Hybridization in Animal Evolution

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Abstract - In the past two decades, it has become clear that hybridization is so common in animal species as to be an almost universal feature of their evolutionary histories. Remnants of both ancient and contemporary hybridization events are present in the genomes of modern species, but their consequences are still not completely understood. In this review, we synthesize what is known about the evolutionary and genetic drivers of ancestry variation across the genome, highlighting mechanisms that play an important role in many species groups including the impacts of the local recombination rate and the role of selection in the earliest generations following hybridization. We discuss advances in our understanding of the long-term evolutionary consequences of hybridization, including the role of introgression in adaptation, and the factors that shape these consequences. We conclude with a discussion of the impacts of hybridization on conservation efforts and outline outstanding challenges in the field.

Significance statement - We now know that hybridization between animal species is widespread and even possibly increasing in rapidly changing environments. These past and contemporary hybridization events have contributed substantially to the genomes of extant species, but not all genomic regions are equally tolerant to the introduction of foreign alleles. The transfer of genetic material between species through hybridization has profound evolutionary consequences, ranging from introducing genetic variants that facilitate adaptation to uncovering deleterious genetic interactions that are harmful in hybrids. We anticipate that advances in the field will help us understand fundamental questions about the interactions

between hybridization and genome evolution and the repeatability of these evolutionary processes across hybridizing species.

Keywords - hybridization, introgression, animal evolution, speciation, reproductive isolation, hybrid incompatibilities

1. Introduction

1.1 Hybridization is a key genetic and evolutionary process that shapes the structure and function of animal genomes

Once thought to be rare, we have come to recognize that evidence of hybridization in animal genomes is so common as to be nearly ubiquitous (Taylor & Larson 2019), with few studies that have tested for evidence of hybridization at a genome-wide scale in animal groups failing to detect it (but see (Forsdick et al. 2021; Satler et al. 2022)). In this article, we trace the evidence that led to this transformation, from the views of the 1930s that "[hybridization is] the grossest blunder in sexual preference, which we can conceive of an animal making" (Fisher 1930) to the recognition today that hybridization is pervasive in animal evolution (Edelman & Mallet 2021). We place this metamorphosis in the context of recent advances in detecting and characterizing hybridization in the genome, what we have learned about how hybridization shapes genome evolution, and the long-term consequences of hybridization. We end this piece with a discussion of future directions in the field that will lead us towards a fuller understanding of the consequences of hybridization in animal species.

1.2 Overview of the field and perspective

Hybridization has been studied in myriad contexts, and we outline some of the most influential approaches and perspectives that shape our discussion here. Many authors have considered the thorny and unresolved problem of when to treat evolutionarily distinct lineages as species versus divergent populations (de Queiroz 2005; Mallet 1995; Stankowski & Ravinet 2021), and this ongoing debate is deeply intertwined with our evolving understanding of hybridization. For the purposes of this review, we treat hybridization as interbreeding between genetically or phenotypically distinct lineages that generates admixed offspring which experience different selective pressures than their parental lineages. In particular, hybrids often have reduced fitness relative to parent lineages, which can indicate that the parent species have diverged genetically, behaviorally, or ecologically. As a result, substantial effort in the field has been devoted to investigating hybrid fitness. Hybrid dysfunction often manifests as reduced viability or fertility, and theory predicts this can result from genetic variants derived from the two parental species that interact poorly in hybrids (*i.e.,* **Dobzhansky-Muller Incompatibilities**). Beyond genetic interactions, reduced performance of hybrids in parental ecological environments is common (Arnegard et al. 2014; Johnsson et al. 2026; Thompson et al. 2024). Hybrids sometimes display “bounded superiority,” displaying similar or even higher fitness than the parent species within areas of range overlap but performing poorly within the typical parental species ranges (e.g. western and glaucous-winged gulls; (Geng et al. 2024). Issues with successful hybrid reproduction due to ineffective mating behaviors (Bridle et al. 2006) or parental care (Behrens et al. 2025) are also common. This pattern of reduced hybrid fitness can drive strong reproductive barriers between parental species and shape the outcomes of species interactions in nature (Anderson & Matute 2025; Irwin & Schluter 2022; Peñalba et al. 2024).

Much research on ongoing hybridization, especially historically, has focused on hybrid zones, or distinct geographic areas where species overlap and hybridization can occur (see section 2; Figure 1A). In recent years, there has been developing interest in **hybrid swarms**, or large populations of hybrid individuals that locally outnumber or have replaced parental lineages. These populations are powerful because they give researchers access to large hybrid populations, potentially increasing power to detect the effects of selection on hybrids (e.g. (Schumer et al. 2018). Fertile or semi-fertile hybrid offspring can facilitate the transfer of genetic material between species via backcrossing with parental lineages through a process known as **introgression.** Genomic and statistical advances across the last two decades have allowed researchers to trace the effects of hybridization and introgression on the genomes of modern species across both ancient and contemporary timescales (see sections 3 and 4) and infer the genetic and evolutionary forces that shape hybridization events (see sections 5 and 6). We view integrating across these diverse timescales and potential outcomes of hybridization as one major challenge for the field going forward (see section 7). Progress in this area will be essential in disentangling the diverse ways in which hybridization shapes animal evolution.

2. Perspectives on the role of hybridization in animal evolution over time

2.1 Classical Era - 1920s to 1990s

Since the modern synthesis, early empirical studies in population and evolutionary genetics began to uncover evidence of genetically based reproductive barriers between described species. Research during this era, based primarily on studies of *Drosophila* species, found overwhelming evidence that hybrids even between closely related lineages had dramatic reductions in viability and fertility (Dobzhansky 1936). This led to the first models describing the genetic and evolutionary mechanisms through which such reductions in viability and fertility can occur, via Dobzhansky-Muller Incompatibilities (Dobzhansky 1937; Muller 1942), along with other important developments in our understanding of the genetic basis and typical patterns associated with reproductive barriers. Particularly influential advances included the development of **Haldane's rule** (Haldane 1922), which laid the groundwork for over a century of research aimed at uncovering the mechanisms that lead to stronger reductions in hybrid viability or fertility in one sex (i.e. the heterogametic sex; section 6.1).

Perhaps because of the dominance of *Drosophila* as a laboratory model in population genetics, researchers well into the 1990s viewed reproductive barriers between closely related lineages as "complete" or nearly complete, meaning that these barriers were so strong that hybrids were almost entirely inviable or infertile. This led to the expectation that introgression between animal species should be exceedingly rare. Most evolutionary biologists embraced the **biological species concept** proposed by Ernst Mayr (1942, 1963) which defined species in terms of their ability to produce viable and fertile offspring. This may explain the prevailing view at the time that hybridization was inconsequential in animal evolution. However, even at the time, some researchers recognized that the biological species concept did not appropriately describe the complexity of genetic exchange in hybrid zones (Anderson 1953; Anderson & Stebbins 1954; Barton & Hewitt 1985). While the biological species concept remains the primary working definition for many biologists today, there is now broad recognition of the immense complexity surrounding species delineation, particularly for modern species whose genomes were shaped by historic (section 3.1) or contemporary introgression. Researchers now broadly accept that reproductive isolation is not a fixed binary (that is, species are either reproductively isolated or not) but rather a quantitative metric that can vary across biological scales (see sections 5 and 6) and across ecological scenarios (sections 3.2 and 6.4).

2.2 Hybrid zones as natural laboratories - 1990s-2010s

In the 1990s to 2010, advances in molecular genetics and theory, as well as several key perspectives that challenged the prevailing viewpoint that hybridization was rare in animals (e.g. (Mallet 1995, 2005), led to a renaissance in the study of naturally occurring hybrid zones and a shift away from the lab models of the previous era. Research in *Heliconius* (Mallet et al. 1990), *Bombina* (Szymura & Barton 1991), crickets (Rand & Harrison 1989), house mice (Dod et al. 1993), and grasshoppers (Virdee & Hewitt 1994), among other animal species, made clear that genetic exchange was occurring between some animal species in nature. Based on these influential findings, the field shifted to viewing hybrid zones as "natural laboratories" (Hewitt 1988) and "windows on the evolutionary process" (Harrison 1990). Researchers began treating hybrid zones as experiments that evolution had already conducted for tens, hundreds, or thousands of generations. Importantly, researchers began to appreciate that different regions of the genome may have different likelihoods of moving across species boundaries (Harrison 1990; Wu 2001). One of the most important insights from work during this period was that although hybridization may be rare on an individual basis, even infrequent hybridization can have substantial evolutionary impacts (Mallet 2005). This led to the development of the first formal hypotheses about the evolutionary and genetic processes that impact where in the genome "barrier loci" arise, and as a consequence, which regions of the genome may resist introgression between species or be more likely to harbor hybrid incompatibilities (such as the **Large X effect**; (Coyne & Orr 1989; Payseur 2010). However, a lack of genome-wide data for most organisms and a focus on a small number of active hybrid zones made it unclear whether the patterns observed in these species were broadly generalizable across animals.

2.3 Evidence of widespread hybridization across the animal tree of life - 2010s-2020s

During the next generation sequencing era, a flood of studies began documenting both ancient and contemporary hybridization across the animal tree of life, cementing the view that hybridization has been common in the evolutionary history of animal species. Evolutionary biologists began to more widely apply tools developed in human genetics like STRUCTURE (Pritchard et al. 2000) and related methods (Alexander et al. 2009; Pickrell & Pritchard 2012), which enabled the detection of relatively recent but cryptic hybridization events (Gompert et al. 2017). The availability of genome-scale data facilitated development and adoption of sensitive genome-wide statistics for detecting both past and ongoing hybridization. Perhaps the most influential among these tools was **Patterson's D-statistic** (Green et al. 2010), which detects deviations from expected patterns of site sharing compared to null expectations under a model of **incomplete lineage sorting**. These approaches opened the floodgates, resulting in the development of a large number of related approaches that could detect more complex patterns of introgression (Pease & Hahn 2015), estimate genome-wide admixture proportions (Patterson et al. 2012; Skotte et al. 2013), or infer the direction of introgression (Hibbins & Hahn 2019). There were also major breakthroughs in statistical and theoretical approaches to infer the timing of admixture (Hibbins & Hahn 2019; Narasimhan et al. 2019) and advances in the development of **local ancestry inference** tools (reviewed in (Moorjani & Hellenthal 2023); see section 4.3). These approaches revolutionized our ability to document patterns of hybridization, including uncovering events that were previously undetectable, either because the hybridization event was between morphologically cryptic parent species (e.g. (DeVos et al. 2023), occurred in the ancient past (Suvorov et al. 2022), or contributed only a small amount of genetic material to modern genomes (Heliconius Genome Consortium 2012).

Research during this period made crucial contributions to our understanding that hybridization has been a frequent part of animal evolution, both historically and in the Anthropocene, which has spurred new interest in the role of human-induced habitat change in hybridization (see section 3 below). Moreover, this period saw the development of several comparative systems to study hybridization, including replicated, independently formed hybrid zones between the same pairs of species (e.g. *Littorina* snails (Westram et al. 2021) and swordtail fish (Langdon et al. 2022)), or mixture events involving one of the same source populations (e.g. humans-Neanderthals and humans-Denisovans; (Sankararaman et al. 2016), allowing researchers to ask more precise questions about the repeatability of the outcomes of hybridization.

2.4 Understanding the genetic and evolutionary consequences of hybridization - 2020-now

In our current era, the focus has shifted from describing patterns of hybridization to disentangling the genetic and evolutionary drivers of ancestry variation along the genome. This work has involved diverse approaches, uniting hybridization research across multiple fields including classical genetics, population and evolutionary genomics, molecular biology and gene editing, field ecology, and studies of behavior. Researchers are now tackling questions such as what genomic variables drive the retention or removal of introgressed ancestry tracts (Vilgalys et al. 2022), what selective processes are most important in driving ancestry variation along the genome (Groh & Coop 2024), and the extent to which these processes are repeatable versus context dependent (Langdon et al. 2024). The major findings of this period, such as the importance of local recombination rate and the outsized role of selection in the earliest generations following hybridization, are discussed in detail in section 5. Moreover, continued methods development (see section 4) has allowed researchers to more precisely date the onset of hybridization and identify environmental or demographic variables that may promote hybridization. In cases of contemporary hybridization, this has led to substantial developments in uncovering their proximate causes, such as shifts in species ranges or mating behavior, especially in the context of anthropogenic disturbance (section 3.2).

3. Synthesis of evidence of hybridization across animal evolution and outstanding questions

Despite significant historical debate over the extent of hybridization in animal taxa, there is now broad consensus that many (if not most) animal species have hybridized with their close relatives over historical or contemporary timescales (Edelman & Mallet 2021; Peñalba et al. 2024; Taylor & Larson 2019). Importantly, research has revealed that the drivers of these hybridization events can differ across time scales. We review what is known about these drivers below as well as possible biases stemming from the biological systems that are most intensively studied that may have shaped and continue to shape the field of hybridization research.

3.1 Ancient hybridization was frequent in animal evolution

Many animal taxa have hybridized with their close relatives during their evolutionary history, and we need to look no further than our own species to see evidence of these patterns.

Some human populations exchanged genes approximately 2,000 generations ago with our now extinct relatives the Denisovans and Neanderthals, with evidence of additional admixture events being continuously discovered (Cousins et al. 2025; Iasi et al. 2024; Sankararaman et al. 2014, 2016). Phylogenomic data supports evidence of ancient hybridization across many species groups including swordtails (Du et al. 2024), *Heliconius* (Heliconius Genome Consortium 2012), *Drosophila* (Suvorov et al. 2022), and felids (Li et al. 2019). Moreover, several extant fish and reptile lineages are **allopolyploids**, including the Amazon molly (Ricemeyer et al. 2026), *Ambystoma* salamanders, and *Aspidoscelis* whiptail lizards (reviewed in (Avise 2015; Ho et al. 2025; Stöck et al. 2021). These rare allopolyploidization events, which are more common in plant taxa (Wang et al. 2025), can be seen as a snapshot of particular ancient hybridization events that “froze” the hybrid genomes at the time of admixture (Ricemeyer et al. 2026; Schartl et al. 1995).

Studying ancient hybridization events gives us insight that hybridization has been pervasive in animal evolution. However, there are many methodological difficulties associated with studying these events. Ancient hybridization events are challenging to distinguish from ancient population structure, especially over deeper timescales. Consequently, we may be underestimating the importance of hybridization in earlier evolutionary time periods. Further, many of these ancient introgression signals propagate along branches, making it difficult to identify source lineages and the direction of introgression, particularly in cases of **ghost introgression** where one or more of the hybridizing lineages has gone extinct. Indeed, even within human evolutionary genetics, there is controversy over whether there was ghost introgression in human lineages with an as of yet uncharacterized population or whether deep population structure could produce similar patterns (Ragsdale et al. 2023). These complexities often prevent us from linking hybridization events to specific biogeographical events, although there are some notable exceptions (e.g. cichlid great lake colonization (Rick et al. 2025)). Nevertheless, the remnants of ancient hybridization that persist in modern genomes have helped us understand the long-term consequences of hybridization on animal genomes (see section 5 below).

3.2 Emerging links between widespread hybridization and environmental change in the Anthropocene

In addition to ample evidence of hybridization in ancient evolutionary history, there are numerous cases of ongoing hybridization that allow us to observe this process in real-time. Contemporary hybridization events vary in their dynamics, but we broadly classify them here into whether hybridization is occurring in older, stable hybrid zones or is driven by recent shifts in species ranges or species interactions. Older hybrid zones are primarily thought to have arisen independently of anthropogenic influence, with many associated with historical changes in species ranges resulting from climatic oscillations including expansions and contractions from glacial refugia (Hewitt 2000; Rick et al. 2025). While the structure of these hybrid zones can vary (i.e. whether they are “wide”, “narrow”, or “mosaic”; (Harrison & Larson 2016)), many appear to be stable over the decades they have been studied. In these cases, it is common for parent species to remain genetically and phenotypically distinct, with hybrids being rare and found primarily in the narrow geographical range where the parental species overlap (e.g. (Llopart et al. 2005). These types of hybrid zones were intensively studied during the Classical

Era (see above). Intriguingly, many of these older hybrid zones are coincident across the same major geographic or ecological transitions, forming **suture zones** (Wait & Peñalba 2025) and providing opportunities to study how species barriers in different taxa respond to a shared climatic or geographic event. Notably, even for older hybrid zones that formed before the Anthropocene, the characteristics of hybrid zones, including their location and stability, can be altered by anthropogenic change (Aguillon & Rohwer 2022).

While we lack broad data to rigorously evaluate this claim, we and others speculate that newer hybridization events may be occurring at an accelerated rate due to anthropogenic change (Ålund et al. 2023; Grabenstein & Taylor 2018)**.** Case studies support the conclusion that the broad environmental changes driven by humans have provided new opportunities for hybridization (Seehausen et al. 2008). Researchers have found that new, anthropogenically induced hybrid zones and hybrid swarms have formed for diverse reasons, including as a result of shifts in species ranges or habitats due to climate tracking (Krapf et al. 2025), novel contact between native and introduced species (Mandeville et al. 2019), changes to habitat connectivity (Dougherty & Carling 2024), disruption of established trophic interactions and niche partitioning (Kinney et al. 2025), and disruption of species communication or mating signals (Banerjee et al. 2023; Ramirez-Duarte et al. 2025). One outstanding research question in this area is whether certain taxa are more prone to anthropogenically induced hybridization due to the nature of their mating barriers or the characteristics of the environments in which they occur (Ramirez-Duarte et al. 2025). Research over the last decade has focused on documenting associations between anthropogenic change and hybridization but identifying the proximate mechanisms of changes in hybridization rates remains an ongoing challenge. An important research priority is determining the extent to which anthropogenic change is increasing rates of hybridization and what types of anthropogenic change have the greatest impact on hybridization outcomes, especially for species of conservation concern (see section 6.4).

3.3 Taxonomic biases in hybridization research in animals

Much of our in-depth knowledge about the consequences of hybridization in animals and conceptual advances in the field have been motivated by research in specific systems, raising the possibility that taxonomic and geographic biases have impacted the broad conclusions we can draw as well as the biological questions we can address. The most obvious source of taxonomic bias in hybridization research is an enrichment in studies of classic lab models (e.g. *Drosophila*, house mice; Figure 1B). Indeed, the extreme patterns of inviability and sterility observed in hybrid *Drosophila* arguably contributed to biologists' view during the Classical Era that hybridization is rare in animals. Taxonomic representation in hybrids studied during the pre-genomics era was also biased towards species with morphological variation obvious to human observers while cryptic species complexes were understudied (Mallet 1993; Scriber et al. 1986). While next generation sequencing has allowed for greater taxonomic diversity at the class level, as shown by the relative increases in the number of studies of Actinopterygii (ray-finned fishes) and Aves (Figure 1C), these changes are driven primarily by decreases in the number of studies of *Drosophila* and *Mus* (Figure 1B). Even today, a persistent source of taxonomic biases is researchers' preference for lab-suited animals with greater perceived tractability (Delmore et al. 2024); Figure 1B). These lab models may vary in how representative they are of dynamics of hybridization in nature, but this challenge is in part mediated by increased availability of genomic data from a broad range of animal species. Despite net gains in taxonomic diversity at the genus and class levels, hybridization research remains heavily skewed at the phylum level towards Chordata and Arthropoda (Figure 1D) suggesting that the improved representation facilitated by next generation sequencing within specific lineages is not yet represented at the phylum level.

Geographic biases in hybridization research are also prevalent. Animals studied in hybridization research are located primarily in North America, to a lesser extent western Europe, and in a few select biodiversity hotspots including Australia, Japan, and Brazil (Figure 1E). This geographic bias is seen perhaps most clearly in studies on the links between anthropogenic change and hybridization (Ålund et al. 2023). There are also geographic biases driven by habitats that are difficult to access, which have been comparatively understudied. One notable example is the open ocean (Viard et al. 2020), which is challenging to study using the spatial sampling approaches that have built evidence for other animal hybridization events (but see (Hobbs et al. 2022). Similarly, we are likely to underestimate rates of hybridization in species that are understudied for other reasons, such as a lack of sampling effort or morphological crypsis.

These biases can impact the questions researchers ask and more fundamentally what we conceive of as biologically possible. For example, sex chromosomes are known to have an outsized role in hybrid incompatibilities, but the most comprehensive studies evaluating these dynamics are based on systems with ancient, highly differentiated sex chromosomes (mammals, birds, *Drosophila*), while the sex chromosomes of species with younger sex chromosomes and high rates of sex chromosome turnover may be less enriched in hybrid incompatibilities, potentially leading to fewer barriers to sex chromosome introgression (Lima 2014; Stöck et al. 2021). Similarly, species with unusual reproductive strategies (*e.g.,* largely clonal systems, obligate sexual parasites) are underrepresented in current research and may conceal unappreciated or unknown biological principles (Figures 1C and D; (Juvé et al. 2025; Vukić et al. 2025). Despite these biases, the past two decades have dramatically expanded the taxonomic diversity in studies of animal hybridization, promising an exciting future of discoveries in the field.

4. Advances in detecting and characterizing hybridization

Advances in our understanding of the frequency of hybridization and its evolutionary impacts have been fueled by massive progress in both genomic data availability for non-model organisms and matched progress in the development of theory and statistical methods to detect hybridization (reviewed in (Gompert et al. 2017; Hibbins & Hahn 2022; Moorjani & Hellenthal 2023; Rannala 2025). Here, we highlight some of the most common approaches and recent advances that are shaping research in the field.

4.1 Accessibility of low-coverage whole genome sequencing

Sequencing techniques used to study hybridization have shifted over time, mirroring technological advances, with early studies using few markers (e.g. allozymes, microsatellites, and mitochondrial genes), later studies applying reduced representation approaches like ddRADseq and exon capture, and present-day studies now regularly leveraging whole-genome sequencing approaches. The major limitations of the older technologies stem from sampling a small slice of the genome and the challenges of extending these interpretations to the entire genome. For example, specific regions of the genome, such as the mitochondria, may reflect distinct patterns of introgression compared to the nuclear genome. More generally, if hybridization is relatively rare on an individual basis, and introgression has on average only contributed to variation in a small proportion of the genome (e.g. 2-5% in humans; (Sankararaman et al. 2016), any method that does not capture a large proportion of the genome may miss evidence of hybridization altogether. Notably, Dagilis and colleagues (2022) found evidence for disagreement between older technologies and whole genome sequencing in signals of introgression based on Patterson's *D* statistic. As a result of both differences in sequencing technologies and analysis approaches, the field is currently limited in the degree to which we can perform comparative analyses (i.e. between animals and plants or across animal taxa) without fears of technical biases (but see (Monnet et al. 2025; Wang et al. 2025).

4.2 Theoretical and software developments

Expanded access to genome-scale sequencing data has driven the development of new computational approaches to infer evidence of hybridization as well as modifications to earlier software to be able to handle data from millions of SNPs (Gompert et al. 2017). The most commonly used methods in the field to detect evidence of hybridization still rely on genome-wide summary statistics (see section 2.3). These approaches have important advantages because they are quite sensitive, even to low levels of hybridization, and can be applied across a wide range of species and contexts. Similarly, at the species-group level, methods such as phylogenetic networks can accurately infer the presence of hybridization but often require user-defined priors to be computationally tractable (Hibbins & Hahn 2022). Ancestral recombination graphs have also shown promise in identifying regions of introgressed ancestry from ancient migration events or from unsampled populations (Hubisz et al. 2020; Zhang et al. 2026). However, to address the most pressing current questions in the field, there has been increasing interest in methods that allow researchers to study variation in ancestry along the genome.

One of the most powerful approaches for understanding the consequences of hybridization has been the development of diverse tools for **local ancestry inference**. These tools enable researchers to infer regions of the genome that trace to distinct parental lineages. Also referred to as ancestry painting, the development of tools that can perform local ancestry inference in diverse species has enabled a renaissance in the study of hybridization (Figures 2A and B), allowing researchers to precisely date hybridization events (Iasi et al. 2024) and identify evidence of adaptive introgression or genetic incompatibilities in the genome. Unlike the approaches discussed above, they can be used to analyze hybridization between any pair of species, whereas phylogenetic and site-based approaches are often restricted to analyzing hybridization between non-sister species. Most methods for local ancestry inference rely on defining informative sites using reference panels of unadmixed parental species and applying hidden Markov models (HMM) that infer the posterior probability of possible ancestry states at these sites along the genome, incorporating error and the possibility of switches in state due to recombination events (Figure 2A). HMM-based methods are powerful and can perform well on both recent and more historical hybridization events (Maples et al. 2013; Wei et al. 2025) but choice of program and parameters can be crucial for accuracy. Recently developed implementations also allow for local ancestry inference in more complex contexts (Corbett-Detig

& Nielsen 2017), such as with multispecies hybridization events involving three or more hybridizing species (Banerjee et al. 2023) or when one of the source lineages in the hybridization event is unknown due to the lineage being extinct or unsampled in the present day (Skov et al. 2018). Other commonly used methods for local ancestry quantification include modifications of the D-statistic (f_d) applied to windows of informative sites along the genome (Malinsky et al. 2021). While these methods have the advantage of being straightforward to apply, some simulation studies have highlighted reduced accuracy under certain admixture scenarios (Martin et al. 2015). Other researchers have used classic population genetic statistics such as variation in F_{st} and D_{xy} in windowed analyses along the genome to detect evidence consistent with local variation in rates of introgression. While these statistics can be applied to accurately infer introgression with sufficient biological knowledge of the system (e.g. (Brandvain et al. 2014), it is important to keep in mind that these patterns can also be impacted by other evolutionary processes unrelated to hybridization (such as background selection; (Hu & He 2005).

Cline analyses represent another suite of approaches that have been used to identify genomic regions potentially associated with reproductive barriers between species. Classic methods measure changes in ancestry at informative markers over geographic space, but more recent approaches have analyzed variation in ancestry of specific loci within a hybrid population relative to patterns of genome-wide admixture to infer the strength of selection acting on specific regions of the genome (Larson et al. 2014) and estimate the strength of reproductive barriers (Francioli et al. 2025). Geographical clines have the advantage of allowing researchers to identify environmental variables that covary with hybridization outcomes, as well as loci that may contribute to reproductive barriers. In the presence of sufficient gene flow between neighboring populations, loci that are not involved in reproductive barriers may show a gradual transition between parental alleles over geographic space. In contrast, the expectation is that clines will be steeper/narrower if a given region of the genome plays an important role in reproductive isolation. However, recent empirical work examining geographic clines at mapped incompatibilities has suggested that this may not be the case in the context of asymmetric incompatibilities or under certain demographic conditions (Robles et al. 2025). Similarly, methods that attempt to leverage variation in ancestry at a specific region compared to average ancestry across the entire genome to prioritize barrier loci (Bayesian Genomic Cline approaches; (Gompert et al. 2024)) have variable performance in simulations (Jofre & Rosenthal 2021). Extensions of these methods have recently been deployed to quantify the total and partial contributions of different reproductive barriers to overall reproductive isolation and position along the speciation continuum (Francioli et al. 2025). As part of this effort, some researchers have adopted a statistic known as the coupling coefficient in an attempt to allow direct comparisons of the strength of reproductive isolation across taxa (Dopman et al. 2024).

Concordant with these methodological developments, advances in simulation methods that allow users to model the process of hybridization and simulate selection have been invaluable. For example, the most recent version of SLiM is rapidly becoming the Swiss army knife of population genetic simulators (Haller et al. 2026) among other widely used admixture simulators (e.g. (Corbett-Detig & Nielsen 2017). In particular, incorporation of tree-sequence recording in SLiM has allowed users to read out local ancestry of simulated individuals. These types of tools enable the discovery of genetic signatures associated with different types of selection on hybrids (Setter et al. 2020) and allow users to test the predicted accuracy of the dizzying number of software and approaches now available for local ancestry inference (Langdon et al. 2024; Schumer et al. 2020; Wei et al. 2025).

4.2 Long-read technologies

We are also beginning to see the impacts of the falling costs of long-read sequencing on hybridization research. At the most basic level, it is now feasible to produce high-quality, well-resolved reference genome assemblies in nearly all animal systems, even for the largest and most repetitive genomes (Meyer et al. 2021). Similarly to the renaissance in methods development that followed lowered costs of short-read sequencing, wider availability of long-read data is currently driving methods development for studying structural variation including via haplotypes and pangenome approaches (Liao et al. 2023). These advances are allowing researchers to address long standing questions in hybridization research (as in (Jansa et al. 2025). Several recent reviews have covered the role of structural variants in hybridization and speciation (Berdan et al. 2024; Lucek et al. 2023; Tellini et al. 2025; Zhang et al. 2021), with a focus on large structural variants, long known to play an important role in local adaptation and reproductive isolation (Noor et al. 2001).

As long-read sequencing becomes increasingly affordable, researchers will soon be able to detect and analyze classes of structural variants that were previously intractable to study at population scales (Edwards & Li 2026), including small scale rearrangements, and especially complex regions such as centromeres, satellites, TEs, and copy number variants. These extremely complex regions may be especially important in shaping the outcomes of hybridization. For example, coevolution between selfish genetic elements and mechanisms that repress them (i.e. centromeric **meiotic drivers** and satellite DNA) have been shown to play a key role in hybrid incompatibilities when selfish elements and their repressors are mismatched in hybrids, particularly in model systems such as *Drosophila* (Brand & Levine 2022; Brand et al. 2026; Searle & Pardo-Manuel de Villena 2024). These advances, coupled with the development of appropriate computational methods for ancestry inference from these data types, will enable researchers studying hybridization to investigate previously inaccessible questions, such as whether small structural variants also resist introgression and maintain linked co-adapted alleles between species (Wellenreuther et al. 2025). The ability to analyze ancestry in these regions of the genome will be especially powerful for inferring the generality of these patterns, particularly in species that cannot easily be crossed in the lab. This wealth of genomic data, including long-read genomes and the software and analytical approaches that are being developed in parallel, promise exciting new frontiers in answering questions about how hybridization shapes the genome.

5. How hybridization shapes the genome

One major goal in the study of animal hybridization is disentangling the complex and interacting ways in which hybridization shapes genome evolution. This is an enormous question, and one where our understanding is most likely to transform in the coming decades. Below, we discuss what we have learned about how ancestry is distributed locally and globally across the genome and outline outstanding questions about the drivers of this variation.

5.1 How hybrid incompatibility genes accumulate in the genome

Most of our early insights into the potential genomic outcomes of hybridization came from genetic crosses performed in laboratory settings aimed at identifying hybrid incompatibilities (Figure 2C). These experiments continue to uncover valuable information about the consequences of hybridization and have provided most of the direct evidence about the presence, number, and genetic architecture of hybrid incompatibilities in animals (Frayer et al. 2025; Kitano & Okude 2024; Presgraves 2010). From these studies, we have learned that even hybrids between recently diverged lineages can have hybrid incompatibilities that have large impacts on viability and fertility (as in *Drosophila* and *Mus*), although there is large variation among taxonomic groups in the degree of genetic divergence at which hybrid incompatibilities begin to manifest (Coughlan & Matute 2020). Research to date has attributed the evolution of incompatibilities to mechanisms such as selfish genetic elements (Searle & Pardo-Manuel de Villena 2024; Sweigart et al. 2019), host-pathogen conflict (Xie et al. 2024), or developmental systems drift (Chang et al. 2021; Schiffman & Ralph 2022), but it is unclear whether the relative frequencies of these mechanisms in mapped hybrid incompatibilities are driven by detection biases (Frayer et al. 2025). Lab studies have also confirmed some of the basic theoretical predictions about how incompatibilities operate and accumulate, including evidence that selection on hybrid incompatibilities is often asymmetric (Frayer et al. 2025; Turelli & Moyle 2007), there is a large effect of the X chromosome on hybrid male fitness (Presgraves 2018), and there is some evidence of faster-than-linear accumulation of incompatibilities with genetic distance (Matute et al. 2010; Moyle & Nakazato 2010; Orr & Turelli 2001). Despite this important progress, hybrid incompatibilities remain difficult to characterize in animal species without powerful genetic resources, and a recent review reported that 90% of known incompatibilities in animals were identified in either *Drosophila*, *Caenorhabditis,* or *Xiphophorus* (Frayer et al. 2025). This is because many approaches to identify hybrid incompatibilities have poor power at weaker selection coefficients. A recent paper estimated that even with nearly 2,000 hybrids, the authors lacked power to identify incompatibilities with selection coefficients less than 0.3 (Robles et al. 2025). This indicates that current studies are likely sampling the tail of the distribution of selection coefficients and argues for developing more powerful approaches to identify incompatibility loci that can be applied in the lab and the wild.

5.2 Beyond mapping hybrid incompatibilities: the distribution of hybrid ancestry across the genome

While lab models have been valuable for mapping hybrid incompatibilities, they often focus on early generation hybrids. Studies of natural hybrid populations and hybrid zones have provided important insights about the long-term genomic consequences of hybridization. Some of the first studies to uncover heterogeneity in introgression along the genome were studies of admixture between humans and our extinct relatives, the Neanderthals and Denisovans. Sankararam et al. (2014, 2016) found evidence for large swaths of the genome in modern-day humans that were unusually depleted in Neanderthal and Denisovan ancestry across individuals (Figure 2B). These early studies found that these genomic regions were associated with a high density of functional base pairs, suggesting that archaic hominin ancestry was especially deleterious in the human lineage in functionally important parts of the genome (Figure 2D). In systems where high quality local ancestry data is available, researchers have tended to find similar patterns (Groh & Coop 2024; Langdon et al. 2024): modern genomes often consist of regions of higher genetic exchange interrupted by **minor parent ancestry deserts**, or regions that are highly depleted in ancestry from the minor parent species (i.e. the species contributing less genetic material to admixed offspring).

Application of new methods that use wavelet variance decomposition to study ancestry variation at different scales have provided insight into how these patterns are established (Groh & Coop 2024). Researchers found that in swordtail fish and Amboseli baboon hybrids, spatial variation in ancestry was likely driven by strong selection repatterning ancestry in the earliest generations after hybridization when ancestry tracts were long (Figure 2D; (Groh & Coop 2024; Langdon et al. 2024). The results of these retrospective studies in hybrid populations mirror available data from experimental evolution studies in animal hybrids. Matute and colleagues (2020) sampled hybrid swarms between *Drosophila santomea* x *D. yakuba* and *D. simulans* x *D. mauritania* across 20 generations and tracked ancestry along the genome. They found clear evidence of genome-wide purging of ancestry from one of the parental species, resulting in ancestry deserts along much of the genome, consistent with theoretical predictions and studies in natural systems (Harris & Nielsen 2016; Juric et al. 2016). Moreover, studies where researchers can track hybridization retrospectively using genomic patterns in addition to studying ongoing hybridization in contemporary hybrid populations are especially powerful. In the case of Amboseli baboons (Vilgalys et al. 2022), *Formica* ants (Heidbreder et al. 2026), and swordtail fish (Langdon et al. 2022, 2024), researchers have directly tested questions about drivers of ancestry variation or changes in the strength and direction of selection. In species where ancient DNA data is available, time series analyses have played a similar role in allowing researchers to detect such shifts (Laine et al. 2025; Sankararaman et al. 2016; Yair et al. 2021).

5.3 Known drivers of ancestry variation along the genome

Both theoretical and empirical work have suggested that the uneven landscapes of introgression observed in many systems are the result of the interaction between linkage, selection, and the timescales on which selection occurs (Groh & Coop 2024; Harris & Nielsen 2016; Juric et al. 2016; Veller et al. 2023). In the early generations after hybridization, few recombination events have occurred, resulting in ancestry linkage disequilibrium across much of the genome. Selection on hybrid genomes will purge alleles that are deleterious in hybrids, such as hybrid incompatibilities, and when selection is sufficiently strong this can remodel ancestry along whole chromosome arms. These broadscale impacts will constrain later evolutionary outcomes by shifting local and global ancestry proportions on these chromosomes (Groh & Coop 2024). Despite these broadscale effects in early generations, later recombination events can decouple adaptive and neutral (or deleterious) alleles, resulting in local increases in introgression against this background. Moreover, changing environmental conditions can also result in introgressed ancestry tracts that were segregating in the population increasing (or decreasing; (Pandey et al. 2025) in frequency long after they were first introduced by hybridization (Jones et al. 2020; Villanea et al. 2025; Yair et al. 2021).

Ancestry deserts are often assumed to be driven by hybrid incompatibilities (Figure 2C), but researchers have also shown that other sources of selection can drive similar patterns. Weakly deleterious alleles can accumulate because of reduced efficacy of selection in small populations, resulting in higher **genetic load** in one lineage (Figure 2E). These alleles individually are likely to experience weak selection (i.e. on the order of ~1/Ne), but when many such alleles are linked in the early generations after hybridization, selection on these regions is strong in aggregate (Harris & Nielsen 2016; Juric et al. 2016). Other studies have demonstrated that regions of the genome that harbor mapped hybrid incompatibilities colocalize with large ancestry deserts, indicating that both processes can drive the accumulation of ancestry deserts (Langdon et al. 2024). These findings layer on to many decades of work demonstrating that certain regions of the genome, such as the sex chromosomes (Figure 2F), tend to be depleted in minor parent ancestry after hybridization (Chevy et al. 2023; Payseur & Rieseberg 2016; Presgraves 2018).

Beyond the sources of selection generating ancestry deserts, researchers have identified genomic variables that correlate with a depletion in minor parent ancestry. One of the first variables appreciated as a major driver of ancestry variation at a genome-wide scale was the local recombination rate (Figure 2G). First reported in hominins and in swordtail fish (Sankararaman et al. 2016; Schumer et al. 2018), several studies have now documented similar patterns and developed theory to explain this behavior (Calfee et al. 2020; Langdon et al. 2022, 2024; Martin et al. 2019; Veller et al. 2023; Vilgalys et al. 2022). Regions of the genome with low recombination rates are especially likely to be depleted in minor parent ancestry at a genome-wide scale, whereas regions of the genome with higher recombination rates are more likely to retain minor parent ancestry.

Because recombination rate variation mediates the degree of linked selection in a region (e.g. low recombination rate regions harbor many linked sites), some of these patterns are likely driven by a higher density of functionally important sites in regions of the genome with low recombination rate. However, in some cases researchers have performed partial correlation analyses or simulations to further explore these drivers and found that recombination rate has a strong effect on ancestry even after accounting for linked coding or conserved basepairs (Schumer et al. 2018; Langdon et al. 2022, 2024). These findings are consistent with theoretical results which have suggested that the impact of recombination rate is so strong that it is one of the most important parameters predicting the equilibrium ancestry proportion following hybridization (Veller et al. 2023).

After accounting for the strong effect of variation in recombination rate, researchers have tended to find that regions of the genome that are enriched in functionally important base pairs are depleted in minor parent ancestry (Figure 2E). In animal species, genomic annotations depleted in minor parent ancestry include regions with a high density of coding and conserved base pairs, large structural variants and sex chromosomes, and classes of enhancers (reviewed in (Moran et al. 2021; Telis et al. 2020). However, there are likely many relevant annotations that have yet to be systematically tested, including connectivity of and centrality in gene regulatory networks (Runghen & Bolnick 2025), number and importance of protein-protein interactions, and variants that contribute to phenotypic traits that differ between hybridizing species.

In addition to regions that are especially depleted in minor parent ancestry, researchers have documented other genomic regions with unusually elevated levels of introgression compared to the genome-wide background (Sankararaman et al. 2014; Vernot & Akey 2014). If hybridization occurred recently, researchers can conclude that regions of the genome with especially high minor parent ancestry are likely to have been positively selected after hybridization and represent cases of adaptive introgression (Flanagan et al. 2025; Heliconius Genome Consortium 2012; Racimo et al. 2015). However, in cases where hybridization occurred deeper in the past, enough time may have passed for neutral ancestry tracts to drift to high frequency (Schumer et al. 2016). Similarly, theoretical results have highlighted the possibility that other evolutionary mechanisms, such as reciprocal masking of recessive deleterious alleles (Harris & Nielsen 2016; Kim et al. 2018; Zhang et al. 2020), can generate signals that are difficult to distinguish from adaptive introgression. As an alternative approach, researchers have leveraged analyses such as functional enrichment (Enard & Petrov 2018) or direct genetic mapping of ecologically important traits and tracing their evolutionary history (Heliconius Genome Consortium 2012; Jones et al. 2018). More broadly, many outstanding questions exist about the frequency of adaptive introgression, the modes of selection that can favor it, and the genetic architecture of traits that are likely to undergo adaptive introgression (see section 6.2).

The search for genomic annotations that correlate with retention or loss of minor parent ancestry is in one sense a question about the repeatability of evolutionary processes within and across hybridizing species. There have been only a handful of studies that have investigated the genomic outcomes of replicated hybridization events between the same pairs of animal species. In these studies, researchers have found evidence for repeatability in ancestry, ranging from modest to very strong covariation in local ancestry (Blain et al. 2025; Langdon et al. 2024; Nouhaud et al. 2022; Westram et al. 2021). A pair of recent studies on swordtail fish (genus *Xiphophorus*) provides an interesting perspective on these dynamics. Researchers studied three independent hybrid populations formed between close relatives *X. birchmanni* x *X. malinche* (~250,000 generations diverged; (Langdon et al. 2022) and two independent hybrid populations formed between more distant relatives *X. birchmanni* x *X. cortezi* (~450,000 generations diverged; (Langdon et al. 2024). While it is important to consider demographic and environmental differences between hybrid populations, these studies found strong evidence for repeatability in patterns of minor parent ancestry variation along the genome within species pairs, and stronger repeatability in the more divergent species pair (explaining up to 50% of the variation in local ancestry). Notably, these studies also highlighted repeatability in local ancestry *across* species pairs, but this appeared to be largely driven by shared genomic architecture (e.g. similar recombination landscapes across species).

6. The long-term evolutionary consequences of hybridization

Another outstanding challenge in the field is uncovering the factors that shape the long-term outcomes of hybridization. Some of the long-term evolutionary outcomes of hybridization have been well-documented whereas others remain poorly understood. When strong reproductive barriers are present between parental lineages, resulting in inviability or infertility in hybrids, hybridization may lead to little or no introgression. In these scenarios, hybridization may drive the evolution of stronger reproductive isolation between the parental species via **reproductive or ecological character displacement** and a reinforcement of species barriers (Stuart et al. 2017). Thus, as a result of hybridization between parent species, the strength of reproductive barriers can become stronger. Over evolutionary timescales, barrier loci can become physically linked or accumulate higher linkage disequilibrium due to epistatic selection (Scarparo et al. 2026). Alternatively, when hybrids do not face significant reductions in fitness or even experience advantages because of hybrid vigor or **heterosis**, this can result in persistent hybridization or even the spread of hybrids outside of the initial contact zone. Notably, even rare hybridization events can allow genes to move across species boundaries. In some cases, parental species can go extinct and be replaced by hybrid swarms (Gilman & Behm 2011; Hasselman et al. 2014; Todesco et al. 2016). In rare cases, hybrid populations can form new reproductively isolated lineages, particularly if they display transgressive phenotypes with improved fitness compared to the parental forms (section 6.3).

6.1 Factors controlling variation in the strength of reproductive isolation and the direction of introgression

The strength and genetic architecture of reproductive isolation between diverging lineages directly impacts the relative fitness of hybrid offspring and the likelihood of several possible evolutionary outcomes of hybridization. Moreover, these factors interact with the environmental context in which hybrids are found and the demographic history of parental species.

A well-established pattern across animal taxa is that the average viability of hybrids decreases with increasing genetic divergence between the parental species (Roux et al. 2016). Intriguingly, there is discordance in the slope of this trend among animal taxa, with some taxonomic groups able to hybridize at higher absolute genetic distances than others. For example, at a given divergence time in generations, the average avian species pair has a higher rate of viable hybrids compared to the average mammalian species pair (Fitzpatrick 2004), and teleost fish species are able to produce viable hybrids at the most extreme genetic distances observed thus far in animals (Káldy et al. 2020). The drivers of these taxonomic differences remain an outstanding question in the field. Similarly, differences in chromosome number and/or karyotype between parent species have long been hypothesized to correlate with reproductive isolation, since these differences can impede successful meiosis in hybrids. However, the evidence for a role of karyotypic divergence in the evolution of reproductive isolation is surprisingly mixed (Lucek et al. 2023). For example, there are around a hundred documented chromosomal races of *Sorex araneus* shrews across Europe, affecting nearly all chromosomal arms, but there is limited evidence that this impedes meiosis (Searle et al. 2019).

An additional factor shaping the dynamics of introgression between species is the degree of symmetry in reproductive barriers as a function of cross direction. Fitness reductions in hybrids are often dependent on which species is the maternal or paternal parent in the cross, a phenomenon known as Darwin's corollary to Haldane's Rule documented as early as the 1800s (Darwin 1859). A major contributor to this asymmetry has been shown to be driven by the sex chromosomes as well as other uniparentally transmitted genetic elements like the mitochondria. Asymmetric introgression can also be driven by asymmetry in the strength of premating barriers (such as weaker preferences for conspecifics in one species) and variation in reproductive strategies (Ordaz-Morales et al. 2026). Finally, ecological selection on hybrids is likely to be asymmetric depending on the environment in which hybrids find themselves, but since most studies, especially lab-based studies, lack explicit ecological context, these dynamics are often difficult to characterize (but see (Johnson et al. 2025). Despite these challenges, existing work indicates key interactions between the environment and hybrid fitness. Ecological context has also been found to play a large role in the repeatability of the outcomes of hybridization from studies of replicate hybrid zones (Raffini et al. 2025), and there are numerous cases of ecological selection limiting introgression after hybridization (Baebler et al. 2025; DeRaad et al. 2025). All these variables can shape the direction and likelihood of introgression between parental lineages.

Asymmetry in introgression can also be driven by demographic processes (see also section 5.3). If one hybridizing species has experienced persistently low effective population sizes, we may expect to see asymmetric introgression since this could improve fitness simply by increasing genetic variation or masking existing deleterious variation (Thompson & Schluter 2022). The direction of introgression can also depend on the geographic context of hybridization. Theory predicts that population expansions in geographic space can result in “surfing” of alleles across species boundaries at range edges (Excoffier et al. 2009). Individuals at the edge of their ecological range will face challenges finding conspecific mates, so these individuals may be more likely to hybridize, shaping the overall direction of admixture.

6.2 Adaptive introgression as a driver of evolution

Although the hypothesis that hybridization has the potential to act as an evolutionary stimulus is many decades old (Anderson & Stebbins 1954), progress in identifying the genetic basis of adaptive traits in recent years and in quantifying local variation in ancestry along the genome has led to a new understanding of the importance of introgression in adaptation. The last decade has seen a flood of studies documenting adaptive introgression across animal taxa, linking introgression to a suite of potentially adaptive traits including cognitive changes in Iberian gray wolves (Lobo et al. 2025; Sarabia et al. 2025), mimicry genes in *Heliconius* butterflies (Heliconius Genome Consortium 2012), poison resistance genes in rodents (Song et al. 2011), pesticide tolerance in moths (North et al. 2025), and immune genes in hominins (Enard & Petrov 2018). Notably, while these regions can encompass a small proportion of the genome, they may have an outsized effect on adaptation (Bennett et al. 2025; Heliconius Genome Consortium 2012; North et al. 2025).

Many researchers have been motivated by the idea that hybridization may be a potent force generating standing genetic variation that forms the raw material for adaptive radiations, including in spectacularly diverse systems such as African cichlids (Meier et al. 2017). Part of this interest is driven by the potential of introgression to allow populations to adapt more rapidly than would be expected if adaptation were dependent on *de novo* mutation, echoing earlier findings on the importance of standing genetic variation in rapid adaptation. Researchers have also observed that hybridization can unmask previously unappreciated trait variation. Due to epistatic interactions between variants in the parental genomes, hybrid trait variation can fall outside of the variation typically seen in either parental species for certain traits. These traits are generally referred to as transgressive traits, and they have drawn attention as likely candidates for adaptation or even speciation in cases where they allow hybrid individuals to be better suited to novel environments.

As discussed in section 5.3, two major approaches are used at present to demonstrate adaptive introgression. In species where a trait is known to confer fitness benefits and the genetic architecture of that trait is described, researchers can trace the evolutionary history of genetic exchange between species to infer adaptive introgression. Alternatively, in scenarios where there is not an *a priori* expectation of adaptive introgression of a particular trait, researchers have performed scans for ancestry outliers or used population genetic signals to investigate how quickly particular ancestry tracts increased in frequency (Svedberg et al. 2021). In addition to these advances, new empirical cases of adaptive introgression have revealed additional complexity in dynamics of introgression across species boundaries. We can now trace the evolutionary history of adaptively introgressed alleles across multiple species, a process called **sequential** or **conduit introgression.** Through this process, alleles can transfer across multiple species boundaries. Notable examples of this process include the MUC19 gene, which transferred from Denisovans to Neanderthals before being positively selected in modern humans (Villanea et al. 2025) and the recurrent transfer of genes underlying variation in carotenoid patterns in manakins (Lim et al. 2024).

While the wealth of genomic data and advances in detecting introgression are allowing researchers to identify more cases of adaptive introgression, there is interest in the field in understanding how these adaptive dynamics interact with selection against minor parent ancestry in the genome-wide background. Other open questions include how prevalent adaptive introgression is relative to other modes of adaptation. In both cases, new theoretical or statistical methods are needed to understand these processes. Moreover, most research on adaptive introgression to date focuses on traits with simple genetic architectures where variation is controlled by one or a few genes. It is unclear whether the process of adaptive introgression itself selects for simple genetic architectures, or if this pattern is an artifact driven by improved power to map traits with simple genetic architectures. Another open question is whether traits under particular types of selection, such as those under balancing selection, may be more likely to undergo adaptive introgression. Since balancing selection allows alleles to persist for long timescales and these alleles can quickly rise to moderate frequency when introduced into a population, this could reflect either a detection bias or the dynamics of selection on balanced polymorphisms (e.g. rapid increases in frequency to an equilibrium value (Horta et al. 2025).

6.3 Hybrid speciation

There has been recurrent interest and substantial disagreement in the field about whether and how frequently hybridization can serve as an evolutionary force driving the formation of new species (Long & Rieseberg 2025; Mallet 2007; Schumer et al. 2014), and what evidence is needed to support putative cases of hybrid speciation in animals, particularly without a change in ploidy (**homoploid hybrid speciation**). There has been a rapid increase in the number of reported homoploid hybrid speciation events since the advent of whole genome sequencing and development of methods for the detection of ancient introgression (Boman et al. 2025; Zou et al. 2022). As a result, there has been renewed discussion in the literature about the interpretation of these cases and attempts to establish consistent approaches for demonstrating that new species arose via hybrid speciation (Blanckaert et al. 2023; Long & Rieseberg 2025).

One common framework requires that (1) the putative hybrid lineage is reproductively isolated from parent lineages, (2) there is evidence of hybridization in the genome, and (3) reproductive isolation of hybrids from parent species is a consequence of this hybridization (Schumer et al. 2014). Given the ubiquity of hybrid ancestry in animal genomes, many species satisfy this second requirement, and in lab-amenable species, or species with ongoing gene flow in nature, it is also possible to test for evidence of reproductive isolation between hybrid and parent lineages. The requirement that is most controversial in the field is whether or how researchers should demonstrate that hybridization resulted in the establishment of reproductive isolation of the hybrid lineage. This criterion remains difficult to satisfy because studies mapping the genetic architecture of reproductive isolation often require techniques such as QTL mapping or GWAS to confidently assess if introgressed regions contribute to reproductive barriers (as in (Rosser et al. 2024), restricting such analyses to particular groups of species. Moreover, in cases of ancient hybridization, it may not be tractable to directly address these questions given the evolutionary change that has occurred between ancestral and present-day lineages. There is also debate in the field over whether the timescale over which hybridization results in reproductive isolation is an important factor, given that longer time periods may favor the evolution of reproductive barriers through genetic sorting in the new lineages (Long & Rieseberg 2025). Ultimately, homoploid hybrid speciation in animals seems to occur rarely in nature, especially compared to plants. While estimates of the frequency of hybrid speciation depends on the criteria researchers follow, it is undoubtedly true that hybridization has had a profound influence on the evolutionary history of animal species.

6.4 Extensions of hybridization research to conservation efforts

Given widespread evidence that hybridization has and continues to shape both the genomes and evolutionary histories of modern species, it is of critical importance for researchers to understand the wide-ranging consequences of hybridization for modern species, particularly for species of conservation concern. One major challenge is in predicting the functional consequences of introgressed alleles, both in terms of their potential adaptive benefits and their potential deleterious consequences. To this end, researchers have begun applying techniques such as genomic forecasting to predict how introgressed alleles may shift in response to changing climates and habitats. Recent research in hares provides one of the most striking applications of these techniques to date. Alleles responsible for changing coat color to winter white or remaining brown in the winter have introgressed between species (Jones et al. 2018), and researchers have leveraged these patterns to predict how species will respond to climate-change driven changes in snow cover (Ferreira et al. 2023). These questions have also been explored in a polygenic context in studies of tolerance to bleaching in coral lineages (Fuller et al. 2020). While long appreciated in crop species, conservation biologists have also begun to explore hybridization as a tool to promote animal conservation (Bell et al. 2019), typically with the goal of increasing genetic diversity genome-wide but also with increasing interest in promoting (or preventing) introgression at specific loci underlying important traits (Aguilar-Gómez et al. 2025). Accordingly, there is widespread interest in the potential for introgression to assist in **genetic rescue** of critically endangered or threatened populations by providing the fuel for adaptation at the speed needed for animal species to keep pace with anthropogenic change (e.g. (DeVos et al. 2023)).

While there is clearly immense promise in using existing genetic variation to reduce extinction risk in our changing world, we and others urge researchers and policymakers to be aware of the unknown factors that could impact the success of this approach (Bell et al. 2019). For most non-human organisms, we still have a relatively poor understanding of the genetic architecture of complex traits, such as physiological traits likely to be important in climate adaptation. Similarly, researchers still do not clearly understand the tempo of the evolution of hybrid incompatibilities across lineages, with theory and empirical studies finding that incompatibilities can segregate within and between populations (Corbett-Detig et al. 2013; Cutter 2012). This raises the possibility that attempts to increase population resilience could instead introduce incompatibilities. Tackling these questions is an urgent priority in the face of rapid species declines in the Anthropocene.

7. Conclusions and future directions

Hybridization is now recognized as nearly ubiquitous in the evolutionary history of animal lineages, but there are foundational unanswered questions about its consequences. We expect that even with rapid progress uncovering the drivers of ancestry variation in the genome in recent years, there are unknown variables that await discovery. Moreover, there are basic questions about the outcomes of hybridization across species groups that remain unresolved, but recent technological and theoretical advances may transform our ability to address these outstanding questions about the importance of hybridization in animal evolution.

A major advance of the past five years is a better understanding of the broadscale drivers of ancestry variation along chromosomes, enabled by theoretical advances interrogating the interactions between selection and recombination rate variation after hybridization (Veller et al. 2023) and how those landscapes are expected to change over time (Groh & Coop 2024). One understudied question is how linked positively and negatively selected sites may even interfere with each other, and consequently, how the changing landscape of linkage over time can unmask variation and change the dynamics of selection (e.g. a recombination event decoupling adaptive and deleterious alleles). More broadly, the interactions between selection and recombination rate make it extremely difficult to distinguish the targets of selection during purging from linked passenger variants. Some researchers have leveraged the distinct recombination histories of independently formed hybrid populations to exclude certain regions as drivers (Moran et al. 2024) but these approaches are still in their infancy.

We also predict that the next five years will see a renaissance in our understanding of other genomic variables that shape the outcomes of hybridization in animals and beyond. New methods such as long-read sequencing are no longer cost prohibitive for most animal species, transforming the classes of genomic features we can analyze. While researchers have studied the dynamics of large structural variants for decades, since these variants were readily detectable with other data types, we have a comparatively poor understanding of how selection acts on smaller structural variants after hybridization (e.g. <1 Mb; (Berdan et al. 2024; Wellenreuther et al. 2025). These variants may be less pleiotropic, less likely to harbor incompatibilities, or disrupt recombination, and thus may interact with selection in fundamentally different ways. At the same time these approaches give us access to variants that are known to impact the outcomes of hybridization based on case studies in model systems but have been intractable to study broadly across the animal tree of life. These include dynamics of introgression involving the Y chromosome (van der Bijl & Mank 2025), centromeres and satellites (Figure 2C; (Brand & Levine 2022; Brand et al. 2026), and transposable elements of different types and ages (Laporte et al. 2019).

Beyond the remarkable advances in long-read sequencing, we predict that the diversity of genomic tools developed to better understand functional interactions in the genome, including both *in vitro* and *in vivo* genome-editing tools, will be invaluable in modeling and interpreting outcomes of hybridization across a broad range of non-model species. Methods development for analysis of single-cell based RNAseq data will also enable researchers to more easily infer the structure of gene regulatory networks and cell-cell interactions involved in hybrid incompatibilities. Deeper knowledge about the functional partners of particular genes can help us better understand the outcomes of hybridization on the genomic level, such as the finding that gene misexpression is common in hybrids (Mack & Nachman 2017).

As the field gains a more mechanistic understanding of the causes and consequences of hybridization, we need to maintain a link between this research and the evolutionary impacts of hybridization in nature. Indeed, a recent review highlights the disconnect between lab-based studies of hybridization, particularly those mapping hybrid incompatibility loci and the genomic outcomes of hybridization in the wild (Frayer & Payseur 2024). While there are good reasons for these findings to diverge, including differences in alleles present in lab and wild populations, as well as environmental and demographic impacts on the nature of selection on hybrid incompatibilities, this result also highlights the gaps in our understanding of these complex interactions.

Finally, although such questions may not yet be tractable to address, another outstanding challenge for the field is understanding the drivers of broadscale variation among animal species in the outcomes of hybridization. For example, why does reproductive isolation evolve so much more rapidly in certain *Drosophila* species relative to swordtail fish despite similar divergence times (in *Ne* generations)? Do broadscale variables driving the evolution of hybrid incompatibilities and outcomes of hybridization also differ between species (e.g. the importance of genetic conflict)? What types of isolating mechanisms are most important in promoting versus limiting hybridization between species? These foundational questions highlight just a few of the unknown variables shaping the evolutionary impacts of hybridization in animals, and they await answers in the coming decades of progress in research on hybridization.

Data availability: All code used in the generation of figures in this manuscript is available at https://github.com/KelsieHunnicutt/Hunnicutt_Schumer_2026_Hybridization_in_Animal_Evolution.

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Terms and Definitions list:

1. Dobzhansky-Muller Incompatibilities - Dysfunctional interactions between alleles derived from parental species that can lead to issues with survival and reproduction in hybrid offspring
2. Hybrid swarm - A population of hybrid individuals that locally outnumbers or replaces parental lineages through interbreeding with other hybrid individuals and backcrossing
3. Introgression - The directional transfer of genetic material between species through the backcrossing and interbreeding of fertile hybrid offspring with parent lineages
4. Haldane’s rule - The principle that if hybrids of one sex are inviable/sterile, it is more likely to be the heterogametic sex
5. Large X effect - The observation that the X chromosome disproportionately contributes to hybrid sterility and inviability
6. Patterson’s *D*-statistic - A summary statistic applied to four-taxon trees that describes the relative frequency of site patterns deviating from the species tree
7. Incomplete lineage sorting - A process where ancestral genetic variation is inherited in daughter lineages and subsequent fixation events result in site patterns that do not reflect the species tree
8. Allopolyploid - Organisms or species that have become polyploids following a hybridization event
9. Suture zone - Geographic regions where many previously separated lineages overlap and hybridize because of a shared geographic or climactic event
10. Meiotic drive - Non-Mendelian segregation of parental chromosomes during meiosis because of selfish genetic elements manipulating meiotic machinery
11. Local ancestry inference - Approaches used to infer the parental source lineage of genomic regions using differences in allele frequencies or states between species
12. Minor parent ancestry desert - Large swaths of the genome that are depleted in introgressed ancestry relative to genome-wide averages
13. Adaptive introgression - The directional transfer of genetic material between species via hybridization with the outcome of increasing the recipient species’ fitness
14. Genetic load - The effect on fitness of segregating deleterious alleles that have fixed or drifted to high frequency in a population
15. Minor parent ancestry - Genomic regions derived from the parent species that contributed less on average to an admixed individual’s genome
16. Reproductive or ecological character displacement - Elevated divergence of reproductive or ecological traits that serve as potential barriers to hybridization in areas of sympatry
17. Heterosis - Increased fitness of hybrid offspring because of increased genetic variation or masking of deleterious variation from parental lineages
18. Sequential or conduit introgression - The transfer of genetic material via hybridization that originated in one species to another species via an intermediate species
19. Genetic rescue - Intentional interbreeding of small, inbred populations to larger, outbred populations to increase genetic diversity
20. Homoploid hybrid speciation - The establishment of new, reproductively isolated lineages via hybridization without a change in chromosome number relative to parental lineages

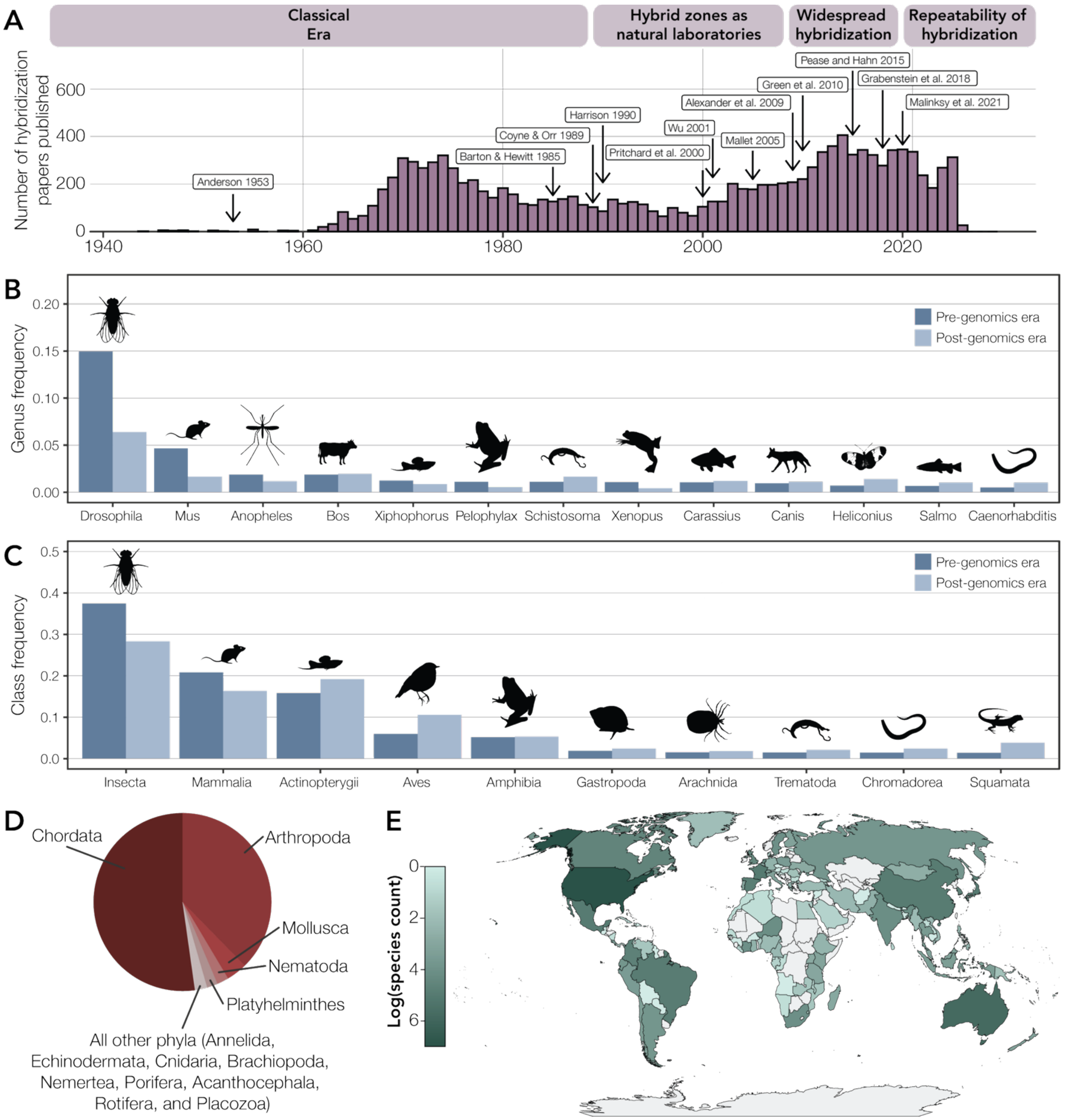

Figure 1: (A) An overview of the timeline of hybridization research using studies identified through NCBI's PubMed database. Select studies that were influential conceptually or in methods development are highlighted above the plot and are discussed more thoroughly in sections 2 and 4. To begin to explore taxonomic biases in hybridization studies, we counted the number of unique genera (B) and unique classes (C) in each abstract, calculated the proportional representation of each genus or class, and subdivided the data into the pre- and post-genomics eras (dark and light blue, respectively; using 2015 as the cutoff date). Note that while only the top 10 genera and classes in each era are visualized, frequencies reflect proportional representation across all genera and classes. We plotted open source animal silhouettes for each class/genus from PhyloPic using the R package rphylopic (Gearty & Jones

2023). (D) Taxonomic distribution of hybridization studies at the phylum level. (E) Geographic distribution of animal species represented in articles on hybridization. We identified unique species names listed in abstracts of hybridization studies (see Supplemental methods). For each unique species mentioned in each abstract, we identified the country with the most occurrence records in GBIF then counted the number of times a country was a represented species' top country of occurrence across all studies and visualized the log-transformed top country of occurrence counts across species.

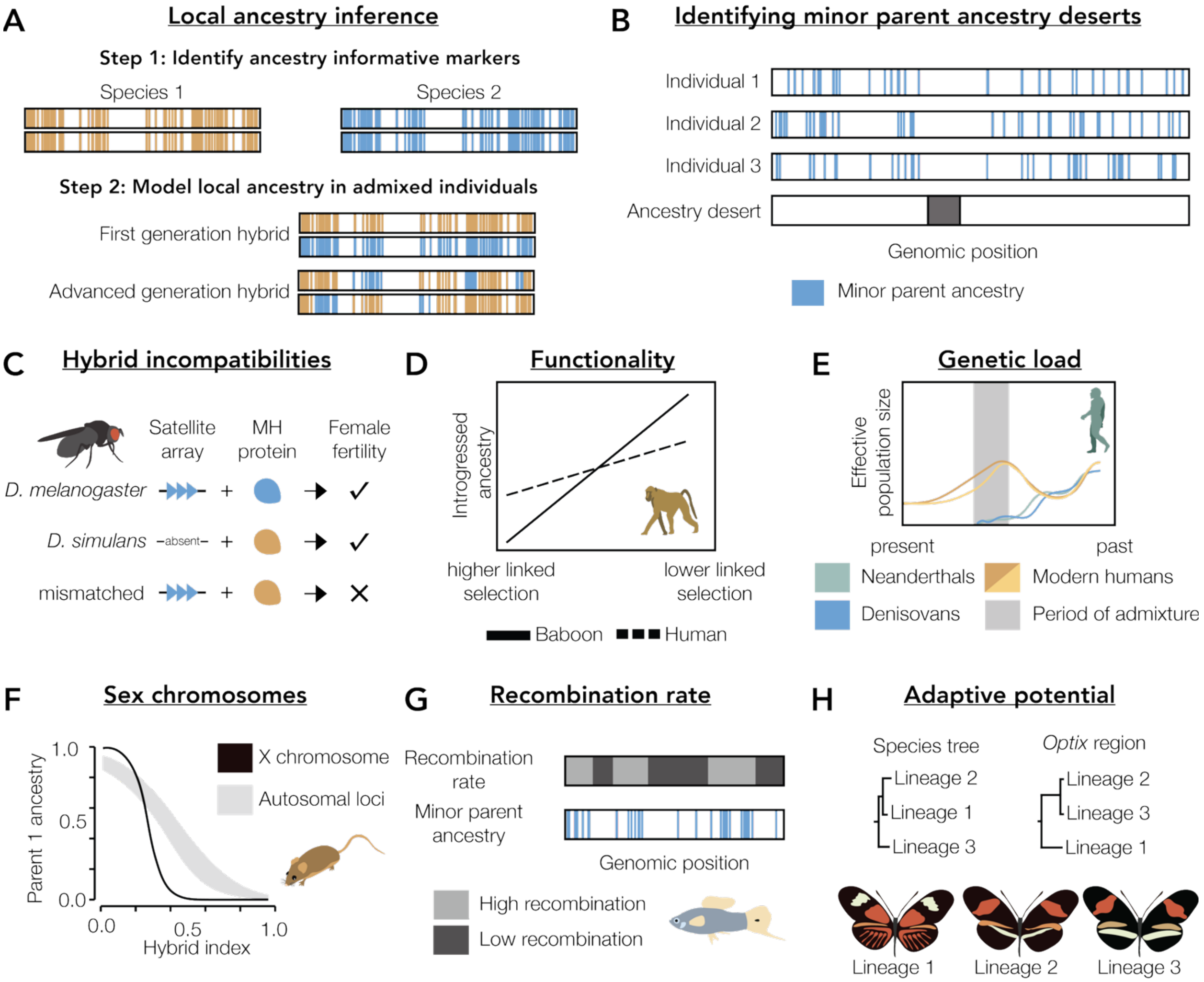

Figure 2: Local ancestry inference (A) has enabled researchers to use differences between parent species to quantify local ancestry of different genomic regions in hybrids. Using local ancestry inference, numerous studies have revealed that minor parent ancestry deserts (B), regions of the genome unusually depleted in minor parent ancestry, are common and emerge rapidly after hybridization (e.g. chromosome 3 in humans; (Chen et al. 2026). Research over the last decade has revealed several drivers of variation in local ancestry. (C) Hybrid incompatibility loci can locally limit introgression. Shown here is an example incompatibility: dysfunctional interactions between the MH protein and DNA satellites derived from different *Drosophila* species can result in increased ovarian cell death and reduced female fertility (adapted from (Brand & Levine 2022; Brand et al. 2026). (D) Baboons and humans have reduced minor parent ancestry in genomic regions enriched in functionally important features like coding-regions and regulatory regions (adapted from (Vilgalys et al. 2022). (E) If one parent species has had persistently reduced effective population sizes, that species is likely to harbor a higher genetic load. In hybrids, many linked deleterious alleles on these ancestry tracts can have large fitness impacts in hybrid offspring (as in Neanderthals; adapted from (Prüfer et al. 2014). (F) X-linked regions in the house mouse hybrid zone have narrower/steeper genomic clines than corresponding autosomal regions and resist introgression across species boundaries (adapted from (Janoušek et al. 2012). (G) Minor parent ancestry is depleted in regions of the genome

with lower local recombination rates in *Xiphophorus* fish (Schumer et al. 2018). (H) Introgression of minor parent ancestry is more likely if introgressed regions allow hybrids to have higher fitness in parental environments as with mimicry wing-patterning genes like *Optix* in *Heliconius* (Heliconius Genome Consortium 2012) which has a different evolutionary history than the species tree.

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Hybridization in Animal Evolution

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Supplemental methods:

We searched for article abstracts on PubMed related to hybridization using the ESearch utility from NCBI (https://eutils.ncbi.nlm.nih.gov/entrez/eutils/). We searched for the following MeSH Terms on February 2nd, 2026: '(("Genetic Introgression"[MeSH Terms] OR "Hybrid Vigor"[MeSH Terms] OR "hybridization, genetic"[MeSH Terms] OR "Reproductive Isolation"[MeSH Terms]) AND "Animals"[MeSH Terms])'. For each article matching our search terms, we retrieved abstracts and publishing metadata using efetch from reutils v. 0.2.5 (https://github.com/gschofl/reutils) and xml2 v. 1.5.2 in R v. 4.5.0. Our search yielded 12,282 total results, and of these, 9,257 PubMedIDs had corresponding abstracts. We used gnfinder v1.1.6 (Mozzherin et al. 2024) to search titles and abstracts for candidate scientific names corresponding to the GBIF species backbone (Telenius 2011). We divided the identified scientific names into two lists: (1) those with good matches to the GBIF species backbone and (2) those that were not confidently identified in GBIF because of an abbreviated genus name. To identify the genera that most likely corresponded to the abbreviated genera in the second set of scientific names, we used the first list of scientific names with good matches to GBIF to generate a list of known genera mentioned in each abstract. We filtered the list of abbreviated scientific names for common words that were not part of the identified scientific names and then we identified the best genus match for each abbreviated scientific name using the candidate genera identified from the good matches list. We identified the most likely genus and species name combination using the name_backbone_checklist function in rgbif v 3.8.4 (Chamberlain et al. 2025) and kept only “EXACT” and “VARIANT” matches. Following abbreviation replacement, we merged our two sets of scientific names, removed scientific names corresponding to non-animal taxa, and removed duplicate entries within each abstract at the genus, class, and phylum level separately.

For each unique species in the dataset, we pulled occurrence records from rgbif using occ_count and restricted records to those with occurrenceStatus = "PRESENT" and hasGeospatialIssue = FALSE. We counted the number of countries with occurrence records for each species and recorded the top two countries by occurrence count for each species. We eliminated widely distributed species based on two criteria (1): species with occurrences in more than 50 countries or (2) species where the proportional difference in occurrence number between the top two countries was less than 0.25. For each species in each abstract, we identified the country with the highest number of occurrence records (i.e., the top country) and visualized the log-transformed counts of the top countries across all abstracts using the world map in the rnaturalearth v. 1.2.0 package (Massicotte et al. 2026).