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# Editorial

## Perspectives on speciation

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The process of speciation lies at the centre of evolutionary biology: speciation is an outcome of evolutionary forces operating within and among populations, and it provides the raw material for the generation of patterns of biological diversity at large temporal and spatial scales. As a result of this central position, many biologists have an interest in speciation but their points of view may be widely different. For example, to a population geneticist the problem is to understand the origin and accumulation of barriers to gene flow through the interaction of mutation, drift, selection, migration, and recombination. For the palaeontologist, the challenge is to document the appearance of new, morphologically defined lineages and to identify factors influencing rates of lineage splitting (and extinction). A macroecologist may be more interested in the way speciation rates contribute to the spatial or taxonomic distribution of biological diversity. In addition to differences in perspective based on disciplines, views of speciation may also differ depending on the taxonomic or methodological focus of researchers. Progress towards a comprehensive understanding of speciation is likely to be enhanced by tackling the topic from many different angles but, critically, it also requires the exchange of ideas and information among researchers with different perspectives.

This special issue is intended to contribute to the interdisciplinary communication needed to bring together the progress made within specialist areas into an integrated understanding of speciation. Most of the papers included are derived from a meeting, 'Perspectives on Speciation', held at the Linnean Society in April 2024, which aimed to bring together a set of speakers, and an audience, representing a wide range of different points of view. The Linnean Society is pleased to acknowledge support for this meeting from The Company of Biologists, Oxford University Press, and the Integration of Speciation Research Special Topic Network (which is funded by the European Society for Evolutionary Biology). [Stankowski et al. \(2024\)](#) provide a more general overview of the need for integration in speciation research and make recommendations for ways to encourage integration: the Perspectives on Speciation meeting and this special issue follow one of their suggested strategies by bringing together scientists who might normally attend distinct sets of conferences and publish in different journals.

One of the barriers to the integration of speciation research is the language used ([Stankowski et al. 2024](#)). There are multiple aspects to this problem, including drift in the meaning of terms over time and divergence in their meaning among disciplines, but also the need for care in the way ideas are expressed ([Walker et al. 2024](#)). Defining 'species' is famously a core problem. [Coyne and Orr \(2004: p. 25\)](#) argue that: 'we cannot study how species form until we determine what they are.' However, one can certainly make the complementary argument that understanding the processes that generate discontinuities in biological diversity helps in finding the best way to define units of diversity. [Dupré \(2024\)](#) argues that species are best viewed as 'processes', rather than the usual treatment of them as 'things' (either individuals or classes). Many biologists are unaware of this philosophical perspective but it is a thought-provoking idea that fits well with the view that speciation can be represented as a continuum running from a set of populations connected in a single lineage through to two or more evolutionarily independent lineages. The starting point of the continuum can be hard to define ([Butlin and Faria 2024](#)) because population structure is a near-universal feature of any species that has a range significantly larger than its dispersal distance. This structure is often driven by local adaptation and, therefore, involves some reproductive isolation implying that speciation has begun. The end point is also hard to identify. Various thresholds can be defined along the continuum that correspond to different operational definitions of species. [Meneganzin and Stringer \(2024\)](#) use the example of *Homo sapiens* and Neanderthals to illustrate how these thresholds may be crossed at different times, without necessarily occurring in any consistent sequence. They also argue that the temporal dimension available in the fossil record helps to interpret relationships between diverging populations at any given point in time. Phylogenetic information can help in a similar way: [Singhal et al. \(2024\)](#) argue that a molecular phylogeny can help to delineate operational taxonomic units that are genetically cohesive and independently evolving. Such comparable units are needed for comparative analysis and may not be provided by current taxonomy, an issue that they illustrate with a study of speciation in *Xantusia* lizards.

[Wiens \(2024\)](#) discusses patterns of speciation and diversification across the whole tree of life [although, like

Stankowski *et al.* (2024), he notes the uneven coverage of taxa in the data available]. It is encouraging that such analyses are possible, and reveal some broadly consistent patterns, such as widespread roles for spatial separation and divergent selection during speciation, implying that there is some consistency in the way species and speciation are defined. Stelkens (2024) also argues for processes of ecological specialization and the evolution of additional barriers to gene exchange in microbes, both of which are shared with multicellular organisms. The specifics of barriers may be different in multicellular eukaryotes, eukaryotic microbes, and prokaryotes but the outcomes are often comparable. One practical implication is that experimental speciation, particularly with eukaryotic microbes, has great potential to address questions of broad relevance.

The analyses described by Wiens (2024) suggest that ‘allopatric speciation’ is common across a wide range of taxa. The general conclusion about the importance of spatial separation is reflected in the analysis of *Xantusia* (Singhal *et al.* 2024). However, broad comparative conclusions can be hard to reconcile with more mechanistic understanding of the speciation process. Wiens (2024) specifically questions how allopatric separation is brought about, arguing that it can be the result of a failure of adaptation to a changing environment. This may explain frequent dissection of species ranges, but a naïve model of allopatric speciation, with a complete external barrier to gene flow maintained until reproductive isolation is complete, clearly does not explain other observations, especially the widespread evidence for introgression. Introgression among persistently differentiated populations that are frequently recognized as taxonomic species clearly shows that contact between divergent populations commonly occurs before barriers to gene flow are complete [see Walker *et al.* (2024) for examples and a discussion of introgression, and Meneganzin and Stringer (2024) for the implications of introgression between Neanderthals and *Homo sapiens*]. Allopatry can also contribute in different ways to evolutionary radiations, contributing to the origin of divergence or to persistence of divergent populations, for example (Gillespie 2024, and see Schluter 2024). Also, allopatry may be common but is not always necessary for speciation, as in the *Howea* palms discussed by Coathup *et al.* (2024).

Perhaps most importantly, allopatry does not, in itself, explain the evolution of reproductive isolation. This occurs by drift, uniform selection (mutation-order effects or one-allele barriers) or divergent selection. The relative importance of these processes is expected to depend on the extent of gene flow, with allopatry making divergence under drift or mutation-order effects more likely but also making divergent selection more effective. How strong and persistent barriers to gene flow typically arise remains uncertain. In this issue, Ayala-Lopez and Bank (2024) consider how complex incompatibilities might evolve and create more effective barriers than simple, two-locus incompatibilities. Kitano and Okude (2024) review the known examples of genes of large effect that contribute to incompatibilities, including cases that do not follow the simple two-locus expectations. On the other hand, Coathup *et al.* (2024) tackle the evolution of strong barriers via a combination of ecological divergence and

assortment, testing for pleiotropic effects of genes that are expected to strengthen barrier effects because the association between divergent selection and assortment cannot be broken by recombination. They use the language of ‘magic traits’, another area where terminology has caused difficulties in communication (see Dopman *et al.* 2024 and references therein).

Multiple different comparative approaches can be used to investigate common factors contributing to speciation, such as periods of spatial separation, or variables that influence the rate of speciation (Singhal *et al.* 2024). Rates may vary across taxa, by geography or in relation to specific traits (Singhal *et al.* 2024, Wiens 2024). Eiserhardt *et al.* (2024) provide an instructive example using the palms of Madagascar. They show that the most species-rich clades of palms on the island had high diversification rates before they colonized the island: the variation in current diversity among clades is more dependent on rate variation than on variation in the time available for speciation since colonization. This is consistent with broad patterns of species richness across taxa (Wiens 2024). Diversification rate variation is correlated with ecological features, but it remains difficult to connect this variation to a mechanistic understanding of the speciation process. Making the connection between macroevolutionary patterns and microevolutionary processes is one of the greatest challenges for the integration of speciation research (Stankowski *et al.* 2024). It is one that requires the joint efforts of biologists with many different backgrounds.

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