimitation methods (such as BPP) and move away from gene-tree-based or subjective species diagnoses. Of course, BPP is not infallible, and may fail to recognize speciation events that involved only a limited number of genes, or will lead to incorrect results when the assumptions of the model are violated [2]. BPP is objective given the clear assumptions of the model, which starkly contrasts with traditional species delimitation approaches that make many, often unidentifiable, implicit assumptions. Nevertheless, all statistical methods aim for objectivity by letting the data speak for themselves. In this case, BPP is a giant leap forward towards objective species delimitation. Our study is a single case, and we urge continued exploration of BPP as a species delimitation tool.

3. SPECIES DELIMITATION AND TAXONOMY ARE CONNECTED

We believe that a strict requirement for describing species using morphological data (or ‘fixed DNA differences’) creates an artificial separation between species discovery and species description where genetic data are relegated to the discovery of new species, but the post hoc discovery of morphological differences (or fixed DNA differences) is necessary to describe those species. Many good species will not exhibit fixed morphological differences or fixed DNA differences across multiple loci. An integrative taxonomy should not force systematists to search for diagnostic attributes that may have no relation to the data or process used for species delimitation [15]. While the traditional method and rules set forth in the Code work for morphological species, we believe that it impedes the timely documentation of many independent evolutionary lineages and cryptic species discovered with genetic data. BEA lament a future where the application of analytical tools, such as BPP, is necessary for properly identifying individuals to species; however, we do not view this as any more laborious than conducting a multivariate analysis of morphometric data to attain the same goal [16]. Furthermore, our goal should be to describe all of the world’s species, not

just the subset of species that meet a subjective minimum standard reflecting ease of identification.

By developing biologically realistic models for analysing genetic data in species delimitation, systematics and taxonomy, we can develop an integrative taxonomy that fulfills Darwin’s goal of classifying life from a genealogical perspective. The relevance for this endeavour is crucial as researchers continue to incorporate new DNA sequencing technologies and coalescent-based inference methods, and as multi-locus genetic and genomic data become progressively easier to collect for a wide range of organisms. A main point of our paper [2] is that objectiveness is necessary *exactly* for the reason of comparability and consistency of executing statistical species delimitation and taxonomy. As species delimitation becomes more objective, we anticipate the scientific community will adjust the ICZN Code in a manner that embraces this objectivity and recognizes the merits of model-based species descriptions as both practical and philosophically advisable.

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