

## Reply to Lukhtanov: Polytypic species: Old wine in a new bottle

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In his letter, Lukhtanov (1) brought a historical perspective to our recent proposition to delimit phylogeographic lineages that have not yet achieved reproductive incompatibility as subspecies (2), noting how it related to the century-old concept of polytypic species.

As argued (1, 2), the general idea that species may be subdivided geographically is not new. Speciation often finds roots in phylogeographic diversifications, hence many widespread species are polytypic, at least at some stage of their evolutionary history. Even though it has often been neglected, the subspecies rank is as old as taxonomy itself—Carl von Linnaeus already featured trinomials in his Systema Naturae, and these were explicitly incorporated in the nomenclatural system by German naturalist Carl Friedrich Bruch during the early 19th century.

What is new is our ability to detect and interpret species' subdivisions in the evolutionary context at a much finer scale. In turn, we can categorize this diversity more objectively and universally to ensure its protection. Rehabilitating subspecies, a rank already recognized by taxonomic and conservation authorities, then appears more relevant than creating new ad hoc categories (2).

Taxonomic disagreements are not driven by species or subspecies concepts as much as by the operational criteria proposed to enforce these concepts (3). The differing views of species and subspecies delimitation have often stemmed from the methodological approaches available in a given time, for a given clade, and to address the evolving challenges of biodiversity conservation. Since the 1970s, the molecularization of taxonomy has tremendously increased our power to distinguish genuine evolutionary lineages from ephemeral genotypes and phenotypes. At the same time, methodological progress has required a nearly constant renewal of the criteria to apply, both to deal with the new "genetic forms" of diversity detectable, and specifically to account for the limitations of molecular tools (e.g., allozymes, barcoding gene sequencing, etc.). Delimiting biodiversity has thus shifted from conceptual to operational concerns (4).

By granting access to the whole genetic background of organisms, next-generation sequencing represents the most significant advance in the field of taxonomy in decades, perhaps since the development of the polymerase chain reaction. With such ultimate resolution to understand the structure of biodiversity, we can finally go back to the classical concepts and unify existing species delimitation practices. The applicability and conservation-effectiveness of our guidelines (2) across all animals and plants will obviously depend on the resources available to taxonomists, in respect to the amount of biodiversity to delimit, as well as the political will to protect this diversity at multiple taxonomic scales. Anyhow, like old wine in a new bottle, the classical polytypic species concept will remain more actual than ever in the genomic era.

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The authors declare no competing interest

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C. Dufresnes, N. A. Poyarkov, D. Jablonski, Acknowledging more biodiversity without more species. Proc. Natl. Acad. Sci. U.S.A. 120, e2302424120 (2023).

S. Conix, V. Cuypers, F. E. Zachos, A. De Block, Taxonomic disagreement about ranks in gray-area taxa: A vignette stud. BioScience 73, 728-737 (2023).

J. M. Padial, A. Miralles, I. De la Riva, M. Vences, The integrative future of taxonomy. Front. Zool. 7, 16 (2010).