The Role of Hybridization in Species Formation and Persistence

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Hybridization, or interbreeding between different taxa, was traditionally considered to be rare and to have a largely detrimental impact on biodiversity, sometimes leading to the breakdown of reproductive isolation and even to the reversal of speciation. However, modern genomic and analytical methods have shown that hybridization is common in some of the most diverse clades across the tree of life, sometimes leading to rapid increase of phenotypic variability, to introgression of adaptive alleles, to the formation of hybrid species, and even to entire species radiations. In this review, we identify consensus among diverse research programs to show how the field has progressed. Hybridization is a multifaceted evolutionary process that can strongly influence species formation and facilitate adaptation and persistence of species in a rapidly changing world. Progress on testing this hypothesis will require cooperation among different subdisciplines.

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The origin of species and the role that "hybridization" plays in it has been of significant interest in evolutionary biology throughout the years. Hybridization is now recognized to be widespread in nature (Whitney et al. 2010; Shurtliff 2013; Taylor and Larson 2019; McEntee et al. 2020) and modern genomic methods have revealed that ancient hybridization (Box 1),[17] and subsequent "introgression" or "gene flow," has been prevalent during the evolution of many taxa (Sankararaman et al. 2014; Irisarri et al. 2018; Suvorov et al. 2022). Because "reproductive isolation" typically takes a long time to build up (Coyne and Orr 2004; Dopman et al. 2023) relative to the rate of geographic range change, there are opportunities for species to hybridize throughout much of their evolutionary history (Fig. 1A). Such hybridization can have important evolutionary consequences, for example, facilitating reinforcement selection for assortative mating (Dobzhansky 1937b; Yukilevich et al. 2023), weakening or removing these barriers to gene flow (Behm et al. 2010; Kearns et al. 2018), producing novel phenotypes (Rieseberg et al. 1999a), permitting the evolution of new independent evolutionary lineages (Olave et al. 2022), or facilitating adaptive radiations (Seehausen 2004).

The term hybridization is often reserved for mating between species. However, the boundary between diverging populations and species is often unclear, such that it is more useful to discuss hybridization as gene flow between genetically distinct lineages (Barton and Hewitt 1985). We introduce the topic to readers new to the field by identifying recent advances that are consistent across organisms and outline open questions that deserve future attention.

THE PROBABILITY OF HYBRIDIZATION

The probability of hybridization can be predicted based on divergence to some extent (Roux et al. 2016). Coyne and Orr (1989) found a positive correlation between genetic divergence and strength of reproductive isolation among *Drosophila* species. Numerous comparative studies in insects (Sánchez-Guillén et al. 2014), amphibians (Sasa et al. 1998; Pereira and Wake 2009), fishes (Bolnick and Near 2005; Stelkens et al. 2010), birds (Price and Bouvier 2002), mammals (Adavoudi and Pilot 2021), and angiosperms (Moyle et al. 2004) show similar patterns. However, the strength of this correlation is complicated by effects of sex determination (Stöck et al. 2021), sexual selection (Rosenthal 2013), sexual conflict (Martin and Hosken 2003), and mating system (selfing vs. outcrossing species; Pickup et al. 2019), among other factors. For example, plants have been suggested to hybridize at greater levels of genetic divergence than animals possibly because they are able to self-fertilize and become allopolyploids (Chapman and Burke 2007). Meta-analyses including systems with different mating and sex-determination systems are needed to elucidate how these factors impact the relationship between divergence and probability of hybridization.

"Hybrid zones" are narrow regions in which individuals of genetically distinct groups meet, mate, and produce offspring of mixed ancestry (Harrison 1990). Hybridization often occurs in areas of inferred secondary contact, especially at the edges of biogeographical regions (e.g., coral reef fishes [Hobbs and Allen 2014]) or at biogeographic barriers (e.g., Amazon River [Rosser et al. 2021]). Geographic areas where many species form hybrid zones, so-called suture zones (Remington 1968; Hewitt 1988), have been attributed to contact between lineages expanding out of Pleistocene refugia in Europe (Hewitt 2001), North America (Anderson 1953), and Australia (Moritz et al. 2009). These geographic areas provide an invaluable glimpse into the speciation process, as pairs of taxa that differ in life history traits (e.g., dispersal rate, generation time) interact in the same extrinsic environment (e.g., age and location of the suture zone).

Human-altered areas are also potentially more prone to hybridization. Habitat perturbation increases the chance of hybridization (e.g., due to lack of mate choice opportunities if population densities are low [Rohde et al. 2015]), removal of physical or ecological barriers, or

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[17] Descriptions of text in quotes are listed in the Glossary (Box 1).

BOX 1. GLOSSARY

- Admixed—when contributions to the genome are from multiple genetically distinct ancestral populations.
- Allopolyploid hybrid speciation—speciation by hybridization, where the new lineage has doubled the chromosome number by combining chromosomes from the two parental species.
- Epistasis—functionally interacting alleles, such that their combined fitness deviates from linearity or additivity.
- Gene flow—transfer of genes between populations (Slatkin 1985) following individual migration between populations at any level of divergence. Gene flow between different taxa (populations, subspecies, or species) is synonymous with introgression.
- Genetic architecture—the underlying genetic basis of a particular trait referring to the number, genomic locations, effect size, and interaction of genetic variants that contribute to the phenotype.
- Homoploid hybrid speciation, combinatorial speciation—hybrid speciation without increase in ploidy.
- Hybrid species—lineage that arose due to hybridization between two (or more) species and that is reproductively isolated from parental species (Grant 1981).
- Hybrid vigor and heterosis—when hybrids (or more heterozygous genotypes) are fitter than their parents (or more homozygous genotypes).
- Hybrid zone—narrow geographic regions in which genetically differentiated populations with parapatric distribution meet, mate, and produce at least some offspring of mixed ancestry (Harrison 1990).
- Hybridization—reproduction between genetically distinct populations producing offspring of mixed ancestry (Barton and Hewitt 1985).
- Introgression—incorporation of alleles from one population from another distinct, population via hybridization (Anderson 1953).
- Linkage disequilibrium—nonrandom association of alleles from two or more loci on haplotypes (Haldane 1919; Lewontin and Kojima 1960).
- Reproductive barriers—behavioral, ecological, temporal, mechanical, or intrinsic (e.g., inviability or sterility of hybrids) barrier that reduces or prevents gene flow between taxa. Some researchers use the term *incompatibility* to refer to all these barriers (as referred to in this article), while other authors use incompatibility to exclusively refer to intrinsic incompatibilities resulting from gene–gene coevolution.
- Reproductive isolation (RI)—reduction in potential gene flow between populations caused by barriers to gene flow (Stankowski and Ravinet 2021). The term is used and measured in different ways by different researchers (Westram et al. 2022).
- Speciation continuum—definitions differ among researchers (Stankowski and Ravinet 2021), but in general the speciation continuum is a concept that acknowledges that speciation is a continuous process, not a single, sudden event.
- Transgressive segregation—quantitative traits in segregating hybrid populations where phenotypes are extreme relative to those of both parental lines (Rieseberg et al. 1999a).

loss of ecological niches (Vonlanthen et al. 2012). Human-assisted movement of species (e.g., for trade or cultivation) also provides many new opportunities for hybridization. In some cases, hybridization between introduced and native species leads to invasive hybrid line-

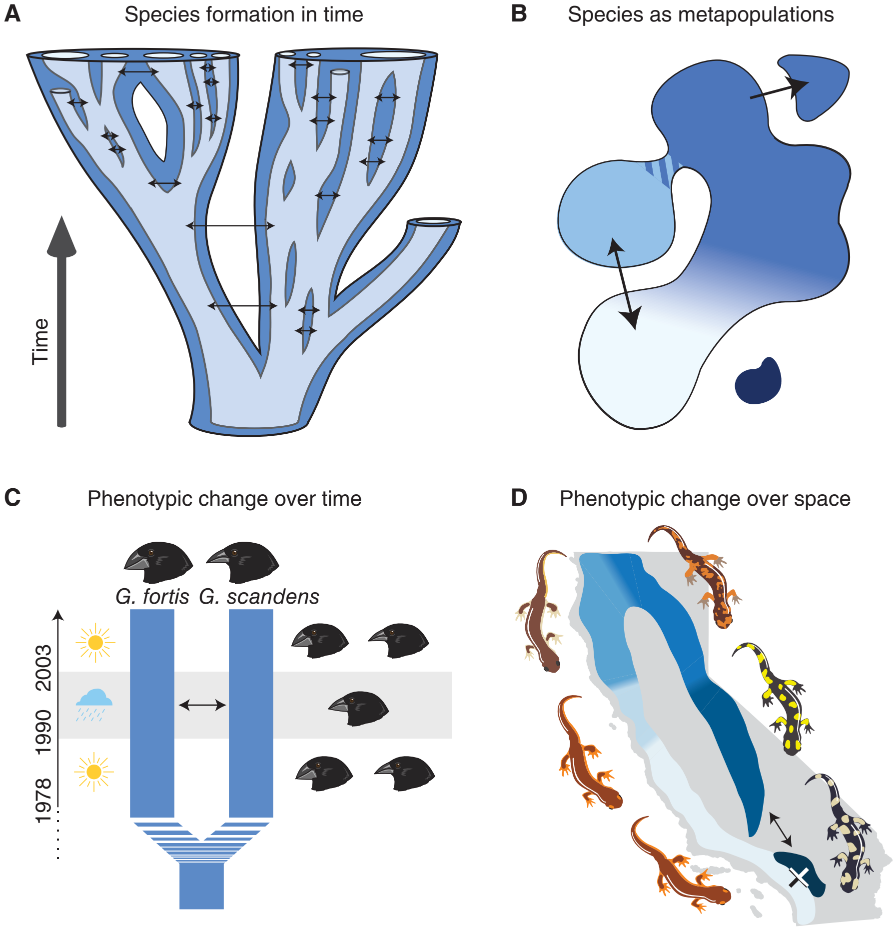

Figure 1. Hybridization over space and time. (*A*) Populations (light blue) and arbitrary species (dark blue) splitting and merging through time with gene flow (black arrows). (*B*) Different shades of blue represent genetically distinct populations with differing degrees of connectivity and gene flow across space. (*C*) An empirical example where rate of hybridization and survival of hybrids varies across *Geospiza fortis* and *Geospiza scandens* system (Grant and Grant 2008). The sun and clouds represent periods of drought and rainfall. The arrow depicts gene flow during the period of rainfall. (*D*) An empirical example of phenotypic change and degree of reproductive isolation among parapatric populations of the salamander *Ensatina eschscholtzii* ring species in California (Pereira and Wake 2009). The "X" between the southern populations represents rare or no hybridization.

ages (Abbott and Lowe 2004; Ainouche et al. 2004; Fitzpatrick et al. 2010), providing exciting systems to understand the genetic basis of adaptation and invasiveness.

The probability of hybridization and persistence of hybrids can also be affected by the ecological context. For instance, "homoploid hybrid speciation," stable hybrid populations, and radiation of hybrid lineages are all more common if new niches exist that are unoccupied by either parental species (Moore 1977; Rieseberg et al. 2003; Meier et al. 2017a; DiVittorio et al. 2020). Allopolyploid hybrids or "hybrid species" are hypothesized to be common in extreme habitats such as the arctic (Brochmann et al. 2004), perhaps due to shielding against loss of genetic diversity in small, isolated populations.

The demographic context also affects the direction and degree of gene flow. If one species is expanding its range into that of another species, the invading species is likely to become more "admixed." This is because, at the expansion front, the invading species is less common leading to asymmetric backcrossing and gene flow toward the invasive species (Excoffier et al. 2009). Moreover, range expansions are predicted to lead to the accumulation of slightly deleterious mutations at the expansion front, and consequently to the purging of deleterious mutations following introgression of more beneficial variants (MacPherson et al. 2022), a hypothesis that needs empirical testing.

SPECIATION AND HYBRIDIZATION

During speciation, a reduction of free recombination and gene flow increases "linkage disequilibrium" (i.e., coinheritance) within the genome and between the traits defining taxa (Butlin 2005; Servedio 2009). Hybridization, on the other hand, combines divergent genomes and can either break up coadapted allele combinations (Barton 2001) or lead to novel adaptive allele combinations (Abbott et al. 2013; Marques et al. 2019; Runemark et al. 2019). Combinations containing both beneficial and deleterious alleles are created simultaneously upon hybridization, and the interplay between these will determine the overall fitness of hybrid genotypes (Kulmuni and Pamilo 2014; Pereira et al. 2014). Traits that cause low fitness in hybrids can contribute to maintenance of genetic distinctiveness of taxa by reducing gene flow between them. These are variously termed "reproductive barriers" or hybrid incompatibilities, and can be behavioral, ecological, temporal, mechanical, or genetic. The initial evolution of these traits is likely a by-product of divergence between parental taxa. However, some barriers may also accumulate via "reinforcement of mating isolation" (Dobzhansky 1937a) if strong selection favors a reduction in gene flow. The mechanisms by which barriers to gene flow arise and the order at which they accumulate are under intense research.

Underlying reproductive barriers are genomic regions referred to as *barrier loci*, *hybrid incompatibility loci*, or sometimes *speciation genes*. These loci hinder introgression at and around their genomic location. The common view of hybrid incompatibilities are as negative "epistatic" interactions between two or more loci. The classic Bateson–Dobzhansky–Muller incompatibility (BDMI) model postulates that derived alleles in one or more loci in one genomic background are incompatible with derived alleles from another genomic background, reducing the fitness of hybrids between them (Bateson 1909; Dobzhansky 1936; Muller 1942; Reifová et al. 2023). Although these authors initially described BDMIs as potentially being dependent or independent from the extrinsic environment, BDMIs have been more commonly treated as environment-independent (i.e., intrinsic incompatibilities). Examples include hybrid necrosis in plants (Bomblies and Weigel 2007), mitonuclear incompatibilities in mice (Ma et al. 2016), or hybrid male sterility in fruit flies (Masly and Presgraves 2007). In contrast, the term "ecological incompatibility" is reserved for coadapted alleles affecting traits that vary in fitness in recombinants in an extrinsic ecological context (see Thompson et al. 2023)—as in stickleback fishes (Arnegard et al. 2014). Assortative mating incompatibility describes incompatibility between the gene(s) underlying a given phenotypic mating trait and the gene(s) underlying the preference for that trait (see Merrill et al. 2023). These can evolve via the Fisherian runaway process of sexual selection, such as in morphologically and ecologically similar species of *Laupala* crickets (Xu and Shaw 2019), or via environment-dependent sensory drive selection, such as in ecologically divergent species of cichlid fishes (Seehausen et al. 2008b). Incompatibilities resulting from these different selective regimes may also differ in how they are expected to decrease fitness in consecutive generations of hybrids (Lindtke and Buerkle 2015). Multiple types of incompatibilities may be present, interacting, and evolving further in any given pair of taxa (Kulmuni and Westram 2017). Additionally, the "genetic architecture" (i.e., number, location, and overall fitness effects) of these incompatibilities will determine the overall degree of reproductive isolation (Bank et al. 2012; Ferris et al. 2017; Dagilis et al. 2019). More theoretical and empirical studies are needed to understand how incompatibilities arise, affect the evolution of other incompatibilities, and ultimately restrict gene flow.

Both speciation and hybridization occur in a variety of temporal and geographic contexts (Fig. 1). What we observe today may mask a history of populations merging and splitting in the past (Mallet et al. 2016; Abbott 2019; He et al. 2019; Peñalba et al. 2019). Divergent lineages can be lost due to extinction or absorption into another population (Zhang et al. 2019; Frei et al. 2022), and changes in selection, the environment or mating dynamics may affect these outcomes (Feder et al. 2003; Han et al. 2017; Nelson and Cresko 2018). Simplifying speciation into bifurcating lineages may lead to inaccurate reconstructions of evolutionary history, while estimates of historical gene flow may be spurious if the possibility of introgression from "ghost lineages" is ignored (Mallet et al. 2016; Barlow et al. 2018; Ottenburghs 2020; Tricou et al. 2022). Researchers are expanding their focus beyond the classical geographic modes of speciation (allopatry, parapatry, and sympatry) to incorporating demographic modes of speciation that allow quantifying periods of divergence with gene flow (Csilléry et al. 2010; Bradburd et al. 2016; Excoffier et al. 2021). We also often study hybridization between a pair of populations as representatives of the entire species. The reality may often be more complex, involving a network of multiple populations across the geography, some of which may hybridize with another taxon, whereas others do not (Fig. 1B). The variation in divergence and gene flow among the subpopulations within the metapopulation as well as the influence of a given allele on fitness in different ecological contexts, may play an important role in determining the evolutionary trajectory of any given lineage. Further development in analytical approaches is needed to be able to simulate more complex two-dimensional configurations containing multiple populations (Bradburd and Ralph 2019; Harvey et al. 2019).

INSIGHTS ABOUT SPECIES BOUNDARIES

Most evolutionary biologists, whether adopting phylogenetic, biological, recognition, or genotypic cluster concepts of species, agree that species boundaries in sexual taxa are maintained by some combination of barriers to gene exchange. Hybridization can reveal the genes and genetic architecture of traits that are relevant to species boundaries. As populations become increasingly reproductively isolated, hybridization can reveal how genomes differentiate and gene flow becomes restricted. Hybridization provides unique insight as it is often difficult to make inferences about barriers to reproduction when populations are diverging in isolation.

Hybrids as Windows into the Genetic Basis of Species Boundaries

When hybridization occurs, rates of introgression are expected to be heterogeneous along the genome, which allows one to identify genomic regions associated with species boundaries. Traditionally, most studies have used experimental hybrids to reveal the phenotypic or fitness effect of an introgressed genomic region in a foreign genomic background (Schumer et al. 2014a). However, this approach is limited to taxa amenable to laboratory culture, where organisms can be crossed over tens (e.g., flies [Masly and Presgraves 2007]) or hundreds of generations (e.g., yeast [Burke et al. 2014]). An alternative approach is to study taxa that hybridize in nature over a larger number of generations, increasing recombinant variation among incompatibility loci and linked neutral genomic regions (Turner and Harr 2014). Natural hybrids have the advantage of being subject to selection and recombination in an ecologically relevant setting, where multiple selective forces act simultaneously and interact (e.g., sexual selection, adaptation, and gene coevolution). While incompatibilities are expected to persist in hybrid zones, due to a balance between dispersal of parental gene combinations and selection against hybrid combinations, these incompatibilities can quickly be purged from hybrid populations that are geographically isolated from their parentals (Li et al. 2022), providing valuable systems to understand the genetic basis of hybrid breakdown and its recovery.

Hybridizing species provide important insights into the nature of selection acting on species boundaries that reduce gene flow between diverging taxa. For example, in sympatric birds (Toews et al. 2016; Turbek et al. 2021), butterflies (Merrill et al. 2019), and crickets (Xu and Shaw 2020), hybridizing taxa are maintained by divergent male signaling and female preferences between species, suggesting that sexual selection may have been involved in species formation (Svensson et al. 2017). Parapatric fish (Haenel et al. 2021), monkeyflowers (Stankowski et al. 2019), and sunflowers (Todesco et al. 2020) show that species or ecotypes can also be maintained by divergent selection coincident with environmental gradients, suggesting a role of ecological selection in species formation. Hybridizing mice (Turner and Harr 2014), weeds (Hämälä et al. 2017), and monkeyflowers (Fishman and Willis 2006) show low hybrid fitness in the form of sterility or reduced cognition, suggesting incompatible gene interactions are also important in species formation (Coughlan and Matute 2020). While strictly intrinsic incompatibilities can only manifest as postmating barriers, behavioral and ecological incompatibilities can act as both premating barriers (McKinnon et al. 2004), and as postmating barriers that reduce the reproductive fitness of hybrids (Gottsberger and Mayer 2007; Arnegard et al. 2014; Bay et al. 2017). The observation that alleles underlying behavioral (Seehausen et al. 2008b; Meier et al. 2017a), ecological (Lamichhaney et al. 2015; Martinez Barrio et al. 2016), and environment-independent intrinsic (Sicard et al. 2015; Fuller et al. 2018) incompatibilities can be older than the split between sister taxa suggest that all these types of incompatibilities may be present before the onset of speciation and may be segregating already in the ancestral population. (Xie et al. 2007; Roberts Kingman et al. 2021).

Hybridization and the Speciation Continuum

Traits and loci reducing gene flow between diverging taxa are expected to gradually accumulate or break down, leading to a continuum of reproductive isolation (Fig. 2; Stankowski and Ravinet 2021). Many population pair comparisons with varying degrees of reproductive isolation are needed to study a "speciation continuum" and understand how a single population can diversify into multiple species over time. The correlation between genetic divergence and the ability to exchange genes (as a proxy for reproductive isolation) across 61 taxa pairs at different stages of divergence suggests a gray zone of speciation where the likelihood of gene flow is rapidly reduced (Roux et al. 2016). The sigmoidal transition between unrestricted gene flow and its abolition is consistent with the idea of a tipping point (Nosil et al. 2017; Riesch et al. 2017; Peñalba et al. 2019). The nonlinear time course has been referred to as a snowball of hybrid incompatibility (Orr 1995; Matute et al. 2010; Moyle and Nakazato 2010; see also literature on coupling by Aubier et al. 2023; Dopman et al. 2023; Ritchie and Butlin 2023). This pattern also suggests that species that have not accumulated sufficient barriers to gene flow may be ephemeral and fuse back into single lineages (Rosenblum et al. 2012; Frei et al. 2022). However, the dynamics of incompatibilities is challenging to study across taxa and there is ongoing debate about the generality of tipping points in speciation (Barton and de Cara 2009). The theoretical expectation of nonlinear patterns of barrier accumulation do not hold, for example, when species emerge from hybrid populations and incompatible gene interactions emerge from sorting of standing variation (see sections below; Marques et al. 2019).

Wu (2001) suggested that speciation can be illustrated as a series of stages of divergence, depicting how genome-wide differentiation and linkage disequilibrium may build up (Fig. 2). In this simplified hypothesis, gene flow is unrestricted in a panmictic ancestral population, is increasingly restricted as more genes are involved in reproductive barriers, and becomes zero when reproductive isolation is complete (see stages in Fig. 2F). Empirical studies have now clarified that the transition between these stages of divergence might be very fast for sympatric radiations and that stages can

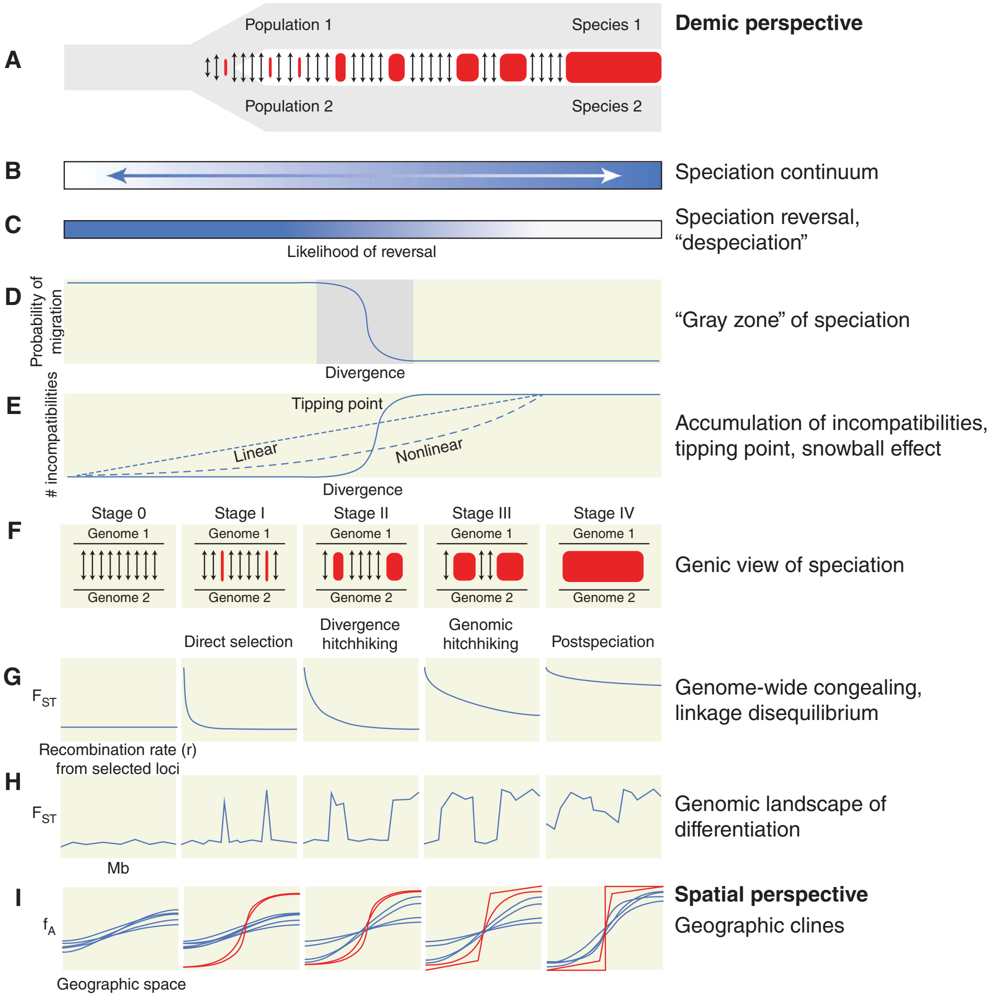

Figure 2. Alternative conceptual depictions of the speciation continuum. There is no implied progression from left to right as populations can move in either direction or stage. (*A*) The demic perspective assigns individuals in one of two demes, which are assumed in panels. (*B*) The speciation continuum depicts continuous variation in degree of reproductive isolation (RI) with arrows indicating that this is not necessarily unidirectional (Stankowski and Ravinet 2021). (*C*) The likelihood of speciation reversal may depend on the number, type, and strength of reproductive barriers and may be narrower than the continuum of RI (Seehausen et al. 2008a; Lowry 2012). (*D*) The gray zone of speciation depicts a narrow range of genetic divergence over which populations transition rapidly between high and low likelihood of gene flow (Roux et al. 2016). (*E*) Hypothetical trajectories reflecting the onset and rate of accumulation of incompatibilities during speciation, which may include both intrinsic (Orr 1995; Yamaguchi and Iwasa 2017) and extrinsic incompatibilities (Nosil et al. 2017). (*F*) The genic view of speciation describes the speciation process in hypothetical stages where gene flow is initially restricted by few loci under selection, followed by restricted gene flow of linked neutral loci until the entire genome is restricted (Wu 2001). (*G*) Increasing linkage disequilibrium among loci under divergent selection is a result of reduction in gene flow, which affect more and more weakly linked loci until the entire genome has restricted gene flow (Feder et al. 2012). (*H*) Levels of gene flow are visualized via the genomic landscape of divergence. The assumption is that with low RI, elevated divergence is localized only at loci under divergent or incompatibility selection, but the affects on neighboring neutral loci becomes apparent with higher levels of RI. The bumpy landscape shows stochasticity due to recombination landscape, linked selection, and demography (Ravinet et al. 2017; Wolf and Ellegren 2017). (*I*) The spatial perspective is an alternative to the demic perspective. Geographic cline analyses show the change in allele frequencies across the transition between a single continuous population to a parapatric pair. Prior to divergent selection, loci may reflect only isolation by distance. Then, only loci under direct selection would show steep clines (red). As more linked neutral loci (blue) are also restricted in gene flow, clines become narrower (Endler 1977).

also follow a reversed order when homogenizing gene flow leads to breakdown of reproductive barriers and ephemeral species revert to a stage of panmixia (Fig. 1A; see references above). Although presented as such, these stages are not discrete occurrences in nature but rather used as a model to frame the different roles evolutionary processes are playing at each stage. One can divide the speciation process in various ways but what is important is to emphasize is what processes are being studied and why they are relevant for a particular speciation event.

ADAPTIVE AND DIVERSIFYING OUTCOMES OF HYBRIDIZATION

Hybridization had long been seen as unimportant in evolution or actively detrimental to biodiversity through the breakdown of species boundaries (Mayr 1942, 1963; Coyne and Orr 2004). Botanists often dissented from this view and recently zoologists' perspectives have also begun to change (Mallet 2008). Although it is known that in some cases hybridization can contribute to biodiversity via reinforcement of reproductive barriers (see Yukilevich et al. 2023) and hybrid speciation, it is unclear whether this is a frequent outcome. Here, we focus on how hybridization can reshuffle existing genetic variation into novel combinations, thereby adding variation faster than that produced by de novo mutation, and so providing novel phenotypes upon which selection can act (Seehausen 2004; Mallet 2007; Arnold et al. 2008; Hedrick 2013; Marques et al. 2019; Nieto Feliner et al. 2020; Kulmuni et al. 2023). We discuss how selection can act on novel phenotypic combinations in hybrid individuals and the potential outcomes of this for populations or species. We then highlight how this may lead to bursts of phenotypic diversity through adaptive radiation and how this diversification can persist over evolutionary timescales.

Transgressive Segregation in Phenotype and Gene Expression in Hybrid Individuals

Hybridization can lead to novel phenotypes that do not exist in parental taxa. Novel phenotypes are classified as "intermediate" relative to parental species (Rieseberg et al. 1993; Thompson et al. 2021), or as "transgressive" when they occur outside the variation found in either parental species (Slatkin and Lande 1994; Rieseberg et al. 1999b, 2003; Parsons et al. 2011; Lamichhaney et al. 2018; Meier et al. 2019). Plant breeders have long relied on hybridization and selective breeding of transgressive phenotypes to obtain varieties of crops with desired extreme traits. In an evolutionary context, "transgressive segregation" can give rise to new ecotypes or species when extreme traits allow hybrid lineages to establish in ecological niches where parental species cannot survive (Arnegard et al. 2014; Selz and Seehausen 2019; Chhina et al. 2022; Schluter and Rieseberg 2022). Speciation through transgressive segregation in ecologically relevant traits occurs in plants such as *Helianthus* (Lexer et al. 2003; Rieseberg et al. 2003; Owens et al. 2023), *Senecio* (Wong et al. 2022), and *Arabidopsis* (Clarke et al. 1995), but also in animals such as in the cichlid adaptive radiation (Seehausen 2004; Kagawa and Takimoto 2018). Moreover, transgression in mating traits can lead to speciation through sexual selection on novel traits (Kagawa et al. 2023).

Transgression in F1 hybrids was found in 20% of the crosses in a meta-analysis (Thompson et al. 2021). Transgression is most common in polygenic traits, and can be caused by heterosis, which masks deleterious mutations in heterozygous sites, a phenomenon seen in early generation hybrids (Rieseberg et al. 1999a; Kagawa and Takimoto 2018). Alternatively, complementary gene action and "epistasis" resulting from recombination of homozygous parental alleles into novel combinations can also cause transgression, an effect that persists in later generation hybrids (Rieseberg et al. 1999a; de Los Reyes 2019; Fraser 2020). Studies with later generation hybrids and recombinant inbred lines are useful to distinguish between these mechanisms and assess the evolutionary significance of transgression (Pereira et al. 2014). The amount of transgression is expected to increase either with genetic distance or (counterintuitively) phenotypic similarity between parental taxa (Stelkens and Seehausen 2009; Stelkens et al. 2009). The genetic architecture of traits can constrain or promote transgression and trait evolvability (Albertson and Kocher 2005; Parsons et al. 2011). For instance, polygenic traits under stabilizing selection in parental populations are likely to be transgressive in F2 progeny (Fraser 2020).

Misregulation of gene expression in early generation hybrids is known to contribute to barriers to gene exchange in, for example, *Drosophila*, sunflowers, mice, and pupfish (Landry et al. 2007; Renaut et al. 2009; Civetta 2016; Larson et al. 2017; Mack and Nachman 2017; McGirr and Martin 2020; Smith et al. 2021). Transgressive gene expression has also been documented in stabilized homoploid hybrid species of both animals and plants (Hegarty et al. 2008; Papoli Yazdi et al. 2022), and novel combinations of divergent regulatory elements in hybrids have resulted in novel phenotypes (Pavey et al. 2010; Singh and Ahi 2022). Hybridization has also been suggested to deregulate selfish genetic elements, such as transposable elements (TEs), resulting in TE insertions during meiosis, increased TE abundance, or higher levels of TE transcripts (Ungerer et al. 2006; Dion-Côté et al. 2014; Hénault et al. 2020; but see Göbel et al. 2018). Accumulation of TEs can cause genome rearrangements and destabilize the genome (Serrato-Capuchina and Matute 2018), alter regulatory networks (Feschotte et al. 2002), or suppress the expression of genes located close to TEs (Whisson et al. 2012). The extent to which novel combinations of regulatory elements and genomic rearrangements can alter patterns of gene expression in hybrids, and how these novel phenotypes can be favored by selection will be an exciting focus for future research.

Adaptive Introgression

Introgression can contribute to adaptation by transferring favored variants between populations. The rate of adaptive introgression is influenced by presence of adaptive variation within structural rearrangements (e.g., inversions), by local recombination rates across the genome (Kim and Rieseberg 1999), and by the presence of genetic incompatibilities that counteract gene flow (Runemark et al. 2019; Moran et al. 2021). For instance, introgression from Denisovans into modern humans of variant alleles enhanced hypoxia resistance in Tibetan people living in high altitudes (Huerta-Sánchez et al. 2014).

In some instances, species shift into novel environments occupied by a preadapted sister species, favoring adaptive introgression from the resident to the newly arriving species (Sánchez-Guillén et al. 2016). For example, an increase of invasiveness of the sunflower *Helianthus annuus* resulted from introgression (Yatabe et al. 2007). In mammals, a rodenticide resistance allele introgressed from *Mus spretus* into *Mus musculus domesticus* (Song et al. 2011). In amphibians, there is evidence for adaptive introgression from an invasive species of salamander into a threatened native species, following human-mediated introductions (Fitzpatrick et al. 2010). In insects, an insecticide resistance allele from *Anopheles coluzzi* introgressed into *Anopheles gambiae* malaria mosquitoes (Norris et al. 2015), and alleles encoding locally favored mimetic color patterns introgressed between multiple species of *Heliconius* butterflies (Heliconius Genome Consortium 2012). Adaptive introgression thus appears to be fairly common and facilitates adaptation and persistence of species in changing environments, but more work is needed to understand when hybridization and subsequent introgression may accelerate speciation.

Hybrid Speciation, the Combinatorial View, and Adaptive Radiations

Hybrid speciation refers to the evolution of a new species from a population formed by hybridization between two pre-existing species. Hybrid speciation thus leads to a net gain in species, while adaptive introgression does not. Hybrid speciation requires emergence of reproductive isolation between the population of hybrid origin and its parental species, which can arise as a direct consequence of admixture. However, because it is very difficult to convincingly show that it was admixture that led to reproductive isolation to both parentals, only a few cases of hybrid speciation are accepted by the strictest definitions (Mallet 2007; Mavárez and Linares 2008; Schumer et al. 2014b). The combination of parental genetic variants may lead to reproductive isolation either because they result in adaptation to a novel ecological niche where parental taxa cannot survive (Rieseberg et al. 2003), or because they result in intrinsic incompatibilities between the hybrid species and both parental species (Hermansen et al. 2014).

In "allopolyploid hybrid speciation," hybridization is followed by chromosome doubling, potentially leading to almost immediate reproductive isolation of hybrid species. This mode of speciation is commonly observed in plants (for review, see Hegarty and Hiscock 2005; Soltis et al. 2014). In contrast, homoploid hybrid speciation (i.e., without chromosome doubling) is more difficult to detect as it is difficult to disentangle from introgression. Advances in genomics have allowed us to sequence more species and larger portions of each genome, revealing new instances of homoploid hybrid speciation that were not apparent from phenotype alone. Among the most widely accepted examples for homoploid hybrid speciation are in plants (e.g., genus *Helianthus* [Rieseberg et al. 1995 but see Owens et al. 2023], yeast [Greig et al. 2002; Leducq et al. 2016], *Heliconius* [Jiggins et al. 2008; Edelman and Mallet 2021], *Amphilophus* [Olave et al. 2022, and *Rhagoletis* Schwarz et al. 2005]).

Reassembly of old variants into new combinations, "combinatorial speciation," can give rise to a radiation of diverse, ecologically differentiated species, each constituting a mosaic of parental lineages both genetically and phenotypically (Seehausen 2004; Kagawa and Takimoto 2018; Marques et al. 2019). These new allelic combinations can take rapid advantage of multiple empty niches resulting in a burst of phenotypic diversity that persists as discrete species emerging from an initial hybrid swarm (Fig. 3). For example, the silversword alliance was seeded by admixture giving rise to an allopolyploid radiation on the Hawaiian archipelago (Barrier et al. 1999). Hybrid swarm origins have also been implicated in the rapid radiations of Lake Victoria region cichlid fishes (Meier et al. 2017a), Caribbean pupfishes (Richards et al. 2021), and munia birds (Stryjewski and Sorenson 2017). After new or empty niches are filled by this initial burst, species radiation can continue through more isolated cases of adaptive introgression or hybrid speciation generating even more phenotypic novelty that may persist as new species (Seehausen 2004; Fig. 3). For instance, species within the radiation of Darwin's finches likely persisted through multiple cycles of fusion and fission (Fig. 1C; Grant and Grant 2008; Han et al. 2017; Rubin et al. 2022). Cyclical shifts in predatory landscape and haplotype diversity fueled by hybridization facilitated the radiation of *Daphnia* in northwest European lakes (Spaak and Hoekstra 1997; Gießler et al. 1999).

PREDICTABILITY OF HYBRIDIZATION OUTCOMES

Despite the often-unpredictable nature of evolution, some predictable patterns of hybridization seem to be emerging. In this section we focus on areas of recent research. Several well-known patterns, like Haldane's rule (Haldane 1922; Orr 1997) and the large X-effect (Dobzhansky 1937b; Coyne and Orr 2004; Payseur et al. 2018; Fraïsse and Sachdeva 2021) are discussed more thoroughly in another article in this collection (Reifová et al. 2023). Growing access to genomic data has now revealed new general patterns very likely driven by the interplay between various selective pressures and recombination. These emerging predictable evolutionary outcomes are discussed below.

Predictability of Introgression at the Genomic Level

When divergent genomes are recombined in hybrids, multiple selective pressures are expected to operate in concert, which can lead to some predictable patterns of admixture. One recently discovered pattern is that recombination rate tends to be positively correlated with the fraction of introgressed alleles in a genomic region

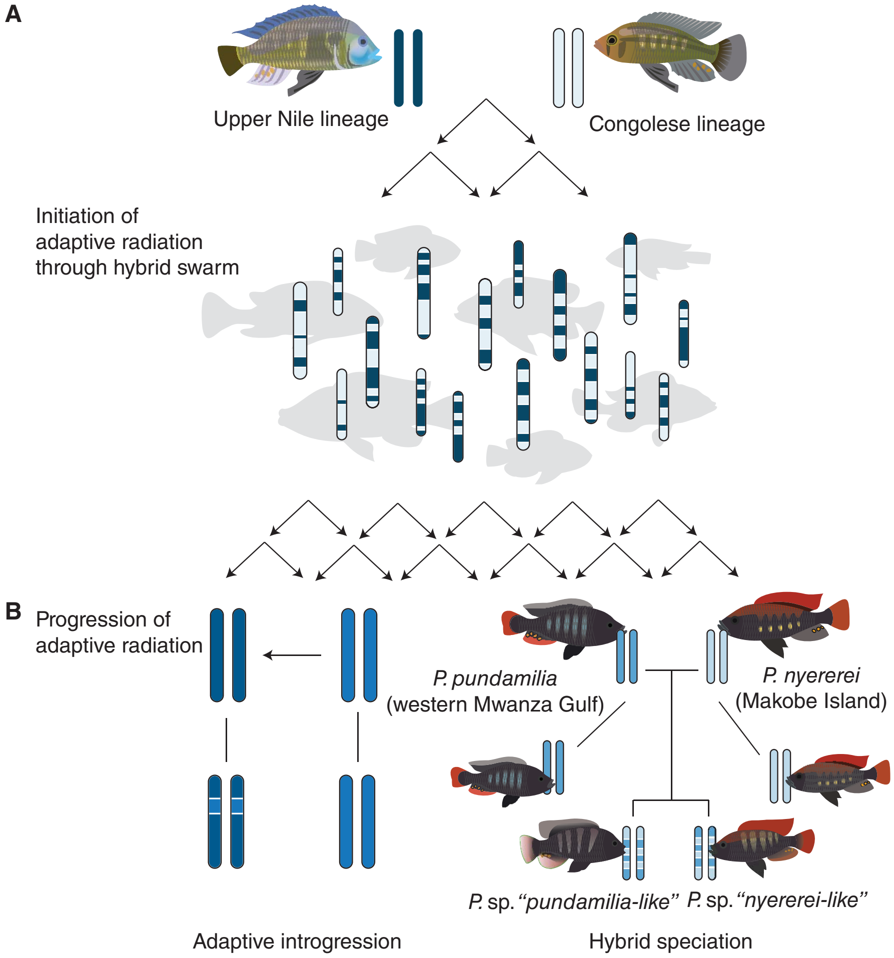

Figure 3. Hybridization can facilitate adaptive radiation. Admixture variation from distantly related species can fuel (*A*) the onset of adaptive radiation, whereby a genetically diverse hybrid swarm gives rise to ecologically diverse species that constitute different genomic mosaics of the parental lineages. The downward pyramids of arrows depict multiple generations of hybridization; and (*B*) the continuation of adaptive radiation, whereby loci affecting ecological adaptation and assortative mating are exchanged and recombined to form novel trait combinations. This can occur through adaptive introgression where a novel trait emerges in one species due to gene flow from another or through hybrid speciation (Meier et al. 2017b) where admixed lineages with new combinations of parental alleles evolve into separate species.

(Nachman and Payseur 2012; Schumer et al. 2018; Leitwein et al. 2019; Martin et al. 2019; Dreissig et al. 2020; Calfee et al. 2021; Duranton and Pool 2022). This correlation is believed to be caused partly by linked selection: if incompatibilities are multilocus and scattered evenly around the genome, selection against incompatible alleles tends to purge larger blocks of linked neutral alleles where recombination rate is low. Recent theory suggests that another important factor is the reduction of ancestry variance due to recombination in later hybrid generations. Due to large variance in fitness, deleterious multilocus variation is removed more effectively in large blocks soon after introgression, rather than later, when recombination already has reduced ancestry variance and therefore reduced variance in fitness (Veller et al. 2023). An interesting corollary prediction is that species with many chromosomes, such as humans, and therefore high genome-wide average recombination rates, will purge deleterious introgressed variation less quickly than species with few chromosomes, like *Drosophila* (Veller et al. 2023). However, an opposite pattern has sometimes been shown where there is more introgression in low recombining regions (Duranton and Pool 2022), a signal that could arise if selection favors introgression. Expectations about the correlation between recombination rate and introgression are still mixed, and more work is needed to clarify the topic.

A second pattern that is beginning to emerge is that, when one of the hybridizing species has a smaller effective population size N_e, that species is more likely to fix slightly deleterious alleles due to genetic drift. As a result, the species with the smaller N_e tends to be a recipient of introgression, rather than a donor. Upon hybridization, deleterious alleles can be purged by introgression of beneficial alleles from the species with larger N_e (Harris and Nielsen 2016; Schumer et al. 2018; Nouhaud et al. 2022).

In a third pattern, when incompatibilities are strong, they will be purged and homospecific allele combinations fixed at the incompatible loci. For example, introgression tends to be rare at nuclear-encoded mitochondrial-localized genes. Due to the uniparental inheritance of mitochondria, heterospecific combinations of nuclear-encoded mitochondrial proteins and mitochondrial-encoded proteins can become incompatible (Barr and Fishman 2010; Trier et al. 2014; Chang et al. 2015; Gaborieau et al. 2016; McFarlane et al. 2016; Shipley et al. 2016; Pereira et al. 2021). Heterospecific combinations of these proteins may lead to suboptimal respiration (McFarlane et al. 2016; Shipley et al. 2016; Wagner et al. 2020). Thus, selection tends to favor homospecific combinations, purging the mismatched allele even if it comes from the species contributing the majority of genomic DNA (Runemark et al. 2018).

Allelic effect size, pleiotropy, and past selective regimes can also affect the likelihood of introgression. If hybrid fitness is low, only alleles under very strong positive selection can cross species boundaries. For example, many known cases of adaptive introgression involve herbicide or pesticide resistance where the introgressed alleles have major effects on survival (Whitney et al. 2006; Heliconius Genome Consortium 2012; Clarkson et al. 2014; Valencia-Montoya et al. 2020). In humans, genomic regions associated with gene expression are purged from archaic introgression, suggesting that altered gene regulation had deleterious effects on the phenotype (Telis et al. 2020; Vilgalys et al. 2022). The purging is most pronounced for highly pleiotropic enhancers (Telis et al. 2020). In hybridizing ants, haplotypes with signatures of past positive selection are more likely to fix in hybrids (Nouhaud et al. 2022) and due to various selective pressures acting in concert genome evolution after hybridization is repeatable across natural population replicates (Fig. 4). In early generation hybrids, introgressed loci will be embedded within large haplotype blocks and the rate of introgression of these blocks will depend on the balance between beneficial and deleterious alleles within the block (Sachdeva and Barton 2018).

Predictability of Hybridization Outcomes at the Level of Fitness

Long-term outcomes of hybridization depend on overall fitness of hybrids. Early generations of hybridization tend to show the strongest hybrid breakdown (Bank et al. 2012). Dominant incompatibilities will appear in the F1 generation, while recessive incompatibilities will become exposed to natural selection in later hybrid generations (Reifová et al. 2023). If incompatibilities are strong and do not have an ecological component they are expected to be purged early (Bank et al. 2012). Incompatibilities are purged from *Tigriopus* copepod recombinant inbred lines in a few generations of recombination, which then recover fitness on par with parents (Pereira et al. 2014). However, in some cases, incompatibilities are environment-dependent so that hybrids experience a reduced fitness in one environment but not in another (Arnegard et al. 2014; Kulmuni et al. 2020; Thompson et al. 2022). For example, in yeast, 24% of viable cross-

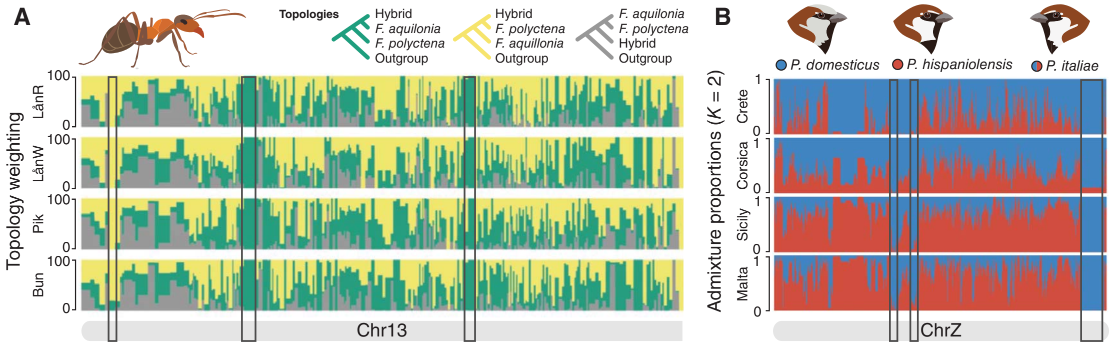

Figure 4. Examples of predictable genomic patterns after hybridization. Dark gray squares highlight specific regions where repeatability is qualitatively observed. (*A*) Hybridization between wood ants *Formica aquilonia* and *Formica polyctena* has led to correlated patterns of ancestry from the parental species across the genome in four independent hybrid lineages: LånR, LånW, Pik, and Bun. As an example, we show the first half of Chromosome 13, but similar correlated patterns of ancestry are found across the genome (Nouhaud et al. 2022). (*B*) Repeated instances of hybridization between the house sparrow (*Passer domesticus*; to the *left* in the row) and the Spanish sparrow (*Passer hispaniolensis*; *middle*) led to the generation of hybrid lineages (called the Italian sparrow, *Passer italiae*; *right*) on four Mediterranean islands. Here, ancestry is illustrated as a sliding window admixture assignment. While the lineages differ in overall contribution from each parent species, some genomic regions are inherited from the house sparrow in all four lineages as seen above. In these regions, there is an enrichment of mitonuclear genes and DNA-repair genes (Runemark et al. 2018).

es become deleterious when tested in another environment (Hou et al. 2015). Hybrid fitness has often been measured in the environment of the parental species, where hybrids may suffer from inviability or sterility relative to parental species (Coyne and Orr 2004). However, in a novel environment, hybrids may even enjoy a fitness advantage compared with parental species in spite of intrinsic incompatibilities (Kulmuni et al. 2023). The extent of hybrid unfitness and hybrid breakdown is broadly correlated with the degree of genetic differentiation. Yet, yeast can produce viable F1 hybrids even between species with 10%–20% nucleotide divergence (Brice et al. 2021) and even though many F2 hybrids are inviable, some persist (Stelkens and Bendixsen 2022). “Hybrid vigor” (heterosis), in contrast, is expected between less differentiated lineages and is dependent on the extent to which hybridization breaks down beneficial or deleterious parental allele combinations (Dagilis et al. 2019). Heterosis across many hybrid classes (F1, F2, etc.) is predicted to occur when parental lineages are highly inbred (Simon et al. 2018). The extent to which hybrid breakdown interacts with hybrid heterosis to facilitate or counteract speciation deserves attention from future studies.

CONCLUDING REMARKS

Many new insights into outcomes and evolutionary consequences of hybridization have been gained in the genomics era. We now know that hybridization is widespread among plants and animals alike, that it can be an important source of genetic and phenotypic variation, and that it can be a target of selection, facilitating species formation and persistence. Historical hybridization events have fueled some of the fastest bursts of diversification in animals (Meier et al. 2017a), and ongoing introgression continues to provide variants that are favored by sexual and environmental selection (Fitzpatrick et al. 2010; Heliconius Genome Consortium 2012), facilitating species persistence in an ever-changing environment. As we discover more about the role of hybridization in speciation some old questions remain, while new questions begin to arise (Box 2).

These questions and continued technological progress in genomics prompt the need for complementary advances in theory and methods. We need analytical tools to improve identification of conditions under which hybridization can lead to novelty and in which environments this might be advantageous, neutral, or disadvantageous. It would also be beneficial to be able to analyze hybridization and gene flow while taking into account two-dimensional space, genetic architecture of traits, and recent demography. Recent improvements in long-range sequencing would benefit from complementary software that incorporates haplotype block analyses in hybridization studies (Sedghifar et al. 2016; Meier et al. 2021). Finally, tackling the long-standing challenge to differentiate between shared alleles due to incomplete lineage sorting or hybridization between sister taxa will allow for a more transferrable metric of gene flow across different levels of divergence.

The role of hybridization in speciation is multifaceted. As we investigate the evolutionary processes shaping the Tree of Life, we reveal more complexity in the role that hybridization plays during and after speciation. More studies across systems will reveal broad patterns we may expect under certain sets of conditions. As we

BOX 2. OPEN QUESTIONS FOR FUTURE RESEARCH

- How does the likelihood of hybridization vary across higher levels of taxonomic organization (e.g., species, genus, family) and taxonomic groups (e.g., animals, plants, fungi, protists)?
- How do different life history traits (e.g., sex determination, mating systems) affect the likelihood of hybridization?
- Does shared extrinsic environment (e.g., climatic history) affect hybridization across codistributed population or species pairs in suture zones similarly, despite different intrinsic factors (e.g., dispersal rates)?
- How does demographic history (e.g., range expansions or contractions) interact with selection (e.g., purging of deleterious mutations) during hybridization?
- Do incompatibilities caused by different selective regimes (e.g., intragenomic incompatibilities, ecological incompatibilities, mate preference incompatibilities) evolve in different ways or can they be generalized under the BDMI model? And how can they facilitate the evolution of each other and restrict gene flow between incipient species?
- How do our predictions change if we expand from a simple two-deme model to a more realistic model of speciation where a species is a set of multiple potentially hybridizing populations distributed across space?
- How general is the pattern of a “tipping point” in speciation and what factors (e.g., neutral and adaptive) influence its occurrence?
- How does allelic reshuffling by hybridization alter gene regulation to give rise to novel phenotypes and barriers to gene flow?
- To what extent can genomic rearrangements change gene expression in hybrids and how adaptive is this phenotypic variation?
- When does hybridization and introgression aid in species persistence versus speciation?
- What is the interplay between recombination, introgression, and selection, and how does this impact evolutionary consequences of hybridization?
- How does the genomic architecture of adaptive phenotypes promote or constrain the evolution of novelty and new species via hybridization?
- To what extent does the interplay between hybrid breakdown and heterosis influence speciation and species persistence?

revisit classic theory with modern methods and expand our collective knowledge, we further reveal new avenues of research to explore the often-contradictory effects of hybridization in speciation and biodiversity.

AUTHOR'S CONTRIBUTIONS

Ideas and conceptualization: J.P., J.K., R.J.P., P.S., G.W., R.S.G., J.I.M., A.R., J.M., O.S. Original draft: J.P., J.K., R.J.P., P.S., G.W., R.S.G., S.J.R., J.I.M., A.R., M.M. Commenting and editing final draft: all contributors. Figures: J.P., J.K., R.J.P., J.I.M., A.R., J.M., M.M. Coordination: J.P., J.K., R.J.P.

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