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Review

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Review

Toward the integration of speciation research

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ABSTRACT

Speciation research—the scientific field focused on understanding the origin and diversity of species—has a long and complex history. While relevant to one another, the specific goals and activities of speciation researchers are highly diverse, and scattered across a collection of different perspectives. Thus, our understanding of speciation will benefit from efforts to bridge scientific findings and the diverse people who do the work. In this paper, we outline two ways of integrating speciation research: (i) scientific integration, through the bringing together of ideas, data, and approaches; and (ii) social integration, by creating ways for a diversity of researchers to participate in the scientific process. We then discuss five challenges to integration: (i) the multidisciplinary nature of speciation research, (ii) the complex language of speciation; (iii) a bias toward certain study systems; (iv) the challenges of working across scales; and (v) inconsistent measures and reporting standards. We provide practical steps that individuals and groups can take to help overcome these challenges, and argue that integration is a team effort in which we all have a role to play.

Keywords: collaboration; diversity, equity and inclusion; scientific practices; synthesis

INTRODUCTION

The core goals of speciation research

Humans conceptualize the diversity of life through the recognition of the more or less distinct units that we call species (Mayden *et al.* 1997, Sigwart 2018, Stankowski and Ravinet 2021a). Broadly speaking, speciation research aims to answer two questions about these units: (i) How do species form? And (ii), what determines variation in speciation rate and species richness across taxa, geographical regions, times, and environments? Many specific questions fall under these two umbrellas and may be expressed and prioritized differently, depending on the perspective of the researcher. For example, biologists who focus on sexually reproducing eukaryotes often state the first question ('How do species form?') as 'How does reproductive isolation evolve?' (Coyne and Orr 2004). Others argue that distinct clusters of organisms in phenotypic or genetic space can be maintained in many ways, not limited to sexual reproduction and reproductive isolation (Barraclough 2019). Depending on whether researchers see speciation as the evolution of reproductive isolation or the formation of distinct clusters, some questions might make less sense than others (e.g. the question 'What is the relative importance of sexual selection in speciation?' when studying the evolution of distinct clusters in asexual organism). Some questions are dependent on specific approaches, such as 'What is the genomic distribution of barrier loci?' (usually tackled with genomic data), while others necessarily require multiple types of data, such as 'How do different phenotypic components of reproductive isolation combine to generate a genome-wide barrier to gene exchange?'

The second broad question (on the determinants of variation in speciation rate and species richness), classically addressed by macroevolutionary research, can be approached using different sources of data, including the fossil record (Sepkoski 1998) or comparative methods (Weir and Schluter 2007). Again, this may lead to different ways of expressing the problem, asking, for example, 'What is the role of mass extinctions in promoting diversification?'; and 'Why is there an imbalance of species diversity across the tree of life?'. Since these questions are intimately associated with explaining patterns of species richness, they frequently require thinking about extinction and geographical range change along with speciation. Thus, they are strongly connected to and, in some cases, largely overlapping with the fields of macroecology (Blackburn and Gaston 2003), macroevolution (Tobias *et al.* 2020), and geology (Hautmann 2020).

An important additional set of issues links the two main questions of speciation research (Reznick and Ricklefs 2009): 'Can we predict patterns of diversity from our understanding of speciation mechanisms?', or, in other words, 'Are macroevolutionary patterns simply generated by the accumulation of microevolutionary processes?' Alternatively, questions can be phrased in

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ways that span the micro–macro divide, such as 'What are the primary drivers of speciation?'

This list of questions, which is far from exhaustive, highlights a major challenge facing the field of speciation research: while interconnected, and sometimes directly relevant to one another, the specific goals and activities of researchers are highly diverse and scattered across a collection of different perspectives. Thus, if we want general answers to the big overarching questions, we will need to integrate our efforts by bringing together diverse scientific findings and the diverse people who do the work.

Ways to integrate speciation research

To integrate means 'to form into a whole'. In science, one can think about integration in two main ways. First, we can aim for scientific integration, through the establishment of connections among different ideas or approaches, or by seeking generalization through formal comparative meta-analyses of many individual studies. Second, integration of the research community can be achieved by creating ways for researchers from diverse geographical regions, subdisciplines, personal identities, or career stages to participate in the scientific process. This matters not only because it is important that scientific opportunities are equitable, but also because the field has much to gain from diverse perspectives.

There are many examples demonstrating how scientific integration has been important in speciation research. In one of the greatest examples of integration across disciplines, Darwin's (1859) book gathered many case studies and drew on agriculture and horticulture, geology, natural history, biogeography and palaeobiology to argue for the origin of species by means of natural selection. The conceptual framework of current speciation research stems from the integration of genetics with these other fields in the Modern Synthesis (Dobzhansky 1937, Huxley 1942, Mayr 1942, Simpson 1949, Stebbins 1950). The mass of knowledge that accumulated in the second half of the 20th century was brought together in the landmark book by Coyne and Orr (2004). Each chapter sought general patterns in empirical data and attempted to integrate them with theoretical expectations. Many of the contributions that are seen as major steps forward in speciation research have been integrative in nature. Examples might include the study of reinforcement (Box 1), the integration of sexual selection with speciation (Lande 1981, West-Eberhard 1983), micro- with macro-evolutionary patterns (Vrba and Gould 1986), ecology with speciation (Schluter 2000), genomics with speciation (Peichel *et al.* 2001, Turner *et al.* 2005), or micro- with macro-evolutionary rates of speciation (Rabosky and Matute 2013).

The need to expand and integrate our research community has not been a historical priority of our field. This is reflected in the list of examples above, the authors of which lack demographic diversity across many axes (e.g. ethnicity, gender, global diversity of researchers). It is our moral duty to broaden access, and ensure that this historical bias does not continue into the future. Diversity within the community will enhance dialogue among researchers with different perspectives and approaches, which will ultimately boost scientific integration of our field. In the private sector, diversity and inclusivity provide companies with a competitive edge (Mayer *et al.* 2018), and socially diverse groups are more innovative and productive than homogeneous groups (McLeod *et al.* 1996). Demographically underrepresented students innovate at higher rates than majority students, but their novel contributions are more likely to be discounted (Hofstra *et al.* 2020). Aside from these, genuine social integration will not be easy, and the specific challenges faced by different individuals will vary depending on their privilege.

Identifying and overcoming challenges to integration

To integrate speciation research successfully, we will need to work to identify challenges to integration, and then create ways to overcome them. As a step towards this, the authors of this article attended a workshop organized by the Integration of Speciation Research (IOS) Network—a Special Topic Network funded by the European Society for Evolutionary Biology (https://speciation-network.pages.ist.ac.at/). The workshop was held at Tvärminne Zoological Station, University of Helsinki, Finland (30 March to 3 April 2023), and aimed to identify challenges to integration of speciation research and propose potential solutions (Supporting Information). Participants of the workshop were selected to maximize diversity across multiple axes, including geographical origin, gender, career stage, training, and study system (Box 2).

The remainder of the article will discuss five key challenges to the integration of speciation research (Fig. 1). First, it is difficult to integrate the ideas, approaches, and findings of researchers from different scientific disciplines, but doing so may help us make progress on stubborn questions and identify new research directions. Second, we argue that the language used in speciation research can be a barrier to effective integration; we need to find ways to foster clear and consistent language to improve communication among speciation researchers and the broader scientific community. Then, we see subdivisions in the field, and benefits to bridging work conducted across two different dimensions: across taxonomic, environmental, and ecosystem gaps, and across spatial and temporal scales. Bridging these dimensions and scales will help us understand the relationship between patterns and processes, allowing us to draw more general conclusions. Finally, given the value of comparative meta-analyses in advancing our understanding, our field needs consistent measures and standards for reporting results, along with infrastructure to support the community-wide sharing of data. Although we share some ideas for overcoming these challenges, our main aim is to increase awareness rather than provide concrete solutions. In doing so, we hope that others will be persuaded to invest the time and effort needed to develop and implement solutions in the future.

CHALLENGE 1: SPECIATION IS A MULTIDISCIPLINARY PROBLEM

Speciation research as a meta-discipline

Rather than a distinct research field composed of sub-fields, speciation research sits at the intersection of multiple scientific disciplines (Fig. 2). For instance, research spanning development, genetics, genomics, organismal studies, and ecology has together contributed to identifying the genetic and developmental basis of colour pattern variation and its role in lineage divergence and isolation in organisms as diverse as *Heliconius* butterflies (Mallet and Barton 1989, Reed *et al.* 2011, The Heliconius Genome

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Box 1. Scientific integration in speciation research: reinforcement as a case study

The study of reinforcement exemplifies how the integration of scientific ideas and practices can lead to new insight (Servedio and Noor 2003). The first step was innovation: the idea of reinforcement was first clearly articulated by Dobzhansky (1937), but has earlier roots tracing back to Wallace (1889) [see Howard (1993) for an historical overview]. Theoretical models and simulations showed that reinforcement is possible, and indicated limits to when it is likely to contribute to speciation (Liou and Price 1994, Kirkpatrick and Servedio 1999). Empirical studies on individual cases demonstrated that reinforcement can occur in the real world, not just in the simplified conditions of theory or simulation (Noor 1995, Sætre *et al.* 1997). However, generalization is also necessary: to go from 'reinforcement can contribute to speciation' to 'reinforcement contributes to X% of speciation events in sexually-reproducing organisms, varying among clades due to Y and Z' requires that multiple studies are brought together and analysed systematically.

The first step in this direction was taken by Coyne and Orr (1989) in their comparative analysis of reproductive isolation in *Drosophila*. Yukilevich (2012) went further, estimating that reinforcement had impacted the evolution of premating isolation in 60–83% of sympatric *Drosophila* species pairs. Theoretical and empirical generalization is also possible: models of reinforcement can be considered special cases of more general models of speciation (Felsenstein 1981, Barton and de Cara 2009). Finally, understanding the place of reinforcement in relation to other speciation processes requires a synthetic step: connecting the contribution of reinforcement to other elements of the speciation process and to variation in speciation rate. This relationship was present at the initial conception of the idea because Dobzhansky saw reinforcement as one step in a speciation process that began with divergence in allopatry, but ideas about this connection have evolved (Butlin 1995, Abbott *et al.* 2013, Butlin and Smadja 2018).

The process illustrated with this example is widely applicable: innovative ideas lead to case studies (empirical and theoretical) which form the backbone for comparative or meta-analytical work aimed at generalization, while attempts are also made to synthesize the idea with other patterns and processes. This need not be a linear sequence. Innovation might emerge from synthesis, for example, or an attempt at generalization might be the stimulus for new case studies. However, no field can truly advance without a combination of these components: that is, without integration.

Consortium 2012, Martin *et al.* 2013, Van Belleghem *et al.* 2023) and *Mimulus* wildflowers (Bradshaw *et al.* 1998, Schemske and Bradshaw 1999, Liang *et al.* 2023). Likewise, the integration of palaeontological and palaeoenvironmental data with DNA sequence data of extant organisms has allowed estimation of past rates of diversification and extinction, while implicating specific phenotypic traits as drivers of speciation and diversification (Benton 1995, Alroy 2008, Quental and Marshall 2010, Pyron, Burbrink and Wiens 2013) (see Challenge 4). Interdisciplinary work can also reveal key knowledge gaps (see Challenge 3), which in itself can drive major advances in addressing or bridging them (Coyne and Orr 1989, Rabosky and Matute 2013). This history and practice of speciation research therefore highlights the power of integrating perspectives and data from disparate disciplines.

There are, however, inevitable disconnects that arise from the interaction of multiple disciplines. For example, disciplines often vary in their core training and methodologies, and in the data they aim, or are able, to acquire (Fig. 2B, C). These differences can hamper communication among areas and amplify misunderstandings arising from distinct usage of language and specialized terminology (Sonneveld and Loening 1993) (see Challenge 2), or in the methods and standards of inference, even when similar questions are being addressed (see Challenge 5). These disciplinary differences can also shape and dictate foundational divides in what is perceived as the core question within a field. Indeed, speciation researchers from different disciplines sometimes aim to answer different core questions (see Introduction). This variation is reflected in, for example, what species concepts are used or preferred (Zachos 2016, Stankowski and Ravinet 2021a) and in the working definitions of reproductive isolation (Butlin 2022, Moyle 2022, Westram *et al.* 2022a).

Divisions may be exacerbated by historical covariation among type of question, methods, and organism that arise because biological features of different systems mean they have conventionally or traditionally been associated in different disciplines. For example, *Drosophila* has provided significant insights into the genetic basis of intrinsic postzygotic isolation, but the significant challenge of performing field studies in this system means that connections between ecology and reproductive isolation have been largely neglected [but see Markow (2015) and Cooper (2018)]. In contrast, numerous classical 'field' systems have a detailed understanding of ecological context but face significant challenges addressing genetic mechanisms. Some of these historical differences might also contribute to potential power dynamics between disciplines, with some researchers perceiving members of other fields as being of 'lower value' or 'contributing less' to the study of speciation, which can reinforce the split or widen the gap between them (e.g. disciplines and researchers with access to advanced technology may be perceived as elite compared with those rooted in observation or natural history). Persistent differences in the core questions asked by researchers from different disciplines could also be a significant challenge to integration.

What can we do to integrate across disciplines?

Resolving inter-disciplinary tension requires an acknowledgement of the importance of diverse perspectives and specializations, and also the development of intentional strategies to promote this disciplinary integration. For instance, one broad element could involve actions designed to overcome or mediate some of the cultural and historical differences identified above. Possible actions include recognizing nuance and discrepancies in terminology (see Challenge 2), respecting distinctive motivating questions across disciplines (see Introduction), sharing of tools and techniques, appreciating

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Box 2. The challenge of integrating diverse viewpoints, illustrated by our workshop

Our workshop illustrates some of the challenges of bringing together diverse scientists. Our first step was to assemble a working group that maximized diversity across many axes (Fig. B1). Apart from the discussion leaders, who were selected by the IOS committee, we broadly circulated an open call to recruit workshop attendees. The application included questions about nationality, gender, career stage, study organism, methodological approach, and motivation to attend (Supporting Information S1). We prioritized participants who were highly motivated, had unique research programmes and experience relative to the other applicants, and who were from the underrepresented global south (Fig. B1; Supporting Information S2). Despite these efforts, there is clearly room to improve: well-populated countries such as China, Russia, India and the entire continent of Africa lack representation or were strongly underrepresented. One practical issue that impacted geographical diversity was the very long visa application and processing times for applicants from underrepresented countries. Workshop participants tend to focus on animals and sexually reproducing eukaryotes, and relatively few of us specialize in macroevolutionary research or use palaeontological or systematic methods (Fig. B1).

We also took several measures to make the activities and discussions at the workshop welcoming, safe, and accessible, and to ensure that all voices were heard. Prior to the meeting, the organizing team established a list of responsibilities and a code of conduct outlining expectations for all attendees, as well as things to keep in mind when communicating in a diverse group (Supporting Information S3, S4). The organizers and discussion leaders also met to discuss ways to facilitate inclusive conversation. Upon arriving at the workshop, we held an introductory session where all members gave a 1-minute talk overviewing their background and approach to research. Midway through the workshop, all participants joined a diversity, equity, and inclusion session that asked participants to discuss case studies in which diversity and equity issues were relevant (Supporting Information S5). Other activities, including a group walk and quiz night, provided opportunities to interact outside of working environments. Throughout the workshop, we provided open and anonymous ways for attendees to give feedback on things that could be improved and report any inappropriate behaviour that they had experienced or observed. At the close of the workshop, the organizing team surveyed the group to get feedback on the experience (Supporting Information S6). Although satisfaction was high, the group highlighted areas for improvement, including more opportunities for interaction, increased diversity of participants, and clearer organization of large joint discussions.

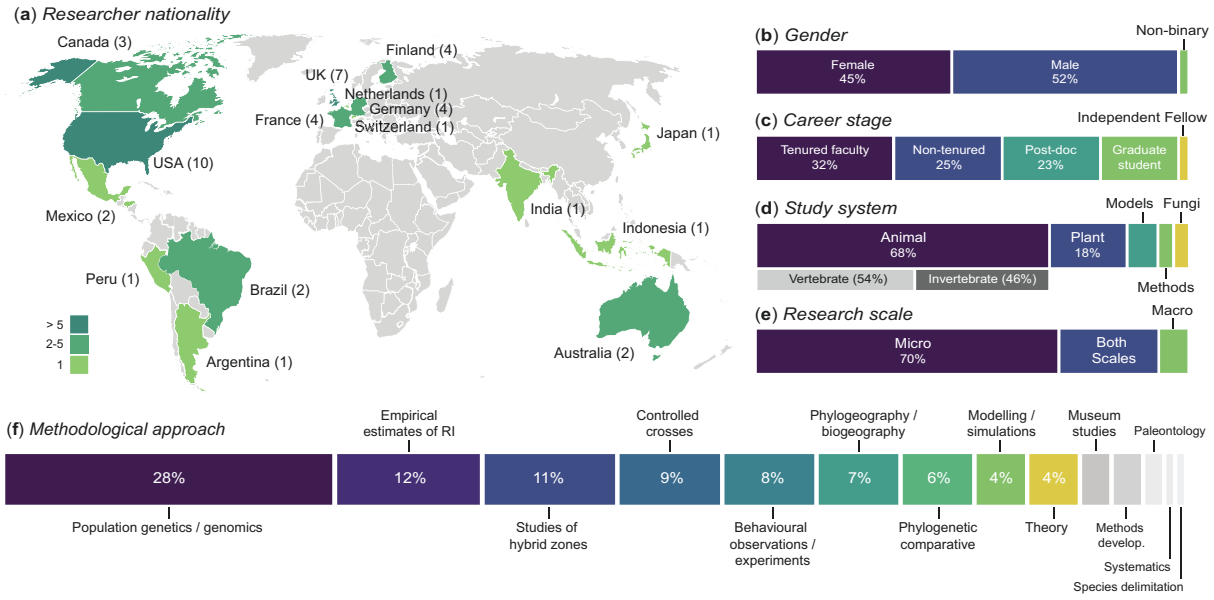

Figure B1. Demography and approaches to research among the authors. A, map showing the nationality of authors. B and C, genders and career stages of the authors. D, rough classification of the systems studied by the authors, where each author could name multiple systems. E, the evolutionary scale at which the authors study speciation. F, the main methodological approaches used, where each author could choose up to three options.

alternative frames of reference, and explicitly acknowledging unstated assumptions. For example, researchers could reduce the risk of misinterpretation by defining key terms when they use them or by referring to published definitions (see Challenge 2; Table 1). Importantly, the primary aim of these mechanisms is to enhance communication between disciplines—they need not involve assimilation or imposition of alternative views.

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Ways to integrate speciation research	Five challenges to integration	Potential solutions
Scientific integration By combining ideas, data and approaches, or by seeking generalisation through meta-analysis **Social integration** By creating ways for a diversity of researchers to participate in the scientific process	(1) Speciation is a multidisciplinary problem (2) The language of speciation is complex, hampering communication among researchers (3) Research is biased toward some organisms, ecosystems and environments (4) Speciation is studied at different spatial and temporal scales (5) Inconsistent measurements and reporting make comparative meta-analysis difficult	• Hold events that aim to unite diverse participants (1,3,4) • Seek collaborations that connect diverse expertise (1,3,4) • Provide training opportunities for diverse researchers (1,3,4,5) • Teach about the exsitence of diverse perspectives (1,2,4) • Make the publishing process more equitable (2-4) • Clarify the meaning of key terms in papers (1,2,4,5) • Create a wiki where language can be clarified (1,2,4,5) • Question and diversify our own research programs (1-5) • Focus on understudied organisms and environments (3,5) • Standardise measurements and reporting standards (1,2,5) • Create and populate a speciation database (1-5) • Identify and question our own biases (1-5)

Figure 1. Ways to integrate speciation research and challenges to integration. We see two main ways to integrate speciation research: scientific integration, and the integration of the research community. These are not independent, as a more integrated research community can improve scientific integration and vice versa. There are, however, many challenges to integration. In this paper, we focus on five challenges, and discuss actions that we can take to overcome them. The numbers show how possible solutions map onto the five challenges.

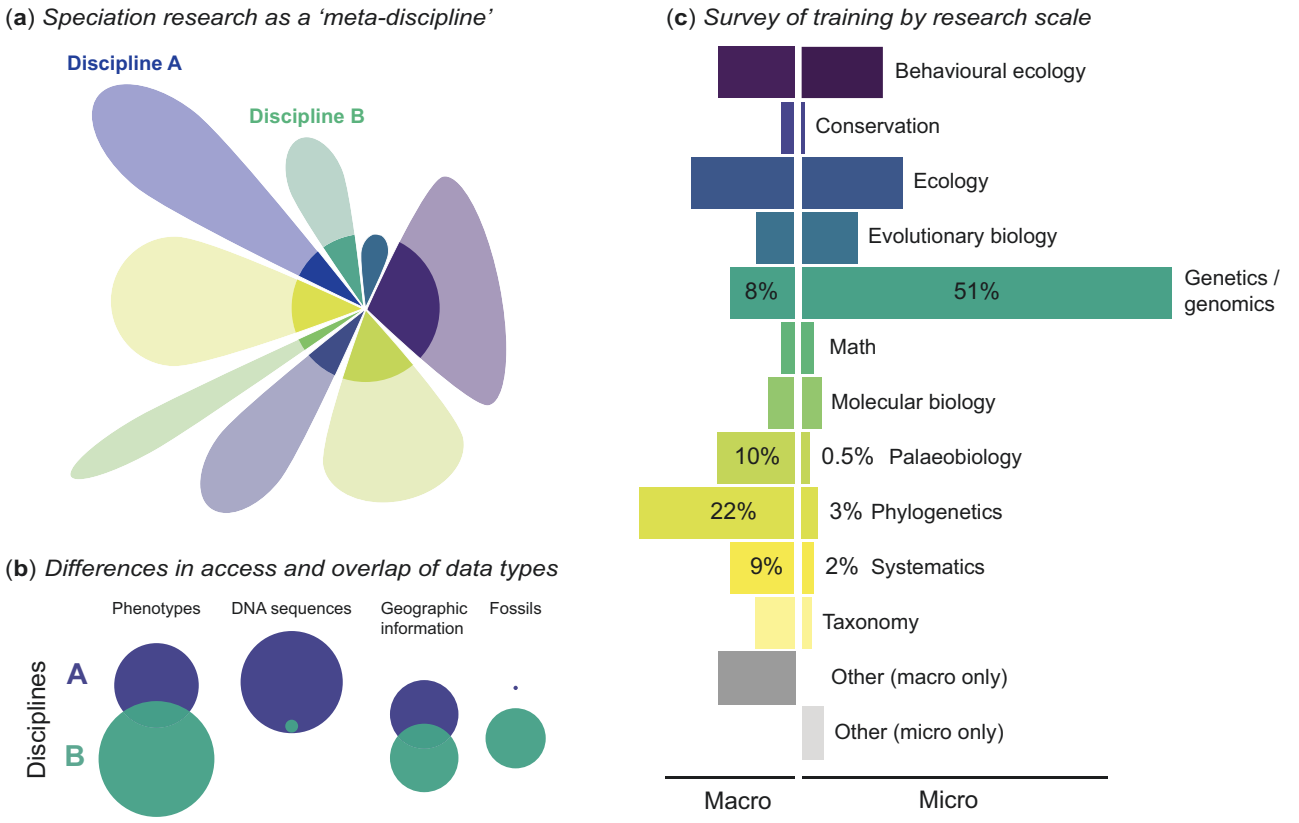

Figure 2. Hypothetical relationships between disciplines and data types, and survey results showing how training varies with research scale. A, speciation research can be viewed as a 'meta-discipline' consisting of many distinct but interrelated disciplines of biological research. This is illustrated hypothetically using different coloured 'petals' that represent different disciplines, and where the darker inner circle indicates the contribution of each to speciation research. Unbalanced contributions may be undesirable, reflecting historical effects, power dynamics, and access of funding available to different disciplines, or may reflect the relevance of a discipline when addressing questions in speciation research. The number and size of each petal will inevitably change over time. B, differences in the access to, and shared fraction of, alternative data types (size and overlap of circles, respectively) between two hypothetical disciplines. C, results from a survey of speciation researchers, showing how primary training varies among researchers who identify as working either at a microevolutionary (N = 165) or macroevolutionary scale (N = 43). Survey participants responded to the questions 'Do you work at the microevolutionary or macroevolutionary scale?', and 'What is your primary training?' [see Stankowski *et al.* (2022) for more details]. The grey boxes represent training that was specific to one group.

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Table 1. A glossary of key terms that appear in this paper, including many terms in the word cloud (Fig. 3).

Term	Definition	Further reading
Admixture	Presence of alleles or haplotypes within one individual that are derived from two or more genetically differentiated populations through hybridization	Marques *et al.* (2019)
Allopatry	Lack of contact between the ranges of populations or species at a specified time-point; sometimes used to mean an absence of gene flow, $m = 0$	Mallet *et al.* (2009)
Barrier effect	The contribution that a barrier locus or trait, some combination of barrier loci or traits, or a spatial or physical barrier makes to overall isolation; ideally a quantitative measure	Butlin and Smadja (2018)
Barrier locus	A locus that contributes to a barrier to gene exchange	Butlin and Smadja (2018)
Barrier to gene flow	Sometimes equivalent to a component of reproductive isolation between populations, such as assortative mating or selection against hybrids, sometimes more specifically the impact on an individual locus	Butlin and Smadja (2018), Westram *et al.* (2022a)
Barrier trait	A trait that contributes to a barrier to gene exchange	Butlin and Smadja 2018
Bateson–Dobzhansky–Muller incompatibility	See 'Dobzhansky–Muller incompatibility'	—
Component of reproductive isolation	Part of the overall reduction in the production of viable and fertile offspring, or of effective gene flow, attributable to a more or less specific mechanism; various levels of resolution are possible—for example assortative mating might be broken down into components due to the timing of receptivity, sharing of pollinators, and fertilization success following pollination	Sobel and Chen (2014)
Coupling	A set of processes that generate coincidence of barrier effects, resulting in a stronger overall barrier to gene flow than either effect would alone	Butlin and Smadja (2018), Dopman *et al.* (2024)
Diversification rate	Increase in the number of species per unit time due to the net effect of speciation and extinction; expected to be highly heterogeneous in time, across taxa, etc.	Morlon *et al.* (2022)
Dobzhansky–Muller incompatibility	Fitness reduction in an individual carrying two or more independently derived alleles that interact negatively; sometimes restricted to epistatic interactions (i.e. excluding dominance), sometimes to interactions between pairs of loci and sometimes to intrinsic barriers	Orr and Turelli (2001)
Ecological speciation	Speciation as a result of divergent selection in contrasting environments that generates reproductive isolation; sometimes restricted to cases of divergence with gene flow	Schluter (2009), Sobel *et al.* (2010)
Effective migration	The rate of gene flow of neutral alleles, accounting for the effect of barrier loci that cause a reduction in gene flow relative to the rate expected from spatial separation and physical barriers to dispersal	Barton and Bengtsson (1986), Westram *et al.* (2022a)
Extinction rate	Number of species lost per extant species per unit time	De Vos *et al.* (2015), Morlon *et al.* (2022)
Extrinsic barrier/Extrinsic isolation	A barrier to gene flow or a component of reproductive isolation that is dependent on the environment; in reality, barriers probably fall on a continuum from extrinsic to intrinsic and the position of some barrier types is hard to define	Anderson *et al.* (2023)
Genetic or genomic architecture	The distribution of loci underpinning a focal trait in the genome or linkage map, their effect sizes, dominance and, sometimes, their interactions; can be applied to barrier effects, barrier traits, or components of reproductive isolation; may include the impact of structural variants such as inversions	Seehausen *et al.* (2014)
Genomic island of speciation	A region of the genome with distinctly greater differentiation between divergent populations or species than the background level of differentiation	Ravinet *et al.* (2017)
Hybrid	An individual with ancestry from more than one genetically differentiated population; the term is sometimes used for F1 offspring specifically and confusion can be generated by a failure to make clear the category(ies) included	Abbott *et al.* (2013)

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Table 1. Continued

Term	Definition	Further reading
Hybrid speciation	Reticulate origin of a new species with genetic contributions from more than one ancestral species; the precise meaning of the term has been vigorously debated	Schumer *et al.* (2018)
Hybrid zone	A geographical area where genetically differentiated populations meet and generate at least some offspring of mixed ancestry	Barton and Hewitt (1985), Stankowski *et al.* (2021)
Incipient species	A population or group of populations with strong but incomplete reproductive isolation from other populations of the same species	Butlin *et al.* (2008)
Intrinsic barrier/intrinsic isolation	A barrier to gene flow or a component of reproductive isolation that is independent of the environment; in reality, barriers probably fall on a continuum from extrinsic to intrinsic and the position of some barrier types is hard to define	Anderson *et al.* (2023)
Introgression	Transfer of an allele or haplotype derived from one genetically differentiated population or species into a background typical of a different population or species	Baack and Rieseberg (2007)
Island of differentiation	See 'Genomic island of speciation'	—
Isolating barrier	Equivalent to 'Reproductive barrier'	—
Lineage	A set of populations or species connected in time by ancestor–descendant relationships	Wiens (2004)
Macroevolution	Patterns of evolution above the level of species, including broad-scale patterns of speciation, extinction, distribution range, and phenotypic change; these patterns may be emergent, in the sense that they are not predictable from microevolutionary processes	Hautmann (2020)
Magic trait	A trait that is subject to divergent selection and also contributes to nonrandom mating; the precise meaning has been debated and an alternative terminology ('multiple effect trait') has been proposed	Servedio *et al.* (2011), Smadja and Butlin (2011), Dopman *et al.* (2024)
Microevolution	Evolution below the species level, consisting of changes in phenotypic and genotypic distributions due to mutation, genetic drift, gene flow, natural selection, and recombination	Kinnison and Hendry (2001)
Mutation-order speciation	Speciation resulting from the independent spread of mutations in different populations due to processes other than divergent ecological selection	Mani and Clarke (1990), Schluter (2009), Sobel *et al.* (2010)
One-allele mechanism	Formation of a barrier to gene flow, or enhancement of an existing barrier due to the spread of the same phenotype, allele, or alleles in two populations	Felsenstein (1981), Butlin *et al.* (2021)
Parapatry	Contact, but not overlap, between the ranges of populations or species at a point in time; sometimes used to mean any degree of contact/overlap short of complete sympatry and sometimes used to mean any level of gene flow that is not allopatry, $m = 0$, or complete sympatry, $m = 0.5$	Mallet *et al.* (2009)
Pleiotropy	Effect of an allelic substitution at one locus on more than one trait—in the speciation context, often a signal and a preference or a signal and a locally adaptive trait (related to the idea of a 'Magic trait'); a 'pleiotropic locus' is a locus where substitutions commonly influence more than one trait	Paaby and Rockman (2013)
Postzygotic isolation	Components of reproductive isolation operating after the formation of a hybrid zygote, including reduced survival, fertility, or mating success of the F1 hybrid and, at least in some uses, fitness reduction of later hybrid generations	Sobel and Chen (2014), Westram *et al.* (2022a) and associated commentaries
Prezygotic isolation	Components of reproductive isolation operating before the formation of a hybrid zygote, including fitness reduction of migrants, assortative mating due to habitat association, mate choice, or pollinator specificity, and post-mating components such as gamete survival and recognition; whether or not spatial separation or barriers to dispersal are included varies among authors	Sobel and Chen (2014), Westram *et al.* (2022a) and associated commentaries

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Table 1. Continued

Term	Definition	Further reading
Reinforcement	Selection favouring enhancement of prezygotic isolation in response to the fitness costs imposed by postzygotic isolation, or the response to such selection; more generally, enhancement of any barrier effect due to the costs imposed by an existing barrier effect	Servedio and Noor (2003), Butlin and Smadja (2018)
Reproductive barrier	Usually equivalent to 'component of reproductive isolation' or 'barrier to gene flow' but might exclude components such as habitat isolation	—
Reproductive isolation	Either reduction in the production of viable and fertile offspring between, relative to within, populations (organismal view) or a quantitative measure of the effect that genetic differences between populations have on gene flow (genetic view)	Westram *et al.* (2022a) and associated commentaries
Sexual selection	The component of natural selection that is due to variation in mating or fertilization success among individuals of one sex	Ritchie (2007)
Snowball	A prediction of some models of speciation that there will be a greater than linear increase with time in the number of Dobzhansky–Muller incompatibilities between diverging populations	Orr and Turelli (2001), Moyle and Nakazato (2010)
Speciation	The origin of new species; operationally, definitions vary among fields: in palaeontology, either due to phenotypic change within a lineage or the splitting of lineages; in phylogenetics and in many comparative analyses, a splitting event creating two descendant species from one ancestral species; in microevolutionary studies, the evolutionary increase of reproductive isolation between groups of populations	Coyne and Orr (2004)
Speciation continuum	The continuous range of reproductive isolation (and/or other characteristics) between populations from panmixis to complete absence of gene flow	Stankowski and Ravinet (2021a), Bolnick *et al.* (2023)
Speciation island	see 'Genomic island of speciation'	
Speciation rate	The number of branching events per extant lineage per unit time; this is distinct from the 'speciation duration', which is the time taken for a speciation process	Coyne and Orr (2004), Morlon *et al.* (2022)
Species	A unit of biological diversity; most commonly, a group of interbreeding populations that is reproductively isolated from other such groups (Biological Species Concept), but different versions of this definition are in use and multiple alternative definitions are available	Mayden (1997), Coyne and Orr (2004), Stankowski and Ravinet (2021b)
Suture zone	A geographical region in which hybrid zones are concentrated	Remington (1968), Swenson and Howard (2004)
Sympatry	Overlap between the geographical distributions of two populations or species at a specified time point; sometimes restricted to complete inclusion of one range within another; sometimes used to mean unrestricted gene flow between populations, $m = 0.5$	Mallet *et al.* (2009), Bird *et al.* (2012)

In addition to clearer conceptual and cultural connection, genuine integration also requires direct interactions. For instance, cross-disciplinary conferences focused on specific questions or problems in speciation research, and other venues for constructive discussion, as well as research collaboration between individuals who each bring distinct expertise, or involving groups of individuals organized around a specific question or shared organism, represent obvious means of empirically bridging across disciplines. Past examples of cross-disciplinary integration within speciation offer some insight into concrete ways to encourage these efforts in the future. One broadly influential strategy has been to identify specific conceptual points of contact or overlap between disciplines, and a general means to resolve them. For example, in a now classic theoretical paper, Felsentein (1981) famously advocated bringing 'genetic and ecological constraints on speciation into a common framework' to achieve a more satisfactory overview of speciation; one element of the common framework in this case was mathematical theory. Coyne and Orr's (2004) book identified many points of contact and disagreement (often between disciplines) and generated some specific hypotheses or predictions to resolve them.

A second influential strategy has involved direct empirical integration at the interface of different disciplinary traditions. Coyne and Orr's (1997, 1989) analysis of patterns of reproductive

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isolation (RI) in *Drosophila*—combining RI measurements from experimental crosses with estimates of genetic distance (from the emerging field of molecular phylogenetics)—was foundational in showing the potential for such direct empirical crosstalk. More recently, Rabosky and Matute (2013) combined similar *Drosophila* experimental crossing data with phylogenetic estimates of species diversification rates. The lack of correlation between rates of RI evolution and speciation rates identified a clear 'gap' in current empirical assessments of speciation: explicit consideration of the role and importance of lineage persistence and/or extinction (see Challenge 4).

Clearly there is still broad untapped potential for direct empirical integration via the inclusion of additional data types that are traditionally associated with different disciplines, such as phenotypic variation, genomic features, spatial information, and palaeontological data (Fig. 2; Challenge 5). It is not necessary that each data type is available in every discipline (e.g. source data will differ between analyses from palaeontology and behavioural ecology); indeed, finding creative ways of combining nonoverlapping yet complementary comparative analyses might provide an important means of integration. Moreover, although each example to date involves 'pairwise' disciplinary linkages (i.e. between two key data types drawn from different disciplines), in principle, data synthesis could extend across multiple disciplines to evaluate important axes of variation or diversification in new ways (Bolnick *et al.* 2023). A primary limiting step for data integration will be the availability of common and/or comparable data types from the same taxonomic groups, issues that are further expanded in Challenges 3 and 5.

CHALLENGE 2: THE LANGUAGE OF SPECIATION IS HIGHLY COMPLEX

Integration of speciation research presupposes that researchers use the same language. Symbols utilized for communication include linguistic representations (technical terminology, analogies, metaphors), as well as mathematical description (statistics, functions, models) and graphic rendition (e.g. a bifurcating tree). As is true for language in general, all of these serve as containers for concepts and represent a compromise among abstraction, generalization, and biological reality. Ideally, all symbols we use have a unique definition and elicit the same connotation in both sender and receiver. Yet, they often do not (Fig. 3). Over the decades, terminology in speciation research has shifted and expanded, paying tribute to the emergence of novel ideas, mathematical models, technological innovation, and model systems (Harrison 2012). The resulting complexity not only constitutes a barrier to entering the field but also to the integration of speciation within and across disciplines. In this section we highlight challenges associated with the language of speciation and at the end provide suggestions for how we may more effectively navigate them.

Some challenging aspects of the language of speciation

Elements of language with varying levels of precision

A central issue in the language of speciation is variation in precision. The representation of concepts ranges from concise mathematical definitions [e.g. 'effective migration'; Barton and Bengtsson (1986)] to rather vague metaphors (e.g. 'genomic islands of speciation'; Turner *et al.* (2005)]. Mathematical models provide transparent definitions that promote clear communication and ultimately clarify thinking even when the underlying models are simplified or idealized (Levins 1966). However, oversimplification can also limit understanding (Turelli *et al.* 2001), and translation of model assumptions and parameters to biological reality and empirically measurable entities is treacherous and may result in unrealistic conclusions. Verbal models are less precise, but can offer intuitive descriptions of complex phenomena (Taylor and Dewsbury 2018), thus helping to guide theory and empirical research. However, we should all question whether metaphors and analogies, both visual and literary, aid understanding (e.g. 'tree', 'entangled bank', 'suture zone') rather than being misleading [e.g. 'magic' traits: Smadja & and Butlin (2011), Maan and Seehausen (2011); and 'speciation islands': Ravinet *et al.* (2017), Wolf and Ellegren (2017)]. Transparency regarding the idiosyncratic imprecisions and evocative nature of metaphors and analogies is important to balance their intuitive appeal.

The discretization of continuous phenomena

Most aspects of speciation are continuous, but we tend to partition them into discrete categories to make them easier for our minds to grasp (Butlin *et al.* 2008, Stankowski and Ravinet 2021b). For example, the geographical context of speciation is often described in categorical terms (allopatric, parapatric, sympatric), when in reality it varies in space and time (Abbott *et al.* 2013) (see Challenge 4). To add to the confusion, these words are also used to describe a parameter (the effective migration rate) in specific models of speciation (Coyne and Orr 2004, Mallet *et al.* 2009). While some argue that this categorization might have been fuelling an unfruitful debate (Butlin *et al.* 2008), it has also motivated research that has guided novel ways forward (Smith 1966, Felsenstein 1981). Moreover, the rarity of strict sympatric speciation has arguably led to the widespread acceptance that at least some spatial separation is essential for speciation (Bolnick and Fitzpatrick 2007). There is a need for balance here, as discretization helps formulate clear hypotheses and simple terms aid communication and education. However, we must be aware of oversimplification and the ways it can restrict our thinking about complex processes (Harrison 2012).

The evolution of language

The meanings of some terms have changed over time which may hinder understanding and communication. For instance, Bateson (1909), Dobzhansky (1937), and Muller (1942) each illustrated models of postzygotic isolation with two interacting loci, but viewed this abstract representation as the 'simplest type, which sufficiently illustrates main principles' (Muller 1942: 87). However, because modern reviews of hybrid incompatibilities often depict the simplest case of a two-locus Bateson-Dobzhansky-Muller incompatibility, it is easy to misapprehend this simplification as a default expectation relative to interactions among more than two loci (Coyne and Orr 2004, Presgraves 2010, Thompson *et al.* 2023) [see Satokangas (2020) for a discussion of higher-order interactions]. As a consequence, modern students of speciation might enter the field with a narrow view of the model articulated nearly a century earlier. Tracing the history

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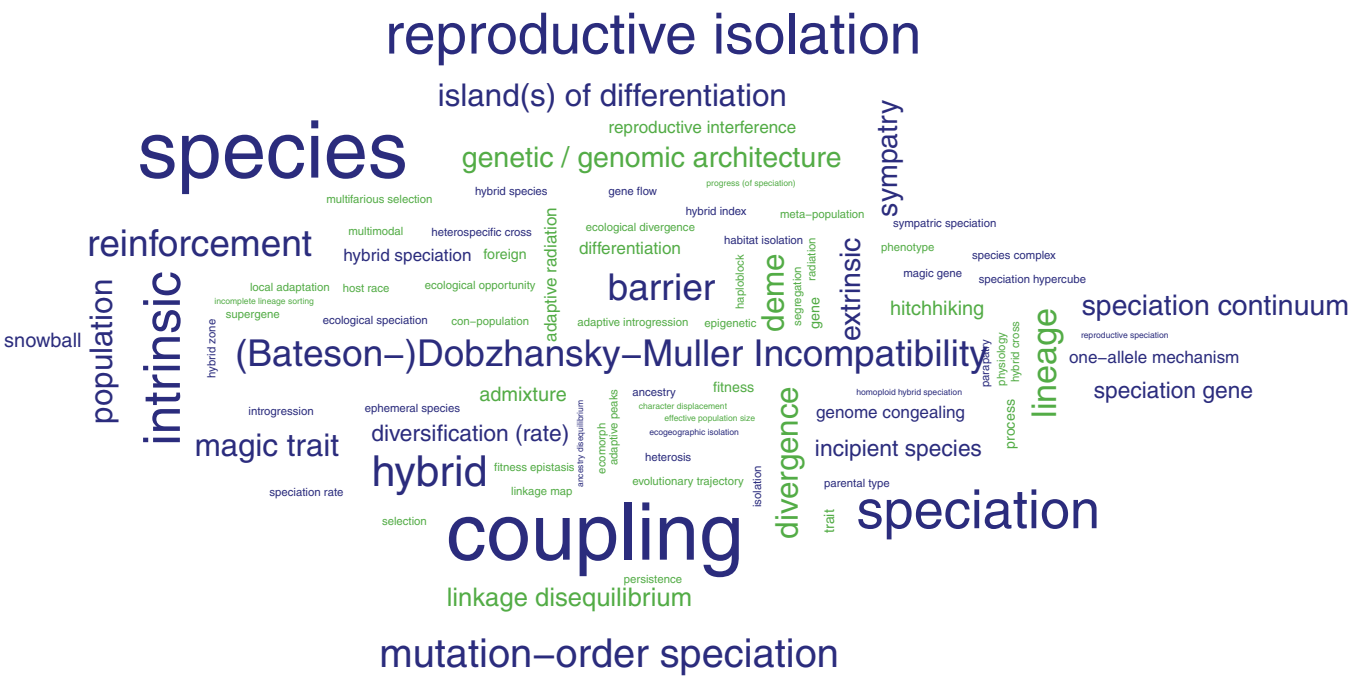

Figure 3. Word cloud of challenging or confusing terms submitted by workshop participants. Participants were asked to: 'Please list words or terms in speciation research that you think might cause trouble, are challenging or which you experience as confusing'. Terms were lightly curated to account for redundancy, spelling errors, and general applicability. Colours indicate a term as being specific to speciation (blue) or referring more generally to aspects of genetics, ecology, and evolution (green). Words in larger fonts were listed more often. For a perspective on numbers, 24% (11) of the workshop attendees listed 'coupling'.

of our terminology is necessary for determining when a change in word use is justified by novel empirical insight, and whether it facilitates or impedes the study of speciation.

The language of speciation has also expanded to include new terms. These may reflect novel discoveries or concepts, but may also be used to convey the impression of innovation in order to gain academic prestige. The latter causes an unnecessary and unproductive increase in language complexity (Harrison 2012). It is critical for authors who wish to introduce a new term to research the historical context, to ensure originality and utility, and to provide a clear and citable definition.

Social dimensions of language

The scientific discourse is a social enterprise that is dominated by strongly represented groups. The language of speciation has mainly been influenced by English-speaking scientists so may not reflect the diversity of views from the entire research community. Non-native English speakers, in particular, might grapple with terms that seem intuitive, self-evident, or evocative to native speakers. A monopoly on defining terms in conjunction with hidden semantic ambiguity for some terms can act as a barrier to entry for new researchers and ideas entering speciation research.

Language also varies according to the questions we are interested in, the taxa we study, and the approaches we use. For example, the use of the word 'pleiotropy' differs between researchers from different disciplines (Paaby and Rockman 2013). Academic genealogy is another factor introducing semantic variation within the community: students are likely to be influenced by the environment they experience early on, leading to clusters of lineage-specific language use. Finally, we should be conscious of how the language we use might be interpreted by nonscientists and we must act to guard against those wishing to use misunderstanding for malicious intent (Saini 2019).

Overcoming challenges in the language of speciation

The first step in navigating these issues is recognizing that ambiguity surrounds even basic and essential terms (Fig. 3). Researchers should engage with multiple sources, expose themselves to different definitions, and research their historical context. Clearly, this will take time for newcomers to the field. Supervisors can provide guidance here and explain conflicts around term definitions rather than merely teaching their preferred definitions and perspectives to trainees. Review and perspective papers can help by providing an overview on the existing variation and controversies (see Table 1) (Butlin and Smadja 2018, Stankowski and Ravinet 2021b, Westram *et al.* 2022a).

While it is tempting to try and arrive at single definitions, it is unlikely that we will ever reach and maintain community-wide consensus on any given term. However, the existence of multiple definitions is not a problem as long as terms are defined in a given context. Once revealed, disagreement can even lead to progress by highlighting conceptual differences between researchers who study speciation from different angles (see Challenge 1) (Moyle 2022, Rosales 2022, Westram *et al.* 2022b). One practical way forward is for authors to define key terms within publications (either in the main text or in a glossary), or by referring to existing definitions in the literature.

In the long term, a dynamic speciation encyclopaedia ('Speciation Wiki') would be a valuable resource to help researchers navigate the language of speciation. Definitions and

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respective references could be collated in one place, historical developments can be tracked, term usage be synchronized, and controversies made apparent. To incentivize quality contributions, a formal consortium may review entries and provide status updates, with membership being equitable and determined by a certain contribution, analogous to standardization attempts in other scientific disciplines (Klionsky *et al.* 2021). We envision that researchers could also contribute entries in their native language.

CHALLENGE 3: RESEARCH IS BIASED TOWARD CERTAIN ORGANISMS, ECOSYSTEMS, AND ENVIRONMENTS

Our understanding of speciation can only ever be as broad as the range of systems that we study. Although studies of speciation have now been conducted across the tree of life, we routinely focus on a biased set of organisms and environments. This bias may limit our ability to detect broad patterns, narrow the scope of our understanding and potentially lead to a distorted view of the speciation process. Below, we provide some illustrative examples of potential gaps, and some ideas and recommendations for how we can identify and fill them.

Examples of bias in speciation research

Bias toward certain taxonomic groups

Some groups of organisms are vastly over-studied relative to their abundance in nature (Fig. 1A, B; Box 2). For example, Hernández-Hernández *et al.* (2021) identified and reviewed more than 3000 studies of speciation. They found that 53% of studies focused on vertebrate taxa, even though vertebrates represent less than 1% of all described species (Titley *et al.* 2017) (Fig. 4A). In contrast, some highly diverse groups, including insects and fungi, were vastly understudied. Similar biases can also be observed on finer taxonomic scales. For example, studies of reproductive isolation in seed plants have tended to focus on certain families, while others have been largely ignored (Christie *et al.* 2022) (Fig. 4B). This matters because taxonomic bias is associated with bias in the representation of biological characteristics that may influence speciation.

Genomic studies focus on taxa that are easy to sequence

Genomic studies of speciation are heavily biased toward taxa with small genomes (<1 Gb; Fig. 4C) and low ploidy (haploid or diploid) due to the technical challenges and cost associated with sequencing of large, complex genomes (Kolmogorov *et al.* 2018). The focus on taxa that are easy to sequence could bias our understanding in several ways. For example, parasitic elements such as transposons or gene copy variants may play a larger role in speciation in organisms with large genomes (Serrato-Capuchina and Matute 2018). If genome size influences speciation, then the study of small genomes may bias our understanding of how speciation occurs.

Studies of RI are biased toward organisms with short generation times

Most detailed studies of reproductive barriers are inevitably restricted to organisms with short generation times. For example, annual plants live and reproduce in a single year, making traits such as lifetime reproductive success easier to measure than in long-lived perennials, such as trees (Fig. 4D). Variation in developmental time across our study species may also bias the traits that we measure. In long-lived species we may unconsciously de-emphasize the importance of later-stage postzygotic barriers simply due to the fact that they are time consuming and difficult to measure (Coyne and Orr 2004). Developmental times of the species we study could therefore affect the conclusions we draw about the evolution of isolating barriers.

Bias toward standard male–female sexual systems

Studies of speciation tend to focus on organisms with typical dioecious female–male sexual systems (Coyne and Orr 2004, Hernández-Hernández *et al.* 2021), missing asexuals (Birky and Barraclough 2009), facultative sexuals (Hartfield 2016), hermaphrodites (except in plants), isogametic systems (in protists), mating type systems (as in fungi) (Giraud *et al.* 2008), alternative life cycles [e.g. bryophytes (Goffinet 2008)], and haplodiploids (Lohse and Ross 2015), among others. This matters because we can reasonably expect the reproductive system to influence the evolution of reproductive isolation, or cluster formation, which is how species tend to be defined in asexual taxa (Birky and Barraclough 2009, Barraclough 2019).

Bias toward organisms that are highly conspicuous

Many study organisms are chosen because of their highly conspicuous traits such as coloration, reflecting our own sensory bias. A focus on conspicuous organisms could distort our understanding of speciation in several ways. First, conspicuous traits are often sexual signals associated with mate choice (Price 1998, Boughman 2002), which may lead to an overestimation of the relative importance of premating barriers and sexual selection in speciation. Second, striking differences in colour are often associated with a simple genetic basis (Toews *et al.* 2016, Campagna *et al.* 2017, Jones *et al.* 2018, Tavares *et al.* 2018, Knief *et al.* 2019), which may lead us to overestimate the contribution of large-effect loci to the evolution of reproductive isolation (Rockman 2012).

Bias toward ecosystems with low biotic complexity

Many studies are carried out in ecosystems with relatively few interacting species. While this low biotic complexity allows us to isolate key variables that contribute to diversification and the evolution of isolating barriers, studies of speciation in ecosystems with high biotic complexity (e.g. tropical forests or coral reefs) are under-represented relative to the number of species they contain (Fig. 4D). In species-rich ecosystems, however, the diversity of interactions among species, from predation and parasitism to competition and symbioses, may act singularly or in concert to influence speciation (Schemske 2009). Thus, by avoiding complex environments, we may be underestimating the role that biotic interactions play in speciation.

Bias against marine environments and their organisms

Relatively few studies of speciation focus on marine organisms, yet the world's seas and oceans contain a broad representation of taxa, with 16 endemic phyla compared with only one that is unique to the terrestrial realm (Faria *et al.* 2021). In addition to harbouring unique taxa, marine environments

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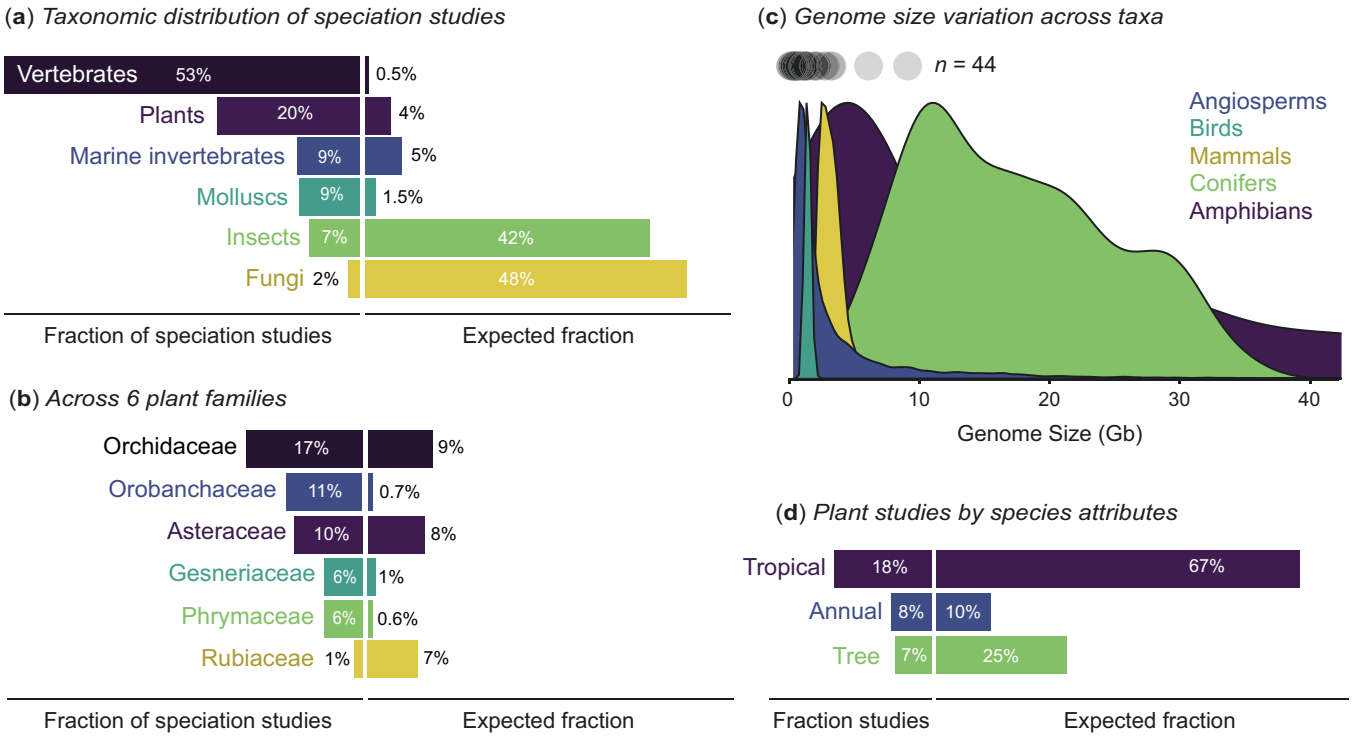

Figure 4. Examples of bias in speciation research. A, the proportion of speciation studies conducted across six broad taxonomic groups, based on the 3099 studies surveyed in Hernández-Hernández *et al.* (2021). The expected fractions are based on the predicted number of species within each group [vertebrates, Wiens (2015); plants, Corlett (2016); fungi, Baldrian *et al.* (2022); molluscs, Bouchet *et al.* (2016); marine invertebrates, Appeltans *et al.* (2012); insects, Stork (2018); and fungi, Baldrian *et al.* (2022)]. B, the fraction of the 89 speciation studies of seed plants reviewed in Christie *et al.* (2022) for six selected families. The expected fraction of studies for each family was determined from the number of described species in each family according to Christenhusz and Byng (2016). In total, 52% of plant species are in families with no speciation studies. C, genome size variation for five example plant and animal groups [data downloaded from the GoaT database (Challis *et al.* 2023)]. Circles at the top of the plot show the distribution of genome size for organisms studied by workshop attendees. D, the fraction of plant speciation studies [also from Christie *et al.* (2022)] focusing on species in tropical ecosystems (versus not tropical), that have an annual life history (versus not annual), and that are trees (versus not trees). The expected fractions were determined from the species richness of species with the same attribute [tropical plants, Pimm and Joppa (2015); annuals, Friedman (2020); and trees, Steege (2016)].

differ from terrestrial ones in a number of striking ways that might impact speciation, including a lack of obvious geographical barriers to dispersal (Palumbi 1994, Faria, Johannesson and Stankowski 2021), and strong abiotic gradients interacting across three-dimensional space (e.g. salinity, light, and currents). Diversification rates in marine fishes show a strong inverse relationship with latitude (Rabosky *et al.* 2018) (i.e. higher rates of diversification away from the tropics)—a pattern not commonly observed in many terrestrial groups (but see Sánchez-Ramírez et al. 2015)). Thus, while working in marine environments can be challenging for a number of practical reasons, more studies are clearly needed.

How do we identify and fill gaps?

The first step in filling gaps is to identify taxa, ecosystems, and environments that have been systematically understudied. Above, we provided a few illustrative examples of areas that we think represent gaps, but our list is by no means exhaustive, and some gaps are supported more by intuition than quantitative assessment. Large-scale literature surveys, (e.g. Hernández-Hernández *et al.* 2021, Titley *et al.* 2017) or, better still, a community-driven database for speciation research (see Challenge 5) would provide a more comprehensive overview of taxa and environments that are understudied, highlighting areas where more work is needed.

Once identified, how should we prioritize gaps to maximize return on our effort? Rather than choosing taxa to study at random, it may be more fruitful to focus on specific clades (e.g. genera or families). A clade-based approach would allow for detailed studies of individual species pairs, followed by broader comparative analyses that seek out general patterns (see Challeng 5). A focus on specific clades has proven fruitful for many groups, including birds (Singhal *et al.* 2021), fishes (Meier *et al.* 2017, Malinsky *et al.* 2018), insects (Coyne and Orr 2004, Fontaine *et al.* 2015, Edelman *et al.* 2019, Suvorov *et al.* 2022), mammals (Vanderpool *et al.* 2020), and plants (Pease *et al.* 2016). Similar taxonomic sampling may be attainable for new clades, enabling nuanced system-specific biological expertise to tease apart biological factors contributing to speciation. Some clades could be chosen from understudied sections of the tree of life, and others to cover the range of factors that we hypothesize might influence speciation mechanisms or rates.

Collaborations between researchers from disparate research disciplines may also help to identify and fill key gaps (see Challenge 1). Taxonomists, systematists, museum and herbarium scientists, land managers, and governmental organizations

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may be in good positions to advise on the biological characteristics that are underepresented or understudied within a specific taxonomic group or across multiple taxa (Mayr and Others 1963). Collaborations with ecologists, environmental chemists, geoscientists, and oceanographers may help to identify understudied environments and ecosystems and understand their relevance to speciation (Faria, Johannesson and Stankowski 2021).

An important way to fill gaps is by improving collaborative links among the global diversity of researchers who study speciation. For example, the reciprocal exchange of ideas, methodological approaches, and knowledge would not only increase the diversity of organisms and environments that have been thoroughly studied, but would also help foster diversity and equity in our research community. Here, it is important to note that by collaboration, we do not mean the one-way flow of resources or information from one area to another (e.g. by providing samples in exchange for authorship). Genuine collaboration among diverse researchers will require all researchers to be involved in the project conceptualization and execution across all stages.

CHALLENGE 4: BRIDGING RESEARCH CONDUCTED AT DIFFERENT SPATIAL AND TEMPORAL SCALES

Speciation processes operate over a wide range of temporal and spatial scales (Fig. 5). However, individual researchers often focus on specific scales: from one or two generations for lab crosses (Sobel and Chen 2014), tens of generations for experimental evolution (White *et al.* 2020), to tens of millions of years for speciation rate variation (Jetz *et al.* 2012). Spatial studies may focus on narrow hybrid zones (Harrison and Larson 2016) all the way up to global patterns of diversification. Where comparisons have been made across vastly different scales, important gaps in understanding have been revealed (Rabosky and Matute 2013). The recent growth of interest in demographic reconstructions from genomic data (Noskova *et al.* 2020, Fraïsse *et al.* 2021) emphasizes that processes over long timescales influence current patterns of genetic variation and differentiation, yet the spatial dimension of these processes is rarely considered. Similarly, the 'speciation continuum' framework (Stankowski and Ravinet 2021b) helps to guide thinking about speciation as a continuous process but lacks spatial and temporal dimensions (Bolnick *et al.* 2023). In reality, spatial and temporal scales are intimately connected so research that better spans broad scales may lead to new insight (Rolland *et al.* 2023). Below, we outline just some of the conceptual and methodological hurdles that we face when trying to bridge research conducted at different scales. However, this challenge overlaps broadly with the others discussed in this paper. For example, researchers working at different scales use different methods, data (see Challenge 1) and terminology (see Challenge 2). Thus, social integration will also be needed to achieve integration in this area.

Understanding and utilizing the spatial distributions of species

Speciation involves the reshaping, breaking, and overlap of geographical ranges over time (Mayr 1963, Endler 1977, Avise 2000) (Fig. 5A). Historical spatial dynamics can therefore help us to understand the ecological, demographic, and geological processes that have shaped range boundaries and broad-scale distributions of species up to the present (Barraclough and Vogler 2000, Weir and Schluter 2007, Hoorn *et al.* 2010, Aguilée *et al.* 2013, Salces-Castellano *et al.* 2020). The geography of a species may also influence its continued evolution and persistence in the future. For example, a species with an expanding range might be more likely to persist through time, and the spatial arrangement of diverging populations influences the potential for gene flow among them (Avise 2000) (Fig. 5A).

Considerable empirical effort has focused on understanding species distributions. In particular, phylogeographical approaches have helped reveal how history, geography and environment interact to generate new species and shape their ranges (Schneider *et al.* 1998, Hewitt 2000, Carnaval *et al.* 2009, Smith *et al.* 2014). Yet, phylogeographic studies have declined following the rise of demographic inference methods that usually ignore spatial context (Marchi *et al.* 2021). However, with large spatial genomic datasets and corresponding environmental data there is tremendous scope to develop and apply powerful spatially explicit analyses. First, we can measure how genetic divergence, ecological divergence, and reproductive isolation accrue over space by applying methods that can distinguish continuous population structure (i.e. isolation-by-distance) from abrupt changes that correspond with hybrid zones, geographical barriers, and sharp environmental gradients or ecotones (Bradburd *et al.* 2018, Bradburd and Ralph 2019). Further, we can test the correlation between these levels of population structure and the heterogeneity in the strength of reproductive barriers across a species range (Barnard-Kubow and Galloway 2017). Thus, spatially explicit analyses are a powerful tool to understand how speciation proceeds over space and time.

More work is also needed to reveal the spatial history of barrier loci (see Fig. 5A). By inferring how, and where, these loci originate and become coupled to form a strong barrier to gene flow, we can begin to understand the complex interplay between *de novo* mutation, ancestral polymorphism, and introgression in shaping species divergence (Richards *et al.* 2021, Campagna *et al.* 2022). Further, we can apply spatial genomic approaches to co-occurring species to determine how taxa with different characteristics are impacted by the same historical events and ecological transitions (Singhal and Moritz 2013, McLaughlin *et al.* 2020, Musher *et al.* 2022). Such work can help us determine how environmental gradients and biogeographical barriers interact with species biology to drive lineage divergence. It is worth noting that these studies, rooted in natural history and biogeography, are particularly accessible to a diverse range of speciation researchers due to their cost-effectiveness and relevance to regions worldwide, thereby fostering global research collaboration (see Challenge 3).

Finally, most current comparative methods represent species as a single tip within a phylogenetic tree (as in Fig. 5B, C). This fails to account for patterns of population structure or range-wide phenotypic variation within a species. These methods could benefit from spatial sampling. For example, the reconstruction of ancestral ranges at deep timescales (Ree and Sanmartín 2009, Goldberg *et al.* 2011) could be improved to include individual-level processes more explicitly, such as dispersal and mating, and population-level information, such as current and past population sizes and patterns of gene flow (Landis *et al.*

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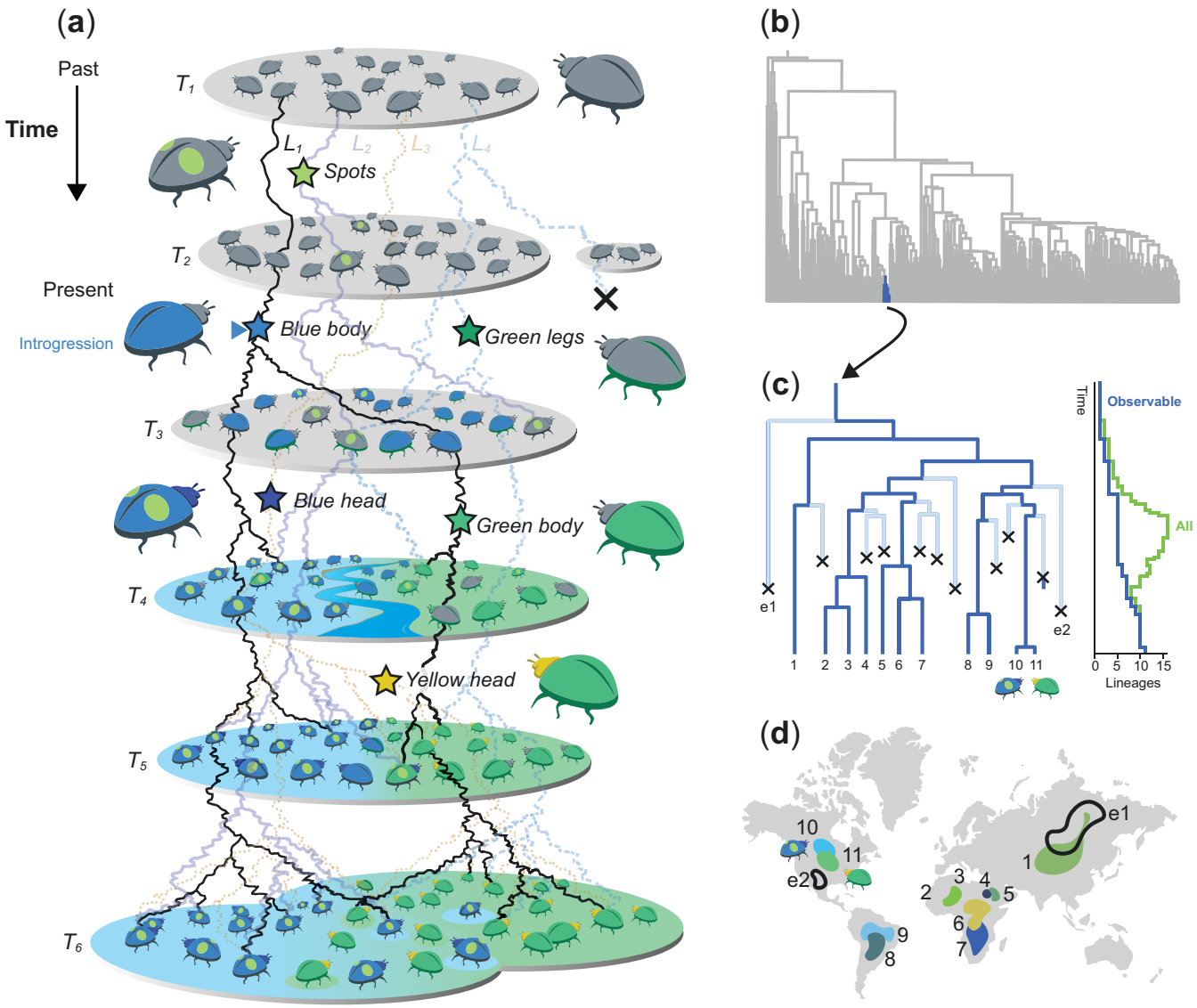

Figure 5. Speciation in space and time. We attempt to depict the spatial and temporal complexity of speciation at two vastly different scales researchers tend to work at, including many factors and processes discussed in the main text. A, the spatial range of emerging species through time (individuals are haploid for simplicity). Lines show partial genealogies for four loci (L_1 to L_4; L_1 is emphasized to make it easier to see); stars indicate when new mutations enter the population. At time 1 (T_1) individuals of a single type of beetle are distributed across the entire range. After T_1, a neutral mutation arises at L_2, giving some individuals spots. By T_2, a new geographically isolated population has arisen, but soon goes extinct. After T_2, a neutral mutation arises at L_4, giving green legs. A globally beneficial allele also enters the population by introgression at L_1 (blue arrow), giving individuals a blue body; this allele rises in frequency and is close to fixation by T_3. Before T_4, two more neutral mutations arise: one at L_3 giving a blue head, and the other at L_1 giving a green body. By T_4, the environment has changed dramatically, represented by a sharp gradient from green to blue, and a river divides the species range. Alleles standing in the ancestral population are now subject to divergent selection, with distinct combinations of traits being favoured in the divergent environments (green body and green legs in the green habitat; blue head, blue body, and spots in the blue habitat). A new neutral allele also arises in the green population, giving a yellow head. At T_5, the populations come into secondary contact, and mate, giving rise to unfit hybrids. The yellow-head allele causes assortative mating between green-bodied individuals, so spreads through the population, reinforcing the barrier to gene flow. By T_6, alleles at all barrier loci are perfectly coupled, and RI is complete, enabling the species to coexist as their niches begin to overlap. B, a large phylogeny depicting the many speciation events that have given rise to thousands of extant taxa. C, a zoom in of one clade, revealing many speciation events that are invisible due to extinction events (in this case a mass extinction). Over microevolutionary scales, there is a tangle of discordant genealogies (as in A), which are only approximated by bifurcating trees over much larger scales (as shown in B and C). The plot on the right side shows how the number of species changes over time compared with those that can be inferred from a phylogeny of extant species. D, geographical distributions of extant species, as well as two extinct species (e1 and e2) whose past ranges can be inferred from the fossil record.

2022). Comparative methods could also be used to evaluate the contribution of processes such as hybridization and secondary contact to speciation rates in a spatially explicit way. The distributions of living and fossil specimens should ideally be used together to inform large-scale distribution patterns and how they have changed through time (Rolland *et al.* 2018). Contemporary and ancient DNA samples can also be used to measure how genetic variation, differentiation, and introgression have changed

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over time (Orlando *et al.* 2002, Harvey *et al.* 2019, Musher *et al.* 2022, Singhal *et al.* 2022).

Linking current processes with patterns of diversity that emerge over deep time

As populations begin to accumulate genetic differences, reproductive isolation may evolve. The strength of isolation will depend on various factors including the evolutionary history in each environment, demographic factors, and the number and effect size of barrier loci (Yamaguchi and Otto 2020, De Sanctis *et al.* 2023). However, even if reproductive barriers remain stable with gene flow and environmental change, the diverged populations may not be able to stably coexist within the same ecosystem if their niches are not sufficiently distinct or if they interbreed too much (Price *et al.* 2014, Weber and Strauss 2016, Germain *et al.* 2021, Irwin and Schluter 2022).

Connecting across timescales requires integration of different data types and approaches. Combining genomic, phenotypic, and fitness data may allow us to make inferences about the origins of isolation in the present (Butlin *et al.* 2014, Anderson *et al.* 2023), and also about the temporal stability of these reproductive barriers in the face of gene flow (Kulmuni *et al.* 2020, Xiong and Mallet 2022). In particular, it is possible to test whether extrinsic (i.e. environment-dependent isolation) is less stable than intrinsic isolation over time, as climates and environments change and allow previously extrinsically isolated lineages to form fertile hybrids and merge back together (Anderson *et al.* 2023).

Answering the question 'when and how do species coexist?' highlights the challenge in connecting speciation patterns and processes across timescales (Rabosky and Matute 2013, Dynesius and Jansson 2014, Freeman *et al.* 2022). This is, in part, because the vast majority of present-day populations will not persist and, therefore, not contribute to long-term species diversity patterns (Rosenblum *et al.* 2012) (Fig. 5C). Conversely, many past divergence events are not detectable in phylogenies as the splitting lineages either merge back together (Taylor *et al.* 2005, Seehausen *et al.* 2008) or go extinct (Harvey *et al.* 2019). Hence, population persistence is particularly hard to measure because it requires that we detect speciation events as soon as they occur (Nee 2006, Louca and Pennell 2020). This might explain the lack of correlation between speciation rates and the level of population isolation observed within species (Singhal *et al.* 2022).

Although disentangling extinction and diversification rates is difficult, it may be possible using data from other sources. Taxa with excellent fossil records [e.g. bivalves: Geary (1987), Steuber (2003)] may provide opportunities for estimating extinction rates, making it possible to distinguish the contribution of speciation to the overall net diversification rate. However, other factors besides persistence, extinction, and lineage merging may contribute to the discrepancy between speciation studied at macroevolutionary and microevolutionary scales (Rabosky 2016). For example we may be incorrectly estimating the number of speciation events closer to the present, as the degree of reproductive isolation is not generally taken into account in defining the tips of our phylogenies (Rosenblum *et al.* 2012). An additional challenge is the disconnection between speciation research and taxonomy (Sauquet and Magallón 2018), because, with macroevolutionary methods, taxonomic species are taken as individually evolving lineages (see Challenge 1). Above all these challenges, deep-time patterns of biodiversity also reflect the impact of one-off geological and climatic events on speciation and extinction (Fig. 5B). Ultimately, short-term population processes may not be directly related to any force acting at geological timescales (Benton 1995, Ksepka *et al.* 2017, Lowery and Fraass 2019, Fenton *et al.* 2023).

CHALLENGE 5: INCONSISTENT MEASURES AND REPORTING STANDARDS

Speciation research has progressed mainly through detailed studies of specific pairs of taxa or radiations, but broad-scale comparative studies and meta-analyses are needed to formally synthesize the results of individual studies toward more general understanding (Coyne and Orr 1989, Rabosky and Matute 2013, Roux *et al.* 2016). However, inconsistent measurement and reporting standards across studies makes comparative meta-analysis of results especially challenging (Rometsch *et al.* 2020, Stankowski and Ravinet 2021b). Considering taxon pairs as the basic unit of comparison, we focus on two broad types of pairwise measures where specific efforts are needed to standardize measurements and improve reporting standards: (i) organismal RI and (ii) barriers to gene flow from genomic data. We focus mainly on these measures because they are of particular interest to speciation researchers, so it is our responsibility to outline best-practices. However, we also consider other variables that are essential for understanding speciation. We conclude by discussing the need for a database to facilitate data sharing and comparative analyses.

Pairwise measures of RI and genetic distance

Organismal measures of RI

Organismal estimates of RI [i.e. the reduction in production and fitness of hybrids inferred from crosses or behavioural observations; Sobel and Chen (2014)] have been fundamental to speciation research, forming the basis of numerous comparative analyses of speciation over the past 30 years (Matute and Cooper 2021). A major challenge for comparative studies is the wide range of barriers that can contribute to RI (e.g. Baack *et al.* 2015). For example, if RI is compared between prezygotic and postzygotic levels, the patterns between studies will depend on which barriers have been assessed. Unfortunately, it is rarely possible to measure all relevant isolating barriers, with most studies focusing on one or a few barriers that are most relevant to their study system or specific research questions. Thus, we do not advocate measuring a particular barrier or set of barriers above others, but encourage the reporting of all barrier(s) that can been measured.

Another problem is the wide variety of metrics used to measure organismal RI. We recommend the framework proposed by Sobel and Chen (2014), which allows the strength of individual barriers to be measured in a comparable way, and combined together to give an estimate of total RI. For example, the equation RI_4 (Sobel and Chen 2014) can be applied to any specific prezygotic or postzygotic barrier, and can capture asymmetries in the strength of RI depending on the direction

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of the cross (Turelli and Moyle 2007, Schilthuizen *et al.* 2011, Lackey and Boughman 2017). Comparative studies focusing on more specific taxonomic groups (e.g. flowering plants) can use these detailed measures to study the evolution of specific barriers (e.g. pollinator isolation), whereas coarser measures of organismal RI (i.e. total prezygotic RI) can be used for evaluating general patterns across broad groups of organisms (Christie *et al.* 2022). Because RI is often context dependent (Matsubayashi *et al.* 2013), measures should be made in the natural environment wherever possible (Westram *et al.* 2022a).

Measuring barriers from genetic data

In addition to organismal measures, which are made over one or a few generations, demographic modelling approaches can be used to quantify the long-term effects of barriers from genomic data while accounting for other confounding processes. For example, it is possible to obtain estimates of the proportion of the genome impacted by barriers, as well as the magnitude of the reduction in gene flow for that set of loci (Gutenkunst *et al.* 2010, Excoffier *et al.* 2021, Fraïsse *et al.* 2021). The newest methods also aim to locate barriers in the genome (Laetsch *et al.* 2022, Baird *et al.* 2023, Burban *et al.* 2023), so can be used to validate candidate barrier loci identified through other means (e.g. through analysis of quantitative trait loci) and identify new ones (e.g. in *Heliconius*; Laetsch *et al.* 2022). These methods are also applicable to any sexually reproducing organism where genomic data can be collected, meaning that the results are amenable to comparative analysis (Roux *et al.* 2016, De Jode *et al.* 2023).

However, all model-based approaches are limited by the simplifying assumptions of the historical scenarios modelled. Given that a large number of models can be used to describe different divergence histories, the fitting of a standard set of models would ensure reproducibility and facilitate comparison across studies. For instance, the *Demes* initiative (Gower *et al.* 2022) intends to fill this gap by providing a file format specification to serve as input for widely used simulation, inference, and visualization tools (see Adrion *et al.* 2020). Similar efforts at standardization would be helpful for estimates of barrier presence (and strength) along the genome, and inferences from hybrid zone samples.

Measuring and reporting genetic distance

Genetic data provide a crucial time axis for comparative speciation studies (Coyne and Orr 1989, Roux *et al.* 2016) and an entry point for modelling the demographic history of speciation. While genetic differentiation (F_{ST}), divergence (d_{xy}), and diversity (π) estimators have straightforward mathematical definitions (see Challenge 2), the complexity of real genomes and variety of sequencing and filtering strategies used has made it difficult to measure them consistently across studies and taxa. Additional confusion comes from the many ways of estimating and interpreting these metrics [e.g. F_{ST}; Bhatia *et al.* (2013)]. We argue that standardized measures of pairwise genetic diversity [π, eq. 22 in Nei and Li (1979)] and divergence [d_{xy} and d_a, eq. 25 in Nei and Li (1979)] should be reported. Given an estimate of the generation time and the *de novo* mutation rate, these measures of genetic distance can be translated into estimates of divergence in units of genetic drift and time in years, the two other timescales that matter for systematic comparisons across speciation events.

A second challenge is to report more complete summaries of genetic variation in addition to the low-dimensional summary statistics mentioned above. Many population genetic measures of interest, including those listed above, can be computed from the joint site-frequency spectrum (JSFS) (Achaz 2009, Ralph *et al.* 2020). Thus, genetic and genomic studies should ideally report the JSFS of putatively neutral partitions (e.g. 4D sites, introns, intergenic sites) to provide a standardized temporal axis in comparative studies.

Other essential variables

A broad range of additional variables are essential for understanding speciation, and should be estimated wherever possible (see Challenge 3). Generation time, dispersal rate, and effective population size determine the spatial and temporal scales over which evolutionary processes occur. Therefore, consistent recording of these three variables is critical, even if precision is difficult to achieve. Ideally, mutation rate would be included in this list of critical variables, but direct estimates are still limited (Bergeron *et al.* 2023). Substitution rate estimates are more widely reported and valuable for dating historical events, but they rely on an assumption of neutrality that is unlikely to be valid (e.g. Chamary *et al.* (2006)).

Information from other sources can also be utilized in comparative analyses (Stankowski and Ravinet 2021b, Bolnick *et al.* 2023). For example, Funk *et al.* (2006) evaluated whether incorporating ecological differentiation would better inform RI than genetic differentiation alone. Phenotypic information (e.g. morphology, behaviour, physiology, development) can provide insights into traits that may contribute to barriers between populations. The geography of the focal taxa and information on the degree of range overlap are also important data to report for a nuanced interpretation. Current and past occurrence information is available through online portals, and other databases systematize information on phenotypic traits (Fraser 2020), sex-determination system (Tree of Sex Consortium 2014), genomic properties (Challis *et al.* 2023), and environmental data (Fick and Hijmans 2017) to name just a few. Many of these resources also report within-species variability, and information at the population level is becoming more common (Barnard-Kubow and Galloway 2017) (see Challenge 4).

A community-driven database for speciation research

While many journals mandate the deposition of data in public repositories, formats vary widely, and the stability and accessibility of supplementary information are not guaranteed. A dedicated speciation database that gathers summary information in a consistent way would alleviate many of these issues (Stankowski and Ravinet 2021b, Bolnick *et al.* 2023). The pairwise measures and essential variables outlined above could act as the foundation of a database for sexual eukaryotic systems. Additional variables and data types may already be available from other external repositories, and could be linked using NCBI taxon identifiers (Schoch *et al.* 2020).

By bringing together results of studies of speciation that span a wide breadth of taxa, approaches, and scales, a database would

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be invaluable for the community. An ideal database would remain flexible and expandable so that new variables could be added, making the addition and curation of new data straightforward and the database easy to use. The entering of data would need to be a community effort to ensure a sufficient coverage of taxa, and would probably require incentives to encourage researchers to participate (Fraser 2020, Kattge *et al.* 2020). In the long run, promoting data gathering and/or entry for under-represented groups and data types will aid in filling sampling gaps, such as those described in Challenge 4. This resource would help define a research agenda, and allow us to test whether patterns in speciation and their drivers are consistent with predictions from theory.

PRACTICAL ACTIONS AND CONCLUDING REMARKS

In this paper, we have identified and discussed five challenges to the integration of speciation research (Fig. 1). Our list of challenges is not exhaustive, but aims to cover a diverse set of scientific and social challenges that could be prioritized. However, there is clearly overlap among the challenges, both in terms of the problems they create and the ways we might overcome them (Fig. 1). The following list provides some practical actions that can be taken by individuals or groups, which should improve scientific integration and lead to a more integrated research community.

1. Organize events, including conferences and workshops, that bring together genuinely diverse sets of participants across all dimensions (challenges 1, 3, and 4). This can be achieved by using selection rubrics that prioritize diversity, providing funding to applicants from under-resourced institutions, and being aware of requirements and timelines for visa applications.
2. Seek out collaborations that connect your own special expertise with different yet complementary expertise in other areas of research (challenges 1, 3, and 4).
3. Provide training opportunities that attract scientists into the field (e.g. *EvoBioCrashCourse*; https://evobiocrashcourse.github.io/index.html) or foster the involvement of scientists who can bring new approaches or perspectives (challenges 1, 3, 4, and 5).
4. Teach students about the existence of different perspectives, definitions, and conceptual debates, rather than presenting a single point of view (challenges 1, 2, and 4).
5. Make publishing more equitable for diverse scientists. Journals can provide more support to authors for whom English is an additional language (e.g. the journal *Evolution*'s English Language Support programme), and can encourage editors and reviewers to focus on the strength of data and conclusions, rather than the technologies used (Challenges 1–3).
6. Clarify the way key terms in speciation research are used in individual research papers (challenges 1, 2, 4, and 5). This can be done by providing a glossary of key terms, or by defining them directly in the text.
7. Create and contribute to a dynamic online wiki where the terminology of speciation can be clarified and discussed (challenges 1, 2, 4, and 5).
8. Individually examine our own research programmes and expand them to cover a broader range of questions (challenges 1–5).
9. Consider expanding or shifting our focus to include understudied taxa or environments (challenges 3 and 5).
10. Improve reporting standards for organismal measures of reproductive isolation, genetic measures of barriers to gene flow, genetic measures of divergence, and key metadata (challenges 1, 2, and 5).
11. Create and populate a speciation database and use it to conduct comparative and meta-analyses that test general predictions about speciation mechanisms, speciation rates, and their connections (challenges 1–5).
12. Identify and question our own biases, as these can affect our judgement, decision-making, and behaviour in a way that restricts the social and scientific diversity and integration within speciation research (challenges 1–5).

It is also important to reinforce that by advocating for greater integration we are not suggesting that all speciation researchers should be doing the same thing. It is positive and creative for a diversity of researchers to study organisms and environments that they understand, using approaches that they find satisfying or have access to, while addressing specific questions that attract their interest. Rather, our main point is that all of our empirical findings should be brought together in a way that makes our efforts more than the sum of their individual parts. Similarly, points of conceptual debate or friction among researchers with different training, backgrounds, or perspectives can sharpen the edges of our thinking, clarify our assumptions, or highlight important gaps or blind spots in our general understanding of the processes and patterns surrounding speciation.

Finally, we want to emphasize that integration is a team effort, and all speciation researchers have a role to play. No one study will give us all the answers, and every study, if done well, makes an important contribution to our general understanding. However, if our workshop taught us one thing, it is that the integration of speciation research will not be easy. True integration requires that we step outside our own scientific and societal comfort zones, confront our own biases, and seek to understand the views of those with very different specific goals, expertise, perspectives, and experiences. Considerable mental and emotional effort, self-reflection, and genuine desire will be needed to bridge these gaps. However, we believe that concerted effort will put us in a much stronger position to address core questions in our field, and will help to change the face of speciation research in the future.

SUPPORTING INFORMATION

Supplementary data are available at *Evolutionary Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

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