Genomics of plant speciation

Dan G. Bock, Zhe Cai, Cassandra Elphinstone, Eric González-Segovia, Kaede Hirabayashi, Kaichi Huang, … Loren H. Rieseberg

2023

Plant Communications
Review article

CellPress
Partner Journal

Genomics of plant speciation

Dan G. Bock[1], Zhe Cai[1], Cassandra Elphinstone[1], Eric González-Segovia[1], Kaede Hirabayashi[2], Kaichi Huang[1], Graeme L. Keais[1], Amy Kim[1], Gregory L. Owens[2] and Loren H. Rieseberg[1,*]

[1]Department of Botany and Biodiversity Research Centre, University of British Columbia, Vancouver, BC, Canada

[2]Department of Biology, University of Victoria, Victoria, BC, Canada

***Correspondence: Loren H. Rieseberg (lriesebe@mail.ubc.ca)**

https://doi.org/10.1016/j.xplc.2023.100599

ABSTRACT

Studies of plants have been instrumental for revealing how new species originate. For several decades, botanical research has complemented and, in some cases, challenged concepts on speciation developed via the study of other organisms while also revealing additional ways in which species can form. Now, the ability to sequence genomes at an unprecedented pace and scale has allowed biologists to settle decades-long debates and tackle other emerging challenges in speciation research. Here, we review these recent genome-enabled developments in plant speciation. We discuss complications related to identification of reproductive isolation (RI) loci using analyses of the landscape of genomic divergence and highlight the important role that structural variants have in speciation, as increasingly revealed by new sequencing technologies. Further, we review how genomics has advanced what we know of some routes to new species formation, like hybridization or whole-genome duplication, while casting doubt on others, like population bottlenecks and genetic drift. While genomics can fast-track identification of genes and mutations that confer RI, we emphasize that follow-up molecular and field experiments remain critical. Nonetheless, genomics has clarified the outsized role of ancient variants rather than new mutations, particularly early during speciation. We conclude by highlighting promising avenues of future study. These include expanding what we know so far about the role of epigenetic and structural changes during speciation, broadening the scope and taxonomic breadth of plant speciation genomics studies, and synthesizing information from extensive genomic data that have already been generated by the plant speciation community.

Keywords:: genomic islands of speciation, structural variation, hybrid speciation, polyploid speciation, reproductive isolation, standing genetic variation

Bock D.G., Cai Z., Elphinstone C., González-Segovia E., Hirabayashi K., Huang K., Keais G.L., Kim A., Owens G.L., and Rieseberg L.H. (2023). Genomics of plant speciation. Plant Comm. **4**, 100599.

INTRODUCTION

In 1859, when Charles Darwin published *On the Origin of Species* (Darwin, 1859), he proposed the enormously important concept of evolution through natural selection and took the first steps toward understanding how new species arise. Departing from the *status quo*, which maintained that speciation is an intractable problem far removed from normal population processes (Wallace, 1889), Darwin suggested that biological diversification is both dynamic and continuous across scales: differences generated by natural selection within species, such as those that can be observed among varieties, eventually amount to splits between species. Since 1859, our understanding of speciation has seen extraordinary progress, building on Darwin's remarkably prophetic views. This was facilitated by several milestones, including rediscovery of Gregor Mendel's principles of inheritance (Mendel, 1965) and the modern synthesis of the 1930s and 1940s, which reconciled population genetics with Darwinian evolution and established the modern unified theory of evolution (Dobzhansky, 1937; Mayr, 1942; Stebbins, 1950).

Studies of plants have been instrumental throughout this time, distinctly shaping our understanding of how new species originate (Rieseberg and Willis 2007; Lowry et al., 2008; Baack et al., 2015). For example, early students of plant speciation considered that hybridization among species can be both frequent and evolutionarily constructive (Anderson, 1949; Anderson and Stebbins, 1954; Stebbins, 1959; Grant, 1981).

Published by the Plant Communications Shanghai Editorial Office in association with Cell Press, an imprint of Elsevier Inc., on behalf of CSPB and CEMPS, CAS.

By contrast, zoological counterparts tended to subscribe to strict reproductive independence of species and regarded cases of hybridization as anomalies that result from occasional failure of isolating mechanisms, with limited reverberations across generations (Mayr, 1942; Mayr, 1963; reviewed in Mallet, 2005). Likewise, in agreement with a perspective that Darwin had formulated decades prior, early botanical workers favored ecological isolation and speciation by natural selection, perhaps also influenced by the primarily sessile habit of their study organisms. For instance, botanists relied on breeding experiments and large-scale transplants and pointed to locally adapted populations and ecotypes as the initial stages in progression toward complete speciation (Turesson, 1922; Clausen, 1951; reviewed in Lowry, 2012). By contrast, zoological counterparts considered speciation unlikely without preliminary geographical isolation (Mayr, 1963) and speculated that the genetic changes leading to adaptive morphological differentiation were fundamentally different from those that lead to reproductive isolation (RI) (Dobzhansky, 1940). Finally, other aspects of plant biology afforded unique advantages for uncovering additional routes to speciation. For instance, given that whole-genome duplication (WGD) is far more common in plants than it is in animals (Otto and Whitton, 2000), it should be of no surprise that polyploidy was discovered in plants (Lutz, 1907) and that most of what we know of polyploid speciation comes from plant systems, even though animal polyploids have also been known for a long time (e.g., Darlington 1953).

The genomic revolution has equipped contemporary evolutionary biologists with the tools needed to resolve many of these debates (see also Seehausen et al., 2014) and to use earlier stances as springboards toward new advances in speciation research. For example, it is now widely accepted that hybridization among species is common and contributes to long-term diversification (Arnold, 1997; Rieseberg, 1997; Mallet, 2005; Abbott et al., 2013), as increasingly illustrated by a range of genome-enabled approaches (Payseur and Rieseberg, 2016; Hibbins and Hahn 2022). Moreover, aside from documenting hybridization, genomic studies have shown that when adaptation and speciation have progressed, chromosomal inversions or other recombination cold spots become crucially important in settings characterized by gene flow (e.g., Todesco et al., 2020). Genome-enabled studies have also supported the disproportionately large role that natural selection has in driving speciation either directly or indirectly (Schluter, 2009; Sobel et al., 2010; Nosil, 2012) by characterizing genes contributing to adaptation and RI (e.g., Wright et al., 2013). Far from providing only answers, however, genomic datasets have also uncovered new problems in speciation research, including the time point when recombination suppression is established relative to reproductive barriers as well as the connection between adaptation and intrinsic postzygotic isolation (Schluter and Rieseberg 2022).

Here, we review recent developments enabled by genome sequencing, focusing on plant speciation. Thus, while we rely on earlier foundational literature, we will not be covering those studies at length. Rather, we look at plant speciation from the vantage point of genomics and ask how our understanding of plant speciation has been shaped by technologies that now allow us to sequence most regions of the genome. We highlight, where possible, aspects of plant speciation that remain challenging and require further study.

THE LANDSCAPE OF GENOMIC DIVERGENCE

A fundamental question in speciation genomics is how divergence across the genome accumulates during and after speciation. Many early evolutionists based their thinking on the biological species concept and viewed speciation as a highly polygenic process involving many coadapted genes (Dobzhansky, 1937). In this model, RI first arises between geographically isolated populations and is then reinforced by selection against hybrids following secondary contact. Introgression is not expected between good species because the degree of coadaptation makes interspecies combinations maladaptive. The amount of divergence between species is therefore expected to be relatively even across genes, given that the genome acts as a single unit.

While the biological species concept was popular in the zoological community, botanists had long appreciated the prevalence of hybridization and introgression between species (Lotsy, 1925; Anderson, 1949). For example, in species complexes appearing to function as "syngameons," taxa were both phenotypically and ecologically differentiated but still hybridized and introgressed frequently (Grant, 1981). Additionally, early botanical work found cases where speciation seemed to be driven by changes at a small number of loci (Hilu, 1983; Gottlieb, 1984; Bradshaw et al., 1995). This evidence, along with theoretical and empirical studies of hybrid zones indicating the permeability of reproductive barriers (Barton and Hewitt, 1985), contributed to development of the genic model of speciation. This model proposes that speciation is initiated by a small number of loci that cause RI (Wu, 2001). If diverging populations are not geographically isolated, then gene flow will be reduced around these loci but unencumbered elsewhere in the genome. As speciation proceeds, regions of reduced gene flow should expand through a process called divergence hitchhiking, leading to greater overall RI (Nosil et al., 2009; Via, 2009; Nosil and Feder, 2012; Via, 2012). Eventually RI accumulates so that the entire genome is protected from interspecific gene flow, and speciation is complete.

An exciting implication of the genic model is that, during the early stages of speciation, genes involved in RI or ecological specialization should be detectable based on genetic differentiation. When comparing genome-wide allele frequencies between species, these genes should have high values of the fixation index (F_{ST}), showing up as so-called "genomic islands." It soon became appreciated that other processes could cause peaks of genetic divergence (Cruickshank and Hahn, 2014). Because F_{ST} is a relative measure of genetic differentiation, when diversity is low, F_{ST} is inflated. This means that an F_{ST} peak may represent the recent sweep of a universally adaptive allele rather than an allele underlying RI (Cruickshank and Hahn, 2014). Background selection, where deleterious mutations are removed by purifying selection, can also reduce diversity, so local genomic variation in purifying selection intensity was also put forward as an explanation for F_{ST} peaks (Zeng and

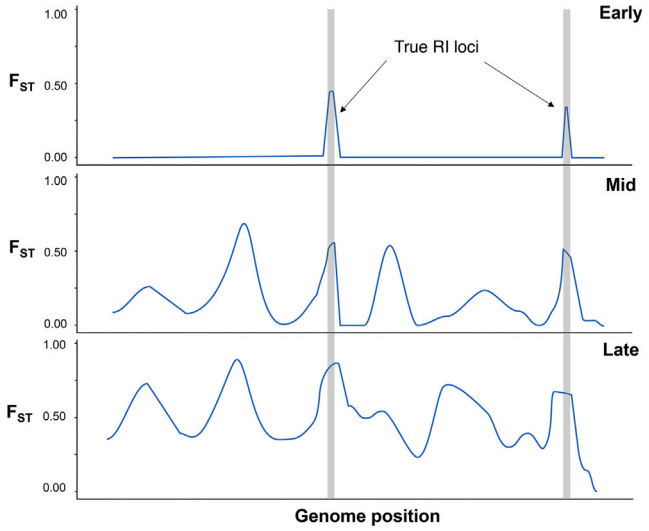

Figure 1. The genome-wide pattern of sequence differentiation at different stages of speciation (early, mid, late).
In the early stages of speciation, RI loci are the only F_{ST} peaks. As divergence proceeds, other processes (e.g., sorting of ancestral variation, local reductions in Ne, linked selection, etc.) cause additional F_{ST} peaks. In late speciation, global rises in F_{ST} further obscure the ability to identify peaks.

Corcoran, 2015; but see Matthey-Doret and Whitlock, 2019). On the flip side, linkage to positively selected alleles could impact neutral sites in a similar way, leading to reduced diversity in genomic regions with low recombination rates (Baird, 2015).

To explore the relative importance of such forces in creating F_{ST} peaks, Stankowski et al. (2019) conducted a comparative study on nine *Mimulus* species. They found that F_{ST} was negatively correlated with genetic diversity as well as tree concordance. This supports the role of linked selection leading to local reductions in effective population size (Ne) along the genome that consequently affects F_{ST}. Was this from background selection or adaptive positive selection? To test this, the authors compared the correlation between genomic factors and the divergence between species to test several hypotheses put forward by Burri (2017) on the effect of linked selection. While correlations with the density of functional elements and recombination rate were observed, simulations using only background selection showed only modest variation in the differentiation landscape, suggesting that background selection was not the primary driver of the differentiation landscape observed. This is consistent with more recent simulations, which found that F_{ST} outliers were unlikely to be driven by background selection (Matthey-Doret and Whitlock, 2019).

But the question is, how can we know whether F_{ST} outliers are truly alleles underlying RI and not the effect of natural selection unrelated to RI? One solution to this confusion involves inclusion of D_{XY} (between-group nucleotide differences), an absolute measure of genomic differentiation, in these comparisons. Under a model of divergence with gene flow, genes contributing to RI should have high F_{ST} and D_{XY}, while a selective sweep in a single species would increase F_{ST} but not D_{XY}.

Several studies in plants have found that regions of high F_{ST} also have high D_{XY}, but, critically, this can also occur in taxa that diverged in allopatry (Wang et al., 2019; Choi et al., 2020; Ke et al., 2022). Without any gene flow between species, these F_{ST} peaks are not caused by localized reduced gene flow. An alternative explanation is that F_{ST} peaks result from differential sorting of ancestral variation (Guerrero and Hahn, 2017). Ancestral variation can be older than species, so when different haplotypes sort into two species, they can cause increased F_{ST} and D_{XY}. In *Primulina*, edaphic species diverged recently (<0.5 million years ago), but F_{ST} peaks between sister species contain haplotypes that were more than 10 times older (>5.4 million years ago) (Ke et al., 2022). The sorting of ancestral variation may also be playing a role in RI (see also Sources of genetic variation underlying RI). In the Hawaiian *Metrosideros* adaptive radiation, F_{ST} outliers were enriched for loci that were differentially fixed between related species. Choi et al. (2021) characterized these as ancestral incompatibilities and hypothesized that the rapid speciation may be facilitated by a pre-existing pool of incompatibilities.

Ultimately it is unlikely for all F_{ST} peaks to have a single cause. Shang et al. (2022) explored the landscape of genomic divergence in five pairs of *Populus* taxa. They characterized F_{ST} outliers into divergence with gene flow or allopatric selection based on whether D_{XY} was elevated. They found that roughly 10 times more regions fit the characterization of allopatric selection than divergence with gene flow regardless of whether the species had a history of gene flow. However, regions contributing to RI were more important in explaining the differentiation pattern of the most recently diverged taxa. It is likely that the window of timing where F_{ST} peaks are exclusively from RI genes is small. Dune and non-dune populations of the prairie sunflower are reproductively isolated but have likely only been diverging for 5000 years (Andrew and Rieseberg, 2013). When comparing their genomes, F_{ST} peaks are almost exclusively in a small number of non-recombining blocks that are linked to RI traits (Huang et al., 2020). As divergence accumulates in the future, other processes will cause F_{ST} peaks, obscuring RI loci that are currently visible (Figure 1). Thus, identification of genomic regions that contribute to RI via the landscape of genomic divergence is most straightforward to achieve in incipient species rather than in species pairs that have progressed farther along the speciation continuum. Moreover, from the perspective of identifying genes contributing to RI, analyses of the landscape of genomic divergence will often require follow-up examination, such as fine mapping (see also The genetics of RI' section). This is because, even in incipient species, F_{ST} peaks can be too large for strong candidate genes to be identified (Andrew and Rieseberg, 2013).

Current work on genomic differentiation is almost entirely based on short-read sequencing and alignment to a single reference genome. One drawback of this method is that complex genomic variants, including structural rearrangements, and large insertions or deletions are not genotyped. For example, Liu and Dawe (2022) recently created a pan-genome for 26 diverse maize lines that had each been assembled *de novo* using long-read technology. They found that the total pan-genome length was 3.7 times larger than an individual genome and that only 4.9%

of the pan-genome was conserved in all individuals while the rest was segregating. This highlights the incredible amount of variation hiding in repetitive regions and rearrangements, which is discussed in more detail in the next section.

STRUCTURAL VARIATION

Structural variants (SVs), such as inversions, translocations, fissions/fusions, insertions/deletions, and duplications, are important genetic differences often found between species. The first hint of structural variation in plants was documented in maize more than 100 years ago, when cytological studies found differences in chromosome length between cultivated maize and its wild relatives (Kuwada, 1915). Later cytogenetic studies proved the existence of chromosomal knobs and inversions in maize and teosintes, and knobs were then used as markers to determine the origin, evolution, and relationships between maize and its wild relatives (Ting, 1964; Wilkes, 1967; Kato Yamakake, 1976). The first evidence of transposable elements (TEs), another important type of structural change, was also found in maize (McClintock, 1950). However, comprehensive exploration of SVs in plants during the 20th century was slowed by technological limitations. Even in the genomic age, a lack of high-quality reference genome assemblies (Yuan et al., 2021) and a focus on SNPs in population genomic studies (Morin et al., 2004; Hoban et al., 2016) have hampered investigation of structural variation and its evolutionary roles. While the emphasis on SNPs in population genomics studies has continued to the present day (Hahn, 2018), because of the recent development of third-generation sequencing, a large number of high-quality genomes have recently become available. Access to such genomes, in combination with enhanced algorithms and tools for SV detection, has allowed detailed interrogation of structural variation in both model and non-model species (Wellenreuther et al., 2019; Huang and Rieseberg, 2020; Lei et al., 2021).

This genomic work has uncovered ubiquitous structural variation of all kinds between closely related species, offering a level of resolution that previous cytogenetic and comparative genetic mapping studies could never achieve (Huang and Rieseberg, 2020; Mérot et al., 2020). The majority of studies of plant SVs have focused on their direct effects on phenotypes, especially for agronomically important traits (Fransz et al., 2016; Qin et al., 2021; Li et al., 2022a, 2022b), although some of these (e.g., flowering time) could potentially contribute to speciation as well (Todesco et al., 2020). Other studies have examined the role of chromosomal rearrangements in speciation via their effects on hybrid sterility (reviewed in Fishman and Sweigart, 2018) or recombination suppression (reviewed in Huang and Rieseberg, 2020; Mérot et al., 2020). However, compared with the number of SVs that have been identified, few SVs have been linked to speciation.

While chromosomal inversions are the most studied SVs, we only briefly discuss them here because their contributions to plant speciation have been the subject of a recent comprehensive review (Huang and Rieseberg, 2020). Inversions may cause RI through direct effects on hybrid fertility (King, 1995), and meiotic abnormalities diagnostic for inversions are sporadically reported in cytogenetic studies (Kenton, 1981; Chandler et al., 1986; Gopinathan and Babu, 1986; Stein et al., 2004). More often, hybrids heterozygous for inversions, especially for inversions that are polymorphic within species, do not show visible reductions in fertility (Kianian and Quiros, 1992; Lowry and Willis, 2010; Fang et al., 2012; Stathos and Fishman, 2014; Ostevik et al., 2016; Huang et al., 2020). However, inversions can also facilitate speciation indirectly by reducing recombination between loci under divergent selection and those underlying RI (Trickett and Butlin, 1994; Kirkpatrick and Barton, 2006; Feder et al., 2011; Dagilis and Kirkpatrick, 2016; Charlesworth and Barton, 2018; Schaal et al., 2022), a genetic architecture commonly reported in plants (reviewed in Huang and Rieseberg, 2020). Such a reduction in recombination can facilitate inversion establishment (Kirkpatrick and Barton 2006) or contribute to the accumulation of phenotypic differences and hybrid incompatibilities after establishment (Noor et al., 2001; Rieseberg, 2001; Navarro and Barton, 2003). While it is not generally known whether traits mapping to inversions arose before or after inversion establishment (Schluter and Rieseberg, 2022), capture of pre-existing combinations of locally adapted alleles has been shown in several cases (Lee et al., 2017; Coughlan and Willis, 2019; Mandakova et al., 2015).

Translocations represent another class of well-studied SVs. Comparative genomics studies frequently report reciprocal translocations between closely related plant species (Huang et al., 2009; Hu et al., 2011; Garcia-Mas et al., 2012), and genetic studies of RI have often mapped barrier traits to translocations (Lai et al., 2005; Rieseberg and Willis, 2007; Fishman et al., 2013; Stathos and Fishman, 2014). Large translocations directly cause hybrid sterility because of mis-segregation during meiosis (King, 1995; Stathos and Fishman, 2014). While such strong underdominance contributes effectively to RI, it represents a major impediment to translocation establishment in the first place. Early models of chromosomal speciation thus suggested that underdominant rearrangements are established via genetic drift (White, 1973; Lande, 1979). However, this is only plausible in selfing species or species that have experienced extreme population bottlenecks. Observations of high rates of translocations in species with very large effective population sizes are also inconsistent with an important role of drift in translocation establishment (Strasburg et al., 2011; Ostevik et al., 2020). Alternatively, translocations may establish because of their effect on recombination suppression (Guerrero and Kirkpatrick, 2014). However, recombination suppression typically is restricted to genomic regions near translocation breakpoints (although see Martin et al., 2020; Figure 2), which limits the applicability of this mechanism. A third possibility is meiotic drive. There is now strong molecular evidence from studies on mice that female meiotic drive of Robertsonian translocations is capable of driving karyotype evolution through their effect on centromere strength (Chmátal et al., 2014). The two examples of female meiotic drive discovered in plants so far, in maize and monkeyflower (Buckler et al., 1999; Fishman and Saunders, 2008; Clark and Akera, 2021; Finseth et al., 2021), are not associated with translocations. However, preferentially transmitted translocations were recently reported in banana (Martin et al., 2020), and several studies have associated translocation breakpoints with centromeres (Schranz et al., 2006; Badaeva et al., 2007; Ostevik et al., 2020), suggesting a possible role of female meiotic drive, but further investigation is needed.

Hemizygosity, resulting from insertion and deletion polymorphisms, should effectively suppress recombination in a similar

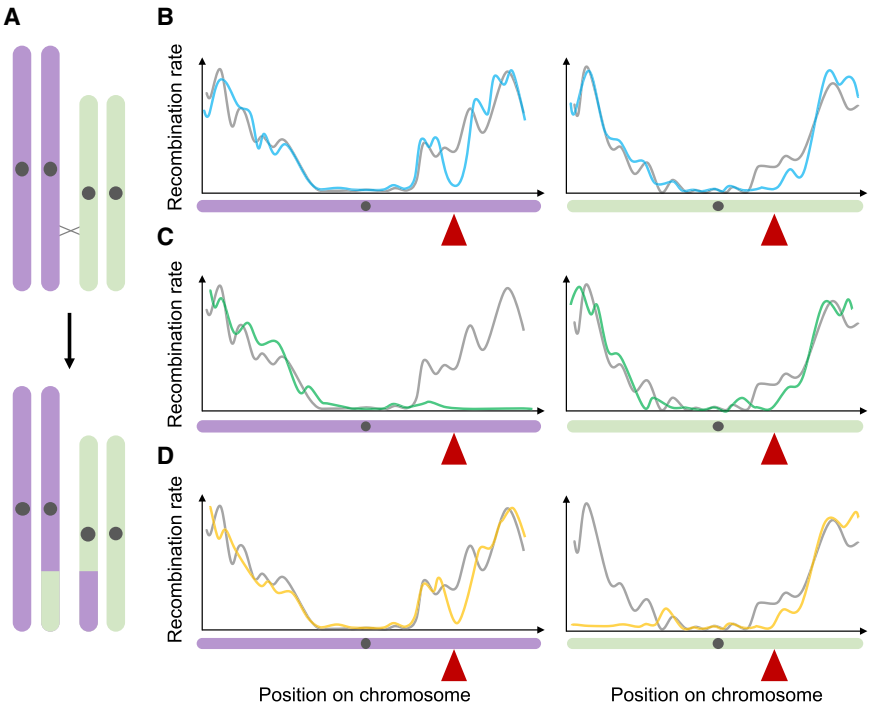

Figure 2. The effects of chromosomal translocation on recombination suppression.

(A) A reciprocal translocation between two non-homologous chromosomes.

(B–D) In different scenarios, recombination rate in heterozygous individuals is reduced **(B)** only around the translocation breakpoints, **(C)** around the breakpoint of one chromosome and in the translocated segment of the other chromosome, or **(D)** around the breakpoint of one chromosome and for the entire chromosome except for the translocated segment on the other. Gray lines represent recombination rate in individuals homozygous for the original karyotype, and blue, green, and orange lines represent recombination rate in heterozygous individuals. The x axes in **(B)–(D)** are used to indicate position along the original chromosomes. Black circles indicate locations of centromeres, and red triangles indicate locations of the breakpoints on the original chromosomes. Note that recombination is also suppressed around centromeres.

way as inversions, thus providing an evolutionary advantage for speciation with gene flow (Ortiz-Barrientos et al., 2016). High hemizygosity has been reported in the genomes of clonally propagated grapevine (Zhou et al., 2019), suggesting that this type of SV might be common in plants and could contribute to RI. An apparent example of the latter comes from sunflower, where hemizygosity or complete loss of a homolog of *FLOWERING LOCUS T* underlies a shift in flowering time between sympatric ecotypes of the silverleaf sunflower (Todesco et al., 2020).

TE insertions and deletions also result in large multigenic SVs. TEs represent an important source of mutations in plant genomes and are known to be the cause of trait variation that could contribute to RI. Examples include differences in flowering time in *Arabidopsis* (Liu et al., 2004) and maize (Castelletti et al., 2014); floral color patterns in morning glory (Iida et al., 2004), snapdragon (Coen et al., 1986), and rose (Li et al., 2022b); and local adaptation in wild barley (Kalendar et al., 2000). It has been speculated that bursts of TE activity, possibly stimulated by abiotic stress, could provide the raw material for rapid adaptation and speciation (McClintock, 1950; Butelli et al., 2012; Cavrak et al., 2014; Zhang and Gao, 2017; Benoit et al., 2019; Wang et al., 2021a). Besides the effects of TE activity on gene expression and function, silencing of TEs through DNA methylation (Slotkin and Martienssen, 2007) may be an important source of recombination rate heterogeneity within and between species (Yelina et al., 2015; Kent et al., 2017; Schluter and Rieseberg, 2022). However, to the best of our knowledge, the potential role of epigenetic modifications in maintaining clusters of adapted alleles and promoting speciation in the presence of gene flow remains to be demonstrated.

Finally, as noted above, additional types of SVs, such as fissions/fusions as well as segmental duplications, could have a role in speciation (e.g., de Vos et al., 2020). Chromosomal fissions/fusions typically have weaker underdominant effects than translocations and milder impacts on recombination than inversions (Jones 1998). In general, fissions are expected to reduce recombination rates, while fusions increase them. Chromosomal fusions are an important component of diploidization and diversification following WGD (Mandáková and Lysak 2018; see also Polyploid speciation). More work is needed to understand the contribution of these types of SVs to speciation. We anticipate that, with continued use of long-read sequencing and associated methods that facilitate assembly of highly contiguous genomes and comparative genomics, this topic will see accelerated progress.

SPECIATION WITH GENE FLOW, INTROGRESSION, AND HYBRID SPECIATION

Gene flow plays a critical role in mediating speciation processes. Gene flow within species holds populations together by impeding differentiation and enabling the spread of advantageous mutations (Morjan and Rieseberg, 2004). Gene flow between species can have a variety of different consequences. On the one hand, it may weaken reproductive barriers, potentially resulting in the merger of species (Todesco et al., 2016; Figure 3). On the other hand, selection against hybrids can strengthen RI through reinforcement (Hopkins, 2013; Figure 3). More frequently though, as theoretical studies indicate (e.g., Buerkle et al., 2003), contact between diverging lineages leads to stable hybrid zones (Barton and Hewitt, 1985). Creative outcomes of hybridization and introgression are possible as well, including transfer of adaptive traits and formation of new hybrid lineages (Arnold, 1997; Figure 3).

Analyses of genome sequence data offer a powerful means for detecting gene flow both before and after speciation (Roux et al.,

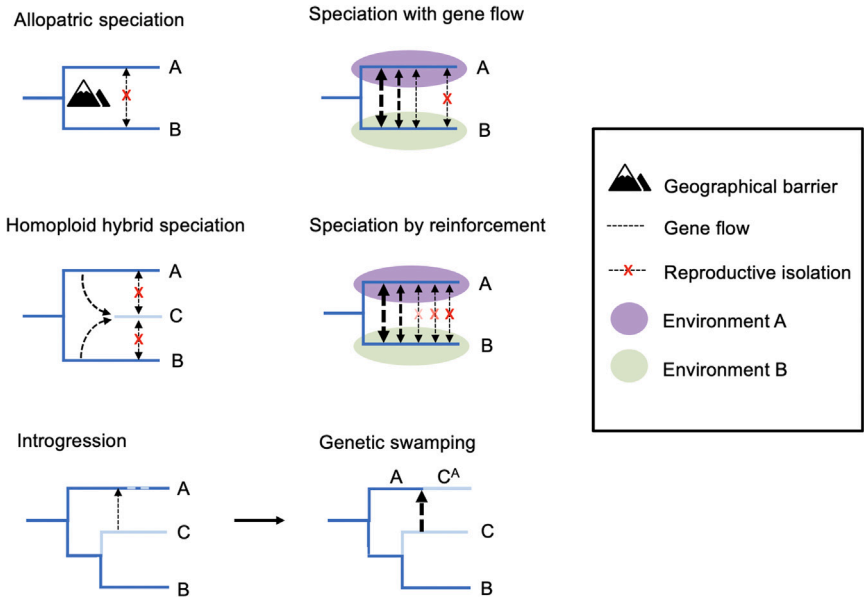

Figure 3. Potential impacts of gene flow (or its absence) on lineage divergence, speciation, or extinction.

Gene flow levels are represented by the thickness of the dashed lines, with thicker lines indicative of greater gene flow. In allopatric speciation, diverging lineages **(A and B)** are isolated because of a physical barrier, represented by a mountain range in the diagram. Biological reproductive barriers are expected to evolve over time, as marked by a red "X." Speciation in the presence of gene flow depicts gene flow diminishing over time as RI strengthens because of adaptive divergence. In homoploid hybrid speciation, hybrids may form an independent lineage **(C)** when they become reproductively isolated from parental lineages. This may occur because of ecological divergence and sorting of genetic and chromosomal incompatibilities (or both). However, if hybrids of low fitness are selected against, then prezygotic barriers between parental lineages may be strengthened over time, as indicated by the darkening of the red "X." Introgression may occur between closely related species **(A and C)**. An increased rate of introgression could lead to extinction through genetic swamping, in which species A becomes indistinguishable phenotypically from species C. This is denoted by C^A.

2016; Dagilis et al., 2021). The many different methods available for such analyses, and their strengths and limitations, have been described elsewhere (Payseur and Rieseberg, 2016; Hibbins and Hahn, 2022). Here we discuss what we have learned from such analyses when applied to plants, focusing on studies that explicitly test for gene flow between divergent lineages as opposed to reports on patterns of genomic divergence, which are described in the two previous sections of this review.

Speciation with gene flow

Geographic isolation is thought to facilitate speciation by eliminating the possibility of gene flow between diverging lineages. If geographic isolation is important to speciation, then sister species are more likely to be allopatric than more distantly related species in a genus, a pattern seen in highly vagile organisms such as birds, insects, fish, and mammals (e.g., Barraclough and Vogler, 2000; Fitzpatrick and Turelli, 2006; Price, 2007). This contrasts with phylogenies of some plant genera in which sister taxa are more likely to overlap in geographic distribution than more distantly related species (Anacker and Strauss, 2014; Grossenbacher et al., 2014; Kantar et al., 2015). Likewise, phylogenetic analyses of plants from remote oceanic islands find *in situ* speciation to be common on some islands (Savolainen et al., 2006; Papadopulos et al., 2011), suggestive of speciation with gene flow, although this pattern is not universal (Igea et al., 2015). Overall, these results imply that geographical isolation may not play a critical role in speciation in many groups of plants, with speciation driven instead by divergent adaptation to different local environments (Anacker and Strauss 2014; Papadopulos et al., 2014). Gene flow between diverging lineages is expected to be common under such speciation scenarios (Kisel and Barraclough, 2010; although see Sianta and Kay, 2022).

There are numerous studies that describe gene flow or introgression in the so-called "gray zone of speciation," in which diverging lineages are distinguishable but RI is not yet complete (Roux et al., 2016; Dagilis et al., 2021). For example, Dagilis et al. (2021) report on 724 such studies across eukaryotes, including 230 plant studies. While these studies indicate that admixture is common, especially in the plant kingdom, most do not make inferences about the timing of gene flow. Thus, it is generally not clear whether the initial divergence of lineages occurred in the presence of gene flow (primary gene flow) or whether there was an initial period of isolation and divergence with subsequent gene flow following secondary contact (secondary gene flow). However, in a subset of studies, demographic model fitting has been employed to examine changes in patterns of gene flow through the evolutionary history of diverging lineages. While results from such analyses should be interpreted with extreme caution (Strasburg and Rieseberg, 2011; Momigliano et al., 2021), primary gene flow is supported in a number of cases. These include examples where gene flow appears to be continuous but declining with time (Chang et al., 2022; Tavares et al., 2022). Other cases represent examples of budding speciation, where a wide-ranging progenitor species has given rise to more narrowly distributed derivative species (Andrew et al., 2013; Chapman et al., 2013; Osborne et al., 2013; Li et al., 2021). Well-studied examples of the latter include a sand dune-adapted species of sunflower from Colorado, USA, that budded off from the widespread prairie sunflower within the past 10 000 years (Andrew et al., 2013) and a high altitude-adapted species of *Senecio* on Mt. Etna, Sicily, whose divergence from a more widespread low-altitude species (~150,000 years ago) is coincident with volcanic activity that increased the elevation of Mt. Etna to more than 2000 m (Chapman et al., 2013; Filatov et al., 2016). Both systems are characterized by divergent ecological selection and ongoing gene flow (Brennan et al., 2009; Ostevik et al., 2016; Wong et al., 2020). Andrew et al. (2013) estimated that gene exchange between the sunflower ecotypes is more than one

effective migrant per generation, which is sufficient to prevent differentiation at neutral loci (Andrew et al., 2013). In contrast, less than one effective migrant per generation is reported for the *Senecio* system (Filatov et al., 2016), indicating that neutral genome-wide differentiation can occur. A caveat is that such estimates are sensitive to inclusion of admixed populations (Filatov et al., 2016), which might account for the apparent difference in gene flow rates between the two systems.

More commonly, speciation appears to be at least partly allopatric (albeit with an important contribution of natural selection; e.g., Melo et al., 2019), with gene flow following secondary contact (He et al., 2019; James et al., 2021). Such gene flow may be intermittent because of climate cycles in which periods of geographic isolation are interspersed with episodes of gene flow (Maguilla et al., 2017; He et al., 2019; Feng et al., 2020). Mangroves from the Indo-Malayan coasts offer a particularly well-studied example of such mixing-isolation-mixing cycles (He et al., 2019). By combining genomic analyses and geographical records, He et al. (2019) linked changes in the ocean levels to intermittent gene flow between Pacific and Indian coasts, which, they argue, permitted higher speciation rates than would be possible under a strict allopatric model.

Introgression

Beyond establishing the importance of non-allopatric speciation in plants, genomic analyses offer insights into patterns and consequences of interspecific gene exchange. In their survey of introgression across eukaryotes, Dagilis et al. (2021) found that rates of introgression are higher (on average) in plants relative to animals and in weakly isolated relative to strongly isolated lineages, which accords with commonly held views in the literature (Barton and Hewitt, 1985; Mallet, 2005). Introgression in organisms affected by human disturbance is significantly elevated as well, as predicted by earlier literature (Anderson, 1948).

Patterns of introgression across genomes also provide insights about speciation, especially the genome architecture of RI. As predicted from hybrid zone theory (Barton and Hewitt 1985), rates of introgression are positively correlated with recombination rates (Brandvain et al., 2014; Owens et al., 2021; Owens et al., 2023). As well, introgression is reduced for genes or genomic regions underlying RI (Barb et al., 2014; Kenney and Sweigart, 2016; Todesco et al., 2020).

Genomic analyses provide examples of other consequences of introgression as well, such as transfer of adaptations and genetic swamping, in which rare taxa are replaced by hybrids. We suspect that adaptive introgression is common in plants, but so far only a relatively small number of examples have been identified from genomic data (Suarez-Gonzalez et al., 2018). Several of these come from *Populus*, in which introgressions have been shown to contribute to climate adaptation in both Europe (Rendón-Anaya et al., 2021) and North America (Suarez-Gonzalez et al., 2016). Another example comes from sunflower, in which introgression of a functional copy of a key regulator of flowering resulted in a 77-day advance in flowering time in silverleaf sunflower (Todesco et al., 2020). The latter study not only shows how introgression can replace genes that have been damaged or lost but also illustrates its potential role in the evolution of RI. Additional instances of adaptive introgression have been reported in systems such as oak (Leroy et al., 2020), cypress (Ma et al., 2019), and *Arabidopsis* (Marburger et al., 2019; Seear et al., 2020).

There are fewer genomic studies of genetic swamping, but a recent analysis of a rare ironbark (*Eucalyptus*) species from New South Wales (Australia) reveals that many populations classified as the rare form are actually hybrids with more widespread species (Rutherford et al., 2019). Genomic studies of admixture have also revealed that extant genomes of plant and animal species often contain "ghost introgressions" from now extinct species (Eaton and Ree 2013; Owens et al., 2023). Whether the donors of these introgressions were driven to extinction by genetic swamping is not clear, but the presence of such genomic remnants offers the possibility of reconstructing extinct taxa through selective breeding (Shapiro, 2017).

Hybrid speciation

In contrast to polyploid hybrid speciation, which is the focus of the next section of this review, homoploid hybrid speciation is thought to be rare because of the challenge of evolving RI from parental populations (Rieseberg, 1997; Buerkle et al., 2000; Schumer et al., 2014; but see Nieto Feliner et al., 2017). Homoploid hybrid speciation is also hard to prove. Schumer et al. (2014) have suggested that the following three criteria are required to establish homoploid hybrid speciation: (1) RI from the parental taxa, (2) evidence of previous admixture, and (3) demonstration that reproductive barriers are derived via hybridization. Genomic analyses are useful for evaluating the second criterion and indeed have often provided evidence of genomic mosaicism (Schumer et al., 2014). However, we emphasize that genomic mosaicism only demonstrates the occurrence of hybridization and that such analyses only indirectly address criteria 1 and 3, which require additional information, including from studies of RI (discussed below). To date, genomic studies have confirmed the hybrid origin of the Oxford ragwort (*Senecio squalidus*) from the two *Senecio* species on Mt. Etna described above (Nevado et al., 2020), identified several potential new cases of homoploid hybrid speciation (e.g., Grünig et al., 2021; Wang et al., 2021b; Wang et al., 2022), suggested a difference in hybrid ancestry for two of the three well-studied sunflower homoploid hybrid species (Owens et al., 2023), and failed to support several previously hypothesized examples of homoploid hybrid speciation, including *Iris hexagona* (Zalmat et al., 2021) and two cases from *Phlox* (Goulet-Scott et al., 2021).

Genomic analyses can also help reconstruct hybrid speciation scenarios, and when linked with phenotypic data, demonstrate how RI evolved. For example, in *S. squalidus*, demographic model fitting showed that the hybridization event responsible for its origin likely took place in the Oxford Botanical Garden rather than earlier on Mt. Etna (Nevado et al., 2020). Given the recency of hybrid speciation, it is not surprising that the hybrid genome contains a unique subset of genomic structural changes and genetic incompatibilities that differentiate its parents (Brennan et al., 2019). A similar pattern has been

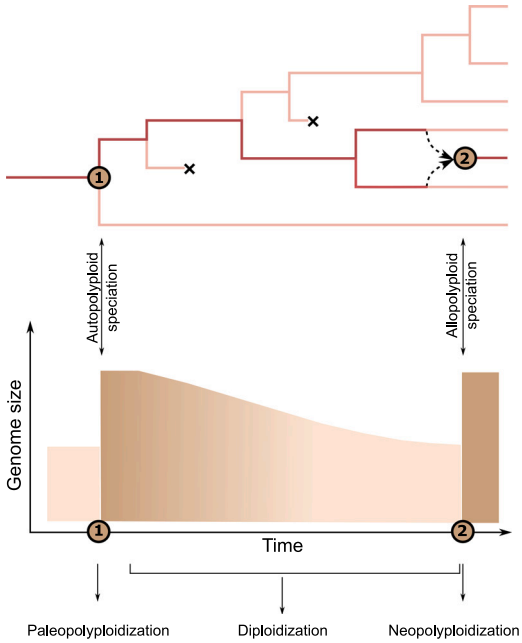

Figure 4. Successive polyploid speciation events and associated genome size dynamics.
The phylogeny on top illustrates a clade that sustained one ancient autopolyploid speciation event (1) and one recent allopolyploid speciation event (2). Occasional extinction events are marked with "X." Note that, while paleopolyploidy events can be a consequence of either auto- or allopolyploidy, discerning between the two possibilities is often not possible for ancient polyploids. The middle part of the figure traces genome size dynamics for a subset of species in the phylogeny shown in darker red. Advances made possible with the help of genomics data include identification of paleopolyploidization events across land plants, understanding the mechanistic basis of diploidization and long-term polyploid evolution, as well as identifying neopolyploids and studying the early meiotic challenges associated with WGD.

reported for a particularly well-characterized hybrid species, *Ostryopsis intermedia*, which inherited alleles underlying flowering time isolation from one parent and habitat isolation via iron tolerance from its other parent (Wang et al., 2021b). The results of Wang et al. (2021b) further highlighted the inheritance of alternate parental alleles involved in premating isolation as a particularly easy route to homoploid hybrid speciation. A more drawn-out hybrid speciation process has been put forward for the origin of *Picea purpurea*, involving a ghost hybrid lineage that formed approximately 6 million years ago, followed by more recent introgression (~1 million years ago) between this ghost lineage and one of its parental species (Ru et al., 2018).

POLYPLOID SPECIATION

Genomics has also contributed to important breakthroughs in our understanding of polyploid speciation—the origin of new species that carry more than two full sets of chromosomes. Here, we review how genome sequencing has been used to test fundamental concepts on this mode of species formation. We start with the origin of polyploids and the earliest genomic responses that occur after WGD and continue with a discussion of genomic changes that unfold more gradually. We conclude by discussing the macroevolutionary significance of polyploid speciation.

The incidence of polyploidy is a topic that has received considerable research interest for more than 80 years. Starting in first half of the 1900s (Müntzing, 1936; Darlington, 1937; Stebbins, 1950) and continuing more recently (Masterson, 1994; Otto and Whitton, 2000), evolutionary biologists have used estimates of base chromosome numbers, the fossil record, and phylogenies to understand the evolutionary significance of this mode of speciation. Genomics has complemented these analyses in important ways, most notably by illuminating signatures of ancient polyploidization (paleopolyploidization; Figure 4) throughout the evolutionary history of land plants, including in bryophytes (Leebens-Mack et al., 2019), ferns and lycophytes (Leebens-Mack et al., 2019; Wang et al., 2020a), gymnosperms (Li et al., 2015; Leebens-Mack et al., 2019; Liu et al., 2022), and angiosperms (Soltis et al., 2009; Jiao et al., 2011; Wendel 2015; Leebens-Mack et al., 2019). These paleopolyploidization events include ones occurring in the common ancestor of all seed plants (~319 million years ago) and again at the base of all angiosperms (~192 million years ago; Jiao et al., 2011; Leebens-Mack et al., 2019). These findings have shaped new questions on the study of polyploidy (Soltis et al., 2010), which increasingly focus on the role of ancient WGDs as catalysts of ecological innovation and evolutionary diversification (Wood et al., 2009; Doyle and Coate, 2019; Baniaga et al., 2020).

As well as identifying paleopolyploidization events, genomics has successfully pinpointed recent polyploidization (neopolyploidization; Figure 4) with important consequences for our understanding of polyploid speciation (Rothfels, 2021). When applied in taxonomically murky clades, genomic analyses often reveal neopolyploids that are morphologically cryptic (e.g., Crowl et al., 2017). Cryptic polyploids illustrate why rates of speciation by WGD are likely to be under-estimated (Soltis et al., 2007), and they can be informative with regard to modes of polyploid speciation. For example, hybrid polyploids (allopolyploids) were traditionally considered to be more frequent than non-hybrid polyploids (autopolyploids; Clausen et al., 1945; Stebbins, 1947), which are often morphologically cryptic. Evidence from phylogenetics and cytology has changed this view, showing instead that autopolyploids are as common as allopolyploids (Soltis et al., 2007; Barker et al., 2016a). Last, knowledge of neopolyploids can be valuable because their parental species might still be present, allowing polyploidization to be repeated experimentally. By comparing established polyploids with very recent or synthetic ones, it is possible to separate ecological and direct genomic effects of WGD from those of evolution after polyploid speciation (e.g., Buggs et al., 2011; Ramsey, 2011).

Outside of tracing polyploidization in exceptional detail across the plant tree of life, genomics has paved the way for answering questions that were almost entirely out of reach for botanical researchers in the early 1900s. For example, during the earliest stages of polyploid formation, how might challenges related to correct segregation of duplicated chromosomes be overcome? While in some systems vegetative or apomictic propagation can facilitate the establishment of new polyploids (Zielinski and Mittelsten Scheid, 2012), stable meiosis is required to achieve

high fertility during sexual reproduction. Until recently, information on this topic has remained limited, with the best-known example coming from the wheat *Ph1* locus (Okamoto 1957; Griffiths et al., 2006). Genomic data have allowed broader investigations of adaptation to WGD (Bomblies et al., 2015; Bohutínská et al., 2021a). In the autotetraploid *Arabidopsis arenosa*, for example, genome scans led to identification of eight meiosis genes with elevated allele frequency differences between diploids and tetraploids that otherwise share extensive polymorphism (Yant et al., 2013). Derived (predominantly tetraploid) alleles for these genes are associated with a reduction in crossover numbers and in multivalent formation (Bomblies et al., 2015; Morgan et al., 2020, 2021), which are important for stabilizing meiosis in autopolyploids (Mason and Wendel 2020). These alleles are present at low frequencies in diploids and are thus readily available for selection to act on, after polyploid speciation (Hollister et al., 2012), and can also be transferred between species via adaptive introgression (Marburger et al., 2019; Seear et al., 2020).

One of the reasons why, prior to application of genomics, many plant species were not suspected to have a polyploid origin is because of genome size. For example, *Arabidopsis thaliana*, which is now known to have experienced at least three rounds of WGDs when considering only events occurring within angiosperms (Blanc et al., 2003; Bowers et al., 2003; Blanc and Wolfe, 2004), has a small genome of only ~135 Mb (Jiao and Schneeberger, 2019). By characterizing the long-term evolution of polyploids and their reversal to a diploid-like state, genomics has helped reconcile these apparently contradictory findings. The process of diploidization unfolds over thousands or millions of years and can occur at different rates even for descendants of the same polyploidization event (e.g., Mandáková et al., 2017). It is also mechanistically diverse, including genome rearrangements and genome downsizing via loss of redundant genes and genome regions (Doyle et al., 2008; Wendel, 2015). As well as facilitating the transition to diploid-like cytogenetic behavior, diploidization may also contribute to ecological diversification and speciation within ploidy levels (Mandáková et al., 2017; Mandáková and Lysak 2018). For instance, the divergent resolution (i.e., loss of different copies) of duplicated genes can lead to the evolution of hybrid incompatibilities and RI (e.g., Scannell et al., 2006), particularly when new polyploids split rapidly into allopatric populations (Muir and Hahn, 2015).

Independent of speciation resulting directly from WGD, the evolution of hybrid incompatibilities after WGD could sustain, over macroevolutionary scales, bursts in speciation and diversification. However, other factors, like reduced efficacy of selection on duplicated genes (Stebbins, 1971) and higher extinction rates, could counteract these effects (Mayrose et al., 2011). Indeed, comparisons between recent polyploids and their diploid congeners support a lower diversification rate for polyploid taxa (Mayrose et al., 2011, 2015; but see Soltis et al., 2014). These findings therefore indicate that most polyploid speciation events do not lead to long-term evolutionary success (Mayrose et al., 2011). When polyploid species do persist, however, the results can be remarkable, as illustrated by families such as Asteraceae, for which WGDs are known to have occurred shortly before large species radiations (Barker et al., 2016b; Huang et al., 2016; Mandáková and Lysak 2018).

THE GENETICS OF RI

As lineages diverge, they accumulate genetic differences that cause RI between them, a process that eventually leads to cessation of gene flow. Identifying the genes that underlie RI, as well as characterizing the evolutionary forces that drive their divergence, has been a major focus in speciation research (Blackman, 2016; Fishman and Sweigart, 2018). Genomics has played an increasingly important role in identification of RI genes and is indispensable for untangling the causative evolutionary forces involved, especially for genes causing postzygotic hybrid incompatibility (Fishman and Sweigart, 2018). In this section, we discuss the approaches used to identify RI genes in plants and illustrate the expanding role of genomics in this endeavor. We then highlight examples where genomics has been used to make inferences about how these genes have evolved. We note that we use the term "RI genes" rather than "speciation genes" because it is difficult to establish whether genetic polymorphisms acted during the splitting of two lineages or, alternatively, whether they originated after speciation (Rieseberg and Blackman, 2010). For a more detailed discussion on RI genes, we direct the reader to Rieseberg and Blackman (2010).

Dozens of genes contributing to RI have been cloned in plants to date (Rieseberg and Blackman, 2010; Blackman, 2016; Ouyang and Zhang, 2018; Vaid and Laitinen, 2019). These genes are involved in the control of diverse phenotypes that act before pollination (e.g., flower color or flower timing), after pollination but before zygote formation (e.g., rejection of pollen from another species), or after zygote formation (e.g., hybrid necrosis or hybrid male sterility; Rieseberg and Blackman, 2010). The majority of these genes have been identified using a forward genetic approach, whereby a trait known to be involved in RI is associated with specific genomic windows using quantitative trait locus mapping and subsequently narrowed to causal genes using fine mapping, genetic transformation, and expression analyses (Blackman, 2016). In principle, this approach does not require a genome or even molecular markers. For example, one of the earliest RI genes identified in plants, *anthocyanin2*, a flower color gene in *Petunia* that leads to pollinator shift, was mapped using phenotypic markers and cloned using transposon tagging (Quattrocchio et al., 1999). However, mapping is greatly facilitated by the availability of a reference genome sequence, and consequently most of the known RI genes to date are from species with advanced genomic and molecular resources, primarily *Arabidopsis*, *Oryza*, and *Mimulus* (Wu et al., 2008; Fishman and Sweigart, 2018; Ouyang and Zhang, 2018; Vaid and Laitinen, 2019).

In addition to the development of high-quality reference sequences, a major way that genomics has contributed to forward genetics is the use of high-throughput sequencing for identifying genetic markers. Using approaches such as genotyping by sequencing, restriction site-associated DNA sequencing, RNA sequencing, and whole-genome resequencing, marker discovery and genotyping are accomplished in a single step. Moreover,

markers are identified genome wide at high density (Poland and Rife, 2012). Together, these benefits over more traditional genetic markers (e.g., Nakazato et al., 2013) have increased the ease and precision of mapping, thus greatly accelerating mapping efforts, including those for RI genes. Chae et al. (2014), for example, were able to map seven causal loci for hybrid necrosis in *A. thaliana* in a single study using mostly genotyping by sequencing on F2 populations for mapping. Likewise, Wilkinson et al. (2021) identified candidate genes for gravitropism (and associated hybrid sterility) by genotyping the tails of the gravitropic distribution in F11 hybrid populations between ecotypes of *Senecio*. In addition to characterizing genetic variation, RNA sequencing in particular can also be employed to winnow down the list of candidate genes obtained from forward genetic studies. An example comes from *Mimulus*, in which hybrids lacking expression of a critical photosynthetic gene are inviable (Zuellig and Sweigart, 2018).

Despite its success in identifying RI genes, forward genetics is nevertheless limited in a number of important ways. To begin with, generating large mapping populations is constrained to species that can grow and flower in the greenhouse or in experimental fields, and rapid-flowering species are favored. A second, more important limitation is that traits must have a clear phenotype and a known or suspected role in RI. This limitation has biased discovery towards traits of large effect, such as flower color, flowering time, selfing, hybrid necrosis, and partial hybrid sterility (Rieseberg and Blackman, 2010), while incompatibilities that are only expressed under certain conditions—for example, those involved in local adaptation—are generally missed, as are traits that are highly polygenic. A third limitation is that genes underlying complete F1 sterility or inviability are also missed, in this case because a recombinant mapping population is difficult or impossible to form. While a taxonomic skew may ultimately have negligible consequences for our understanding of the genetics of RI in plants more generally, the selection bias introduced by forward genetics precludes resolution to important questions, such as whether RI evolves most commonly by loci of large effect or typically has a polygenic basis.

Genomics, however, has begun to compensate for the limitations of forward genetics. For example, studying a case of hybrid necrosis in *A. thaliana* that kills F1 hybrids at the cotyledon stage, Barragan et al. (2021) overcame the inability to form an F2 mapping population by using genome-wide association analysis; the occurrence of necrosis in F1s from a large number of crosses between *A. thaliana* accessions was associated with a causative locus using variant information from the parental accessions. Although still limited to cases where incompatibility has a clear phenotype, genome-wide association studies hold great promise for identifying hybrid incompatibility loci, especially in natural hybrids (Powell et al., 2020). Another genomics approach is the use of population genomic scans between divergent species or populations (see The landscape of genomic divergence) to search for genomic regions with signals of natural selection (e.g., increased differentiation, decreased diversity, increased linkage disequilibrium, and differential gene expression). In *Mimulus*, an R2R3-MYB transcription factor, *MaMyb2*, which was identified as a candidate gene for differences in floral pigmentation (Streisfeld et al., 2013), has been shown to locate in a sharp peak of genomic differentiation (Stankowski et al., 2019). By performing a gene-based Hudson-Kreitman-Aguade test using population genomic data, Wang et al. (2021b) found a hybrid species of *Ostryopsis* to be isolated from its parents through inheritance of different alleles of parental isolating genes (see Speciation with gene flow, introgression, and hybrid speciation). In *Populus*, genome scanning was performed between *Populus euphratica* and *Populus pruinose*, and several highly diverged proteins were identified that are putatively involved in post-mating isolation between lineages (Ma et al., 2018). Such genome scans are particularly powerful when combined with genome-wide association analyses of phenotypic or environmental data. For example, by determining the timing of flowering, homologs of *FLOWERING LOCUS T* have been shown to facilitate ecotype formation in aspen (Wang et al., 2018) and sunflower (Todesco et al., 2020).

Although genomic methods have been successful in identifying candidate RI regions differentiating ecotypes or species, in most cases, the underlying genes and mutations have not been functionally validated or causally linked to RI barriers. There are a number of reasons for this. First, outlier loci from genome scans are not necessarily related to RI (as discussed in The landscape of genomic divergence). Second, incompatibilities between alleles or genes are poorly predicted from genomic data. Thus, functional analyses are still required to validate suspected RI genes. This is time consuming and technically challenging even in model species and can be further complicated by the polygenic architecture of RI seen in many systems (e.g., Zuellig and Sweigart 2018; Stankowski et al., 2019) and by the diversity of possible mutations underlying RI, which range from amino acid substitutions to regulatory changes to SVs (Rieseberg and Blackman, 2010). Last, even when RI genes have been functionally validated, only rarely has fieldwork been conducted to fully verify their role in RI.

While a purely genomics approach to identifying RI genes remains challenging, population genomics analyses can offer critical insight into the evolutionary history of known RI loci. Hybrid necrosis, for example, is typically caused by Bateson–Dobzhansky–Muller incompatibilities between immune system genes whose evolutionary dynamics are thought to be shaped by balancing selection because of varying pathogen pressures (Bomblies and Weigel, 2007; Li and Weigel, 2021). Arguably the strongest evidence of this comes from population genomics studies of two immune system genes, *NPR1* and *RPP5*, in the annual crucifer *Capsella grandiflora*. Here, balancing selection appears to have maintained compatible and incompatible alleles at *NPR1* in *C. grandiflora*, an ancient outcrosser, whereas alternative alleles are fixed in its selfing derivatives, *Capsella rubella* and *Capsella orientalis* (Sicard et al., 2015). In *Mimulus guttatus*, a hybrid necrosis allele has been swept to high frequency because of genetic hitchhiking with a copper tolerance allele favored by local selection to copper mine tailings (Figure 5; Wright et al., 2013). The locus controlling hybrid necrosis (*Nec1*) is tightly linked to the copper tolerance locus (*Tol1*), and markers linked to both exhibit high F_{ST} relative to unlinked markers (Figure 5; Wright et al., 2013). The nature of selection acting on these cases of hybrid necrosis is fairly clear, but this is not true for other classes of RI genes, such as those causing hybrid sterility. For example, an allele causing hybrid male sterility in *Mimulus* has undergone a strong selective

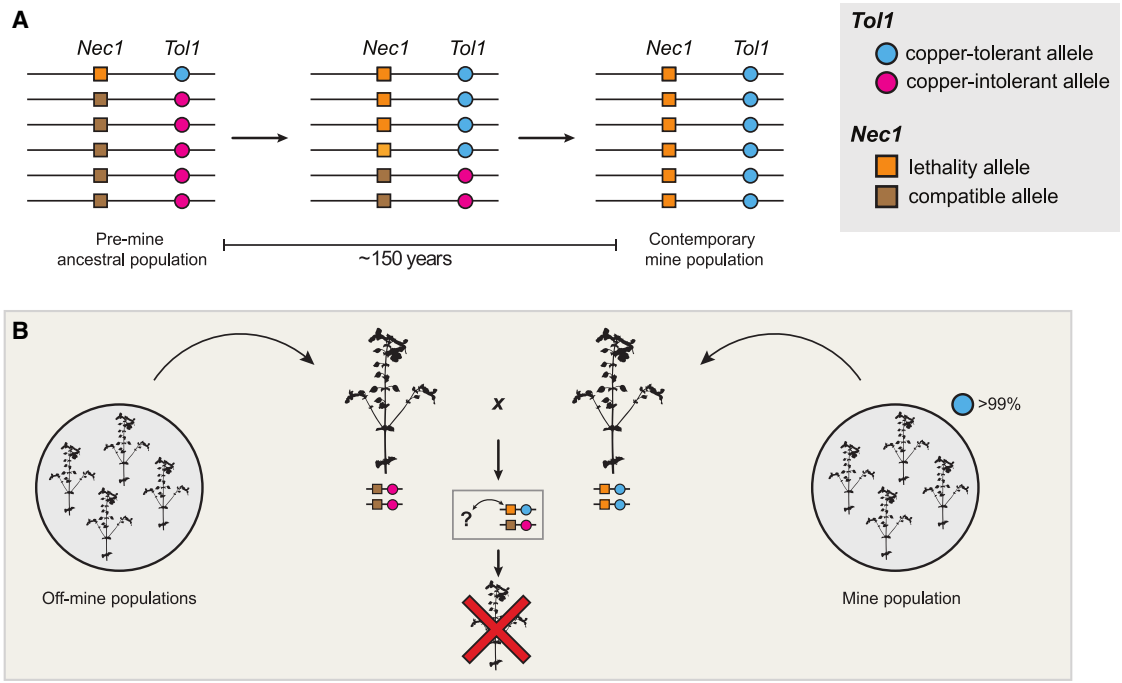

Figure 5. The evolution of a Bateson–Dobzhansky–Muller hybrid incompatibility because of genetic hitchhiking.
Results from Wright et al. (2013), focusing on *M. guttatus*, are used to illustrate this process.
(A) An allele at the *Tol1* locus that confers copper tolerance (blue circle) has swept to near-fixation (>99% frequency) in a copper mine population in California since the mine's inception around 150 years ago. A hybrid lethality allele (orange square) at the adjacent *Nec1* locus has been swept to high frequency alongside the copper-tolerant allele.
(B) The swept allele at *Nec1* causes hybrid necrosis in crosses between mine population plants and off-mine populations plants, interacting with several unknown loci to cause necrosis.

sweep (s = 0.15; Sweigart and Flagel, 2015), but what drove the sweep is not known (although genetic conflict has largely been ruled out; Kerwin and Sweigart, 2017). For several other cases of hybrid sterility, such as those in *Oryza*, population genomics analyses have yet to be performed. Such analyses will provide much-needed evidence toward whether these genes have evolved neutrally, through genetic conflict, or through some other form of selection (Fishman and Sweigart, 2018).

SOURCES OF GENETIC VARIATION UNDERLYING RI

Another important issue in speciation that can be addressed with genomics is the extent to which the evolution of RI arises from new mutations versus re-use of pre-existing variation (i.e., standing variation). This matters because evolution from standing variation can occur more quickly than when new mutations are required (Barrett and Schluter, 2008). Another advantage of standing variation is that alleles are older, permitting accumulation of multiple favorable mutations within alleles or assembly of cassettes of co-selected alleles held together by recombination suppressors, such as inversions (see Structural variation). Also, such alleles or cassettes may have already been tested by selection in an ancestral population or in a compatible congener when originating through introgression. Note that, while genetic variation originating from adaptive introgression may differ from intraspecific standing genetic variation in attributes such as initial frequency (Hedrick, 2013), we do not differentiate between the two here. If RI is a by-product of divergent natural selection, then evolution through standing variation can impact the genetic architecture of isolation by easing the conditions necessary for establishment of mutations with small or recessive effects (Hermisson and Pennings, 2005). Last, reliance on standing variation is expected to increase the repeatability of evolution (MacPherson and Nuismer, 2017; Thompson et al., 2019).

Mutation is the ultimate source of genetic variation, so whether evolution is from standing variation versus new mutations is a matter of timing and geography. Barrett and Schluter (2008) suggest three lines of evidence that would support evolution from standing variation: (1) the allele is present in ancestral or donor populations, (2) the allele is older than the ecotype or species in which it is found, and (3) the allele displays a signature of selection that is indicative of evolution from standing variation (Peter et al., 2012). In general, inferences based on (1) or (2) are more robust than (3) because they do not specify the mechanism by which an allele rises to high frequency and are largely unaffected by population structure or deviations from demographic assumptions that can distort signals from selective sweeps. In addition, inferences from the signature of selective sweeps will only be possible for very recent speciation events because the genomic footprint of selection is rapidly eroded by mutation and recombination (Racimo et al., 2014).

So what have we learned about the sources of variation from genomic studies of plant speciation? As expected, standing variation appears to play an important role in rapid speciation events, at least when speciation is driven by divergent natural selection.

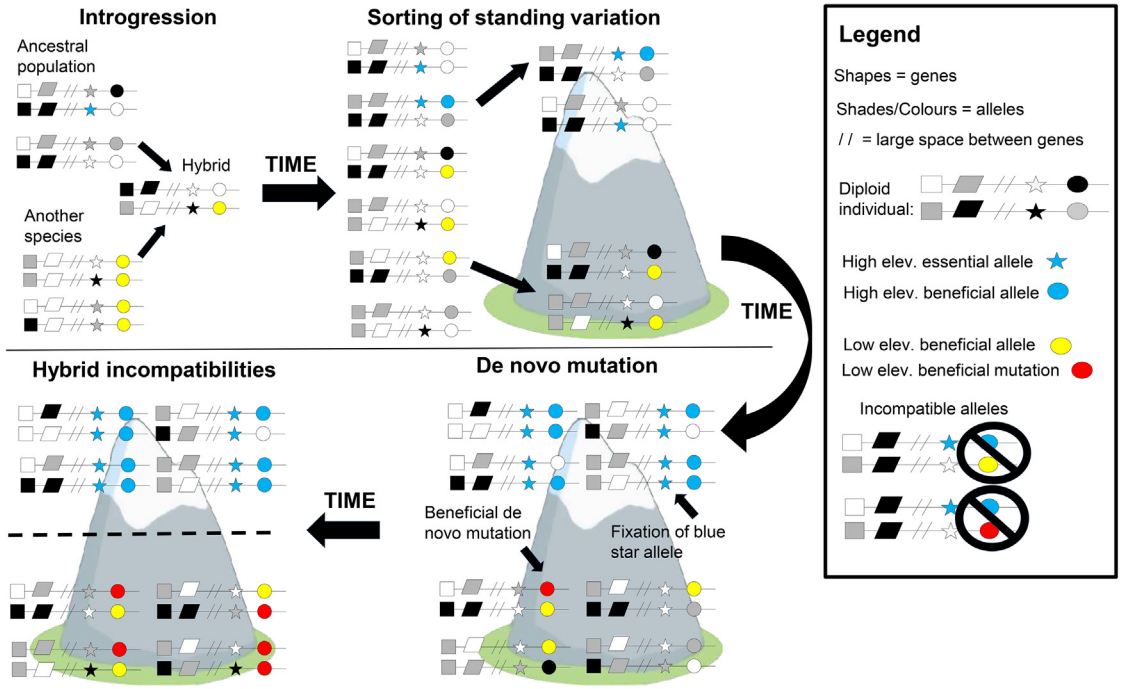

Figure 6. Hypothetical scenarios showing the influence of time and geography on introgression, selection on standing variation, and hybrid incompatibilities from *de novo* mutations.

Genetic loci are shapes. Alleles are shades/colors. Each species is shown as a few sample individuals. Each individual is diploid with two copies of each gene. Tightly linked genes are shown close together, far genes are separated by //. The ancestral blue alleles of the star and circle loci are essential or facilitate, respectively, survival at higher elevations. The yellow and red circle alleles are beneficial to low-elevation populations but cannot mix with the blue circle allele, impeding gene flow between high and low species. Introgression introduced the yellow allele to the ancestral population. Elevation is used as a visual example here, but this could equivalently be different niches of any type in the same location or different locations.

Examples include the origin of dune sunflower ecotypes in the southwestern US, in which traits associated with dune adaptation and RI map to inversions, which are old and pre-date ecotype divergence (Ostevik et al., 2016; Huang and Rieseberg, 2020; Todesco et al., 2020). Likewise, the *Metrosideros* adaptive radiation across the Hawaiian Islands appears to have been shaped by recurrent use of ancient variants (Choi et al., 2021). In *Arabidopsis*, parallel adaptation to high- and low-elevation environments is a consequence, in part, of re-use of ancestral standing variation (Bohutínská et al., 2021b). Other examples come from studies of adaptive introgression or homoploid hybrid speciation (see Speciation with gene flow, introgression, and hybrid speciation), in which alleles or SVs critical to RI have been identified in parental populations (Nevado et al., 2020; Todesco et al., 2020; Wang et al., 2021b). Finally, standing variation is also known to indirectly facilitate speciation by contributing to the persistence of new lineages. A notable example is adaptation to WGD in autotetraploid *Arabidopsis*, which was shown to involve standing genetic variation (Hollister et al., 2012; see also Polyploid speciation).

There is also ample evidence for the evolution of RI through new mutations. The clearest example is polyploid speciation (see Polyploid speciation), where RI is the result of a macro-mutation (i.e., WGD). There is also evidence that hybrid incompatibility barriers arising because of genetic conflict often rely on new mutations. For example, hybrid necrosis is now known to result from deleterious interactions between rapidly evolving disease resistance genes (Li and Weigel, 2021). Likewise, incompatibilities resulting from the spread of selfish genetic elements, such as cytoplasmic male sterility, typically appear to be a consequence of new mutations (Case and Willis, 2008; Rieseberg and Blackman, 2010).

In most cases, speciation will likely involve both standing variation and new mutations, with standing variation dominating during the early stages of speciation and new mutations at later stages (Figure 6). This expected progression is seen in experimental yeast populations exposed to different stress-inducing substances; some populations (but not others) rapidly depleted pre-existing variation in the first 30 generations, increasing their reliance on new mutations in later generations (Ament-Velásquez et al., 2022). In plants, changes in the relative importance of standing variation and new mutations over time have been inferred from observations that the repeatability of evolution is negatively correlated with genetic distance (Bohutínská et al., 2021b). Phylogenomic studies also offer the potential to estimate the relative importance of different sources of variation. This is illustrated by analyses of the wild tomato clade (*Solanum* section *Lycopersicon*), in which ancestral standing variation, introgression, and new mutations have contributed approximately equally to this recent adaptive radiation (Pease et al., 2016). We suspect that if a similar analysis was conducted of an older group, the relative importance of these different sources of variation would shift toward new mutations.

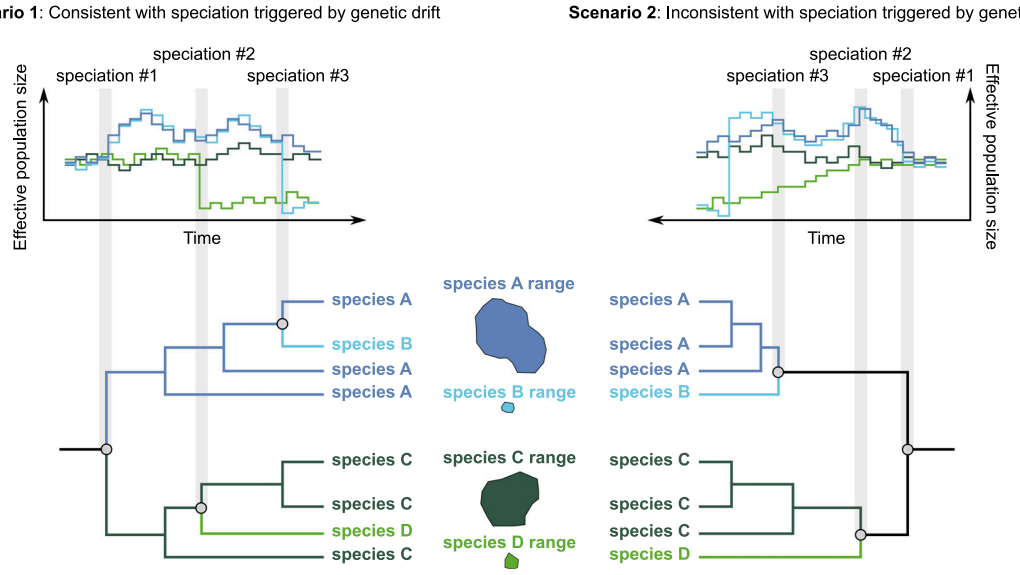

Figure 7. Genomics can facilitate the study of speciation that is triggered by genetic drift via phylogenomics and the reconstruction of demography.

Two hypothetical scenarios are considered, both of which result in the same contemporary differences in range size and population size among species. Only scenario 1 (left) is consistent with speciation triggered by genetic drift. In this case, two of the three speciation events (i.e., speciation 2 and speciation 3) could have been the direct result of drift-induced genetic changes because the timing of speciation (gray shading) coincides with sharp decreases in effective population size (top panels). Consistent with speciation triggered by genetic drift, the phylogeny on the left also identifies species A and C as paraphyletic.

THE DEMOGRAPHY OF SPECIATION

The contribution of reductions in population size to speciation has been the focus of substantial research interest and debate during much of the 20th century (Coyne and Orr, 2004). This was based on observations that (1) local or "budding" speciation appears to be common (reviewed in Crawford, 2010), (2) founding events on oceanic islands often lead to spectacular diversification (e.g., Carlquist, 1965), and (3) species differ by underdominant chromosomal rearrangements that could become established through genetic drift in small populations (White, 1973; Lande, 1979; reviewed in Huang and Rieseberg, 2020).

Models of speciation by genetic drift developed during this time viewed progenitor populations as evolutionarily static on account of their large size (Barton and Charlesworth, 1984; Charlesworth, 1995; Coyne and Orr, 2004). When new (descendant) populations were founded by a small number of individuals, however, it was suggested that decreases in genetic diversity could break evolutionary inertia, occasionally leading to RI. Under Mayr's genetic revolutions model, for example, a sudden reduction in genetic diversity was hypothesized to set off a genome-wide chain reaction, resulting in transition to new combinations of coadapted alleles that are advantageous in a more homozygous background and that confer some isolation from ancestral combinations of alleles (Mayr, 1942, 1954, 1963). Other models involving abrupt reductions in population size included the catastrophic speciation model (Lewis and Raven, 1958; Lewis, 1962) and the closely related quantum speciation model (Grant, 1981; Gottlieb, 2004) as well as the founder–flush–crash model (Carson, 1968, 1975, 1982) and the transilience model (Templeton, 1980, 1982).

Speciation by genetic drift has been put to the test using theoretical and experimental approaches. These studies provided little support for a causal role of population size contractions in speciation (Barton and Charlesworth, 1984; Charlesworth, 1995; Coyne and Orr, 2004). Theoretical work has criticized, for example, the assumption that large populations are more resistant to evolutionary change than small populations (Barton and Charlesworth, 1984). Also, studies using experimental populations offered limited evidence that RI could arise as a by-product of population bottlenecks (e.g., Moya et al., 1995; Rundle et al., 1998).

Genomics can complement theoretical and experimental tests of speciation by genetic drift via phylogenomics and reconstruction of long-term demography (Figure 7). Phylogenomics has been used, for example, to verify one of the predictions of speciation by genetic drift: that the descendant species is monophyletic within the paraphyletic progenitor (e.g., Andrew et al., 2013). In the case of *Clarkia franciscana*, which was considered a classic example of catastrophic speciation (Lewis and Raven, 1958), phylogenomics did not support this phylogenetic placement, refuting the possibility that speciation occurred by budding (Sianta and Kay, 2022), in line with earlier suspicions based on isozymes (Gottlieb, 1973). Reconstruction of long-term demography could be equally informative, although these methods have been used most often to establish whether divergence occurred with or without gene flow (see Speciation with gene flow, introgression, and hybrid speciation). Comparatively less emphasis has been placed on inferring changes in effective population size (Ne) at time points that overlap with speciation events despite the potential utility of such analyses (Figure 7). This is likely because obtaining

estimates of Ne at scales that exceed hundreds of thousands of generations remains challenging (Nadachowska-Brzyska et al., 2022). Demographic models could also be used to identify population bottlenecks that are coincident with speciation, and failing to account for this may lead to spurious speciation scenarios (Momigliano et al., 2021). Nonetheless, the small number of examples currently available do not support speciation by genetic drift. For example, in the budding speciation of *Mimulus nasutus* from *M. guttatus* (Brandvain et al., 2014) or of *C. rubella* from *C. grandiflora* (Foxe et al., 2009), reduced Ne in the descendant species has been attributed to the transition to selfing, which then contributed to speciation. As well, in island radiations such as that of *Metrosideros*, there is limited evidence that reductions in Ne track within-island diversification (Choi et al., 2021). In wild emmer wheat, recent sympatric speciation followed a population bottleneck, but other work suggested that RI was driven by disruptive ecological selection (Wang et al., 2020b). Broad re-analyses of genomic data from multiple systems with consistent methodology is needed to characterize the frequency of bottlenecks occurring shortly before or coincident with speciation.

CONCLUDING REMARKS

So what have we learned about speciation from genomic studies of plant species? Analyses of genomic differences between diverging populations and species have shown that the landscape of genomic divergence is highly heterogeneous, regardless of the stage or geography of speciation (see The landscape of genomic divergence). These observations, along with conceptual and theoretical advances, indicate that evolutionary factors responsible for this heterogeneity are complex and that such patterns reveal less about the genes and processes underlying RI than originally hoped for. However, such studies, when combined with comparisons of high-quality reference genomes, have revealed that genomic structural differences between species are far more abundant (see Structural variation) and play a much larger role in adaptive divergence and speciation than previously believed, especially via their effects on recombination suppression.

Genomic approaches have also proven to be highly effective in documenting gene flow and hybridization (see Speciation with gene flow, introgression and hybrid speciation). These studies have confirmed the importance of speciation with gene flow in plants, demonstrated the ubiquity of introgression, and revealed new instances of homoploid hybrid speciation while calling several earlier examples into question. Likewise, genomic studies have confirmed the ubiquity of polyploid speciation throughout the history of the plant kingdom, revealed the many genomic changes following polyploid speciation, and offered insights into the timing, mechanisms, and consequences of such changes (see Polyploid speciation).

As alluded to earlier, genomic studies have not offered a simple approach for identifying the genes and mutations underlying RI that was initially anticipated. Instead, genomic tools have mainly served as a means for speeding up forward genetic studies for RI gene identification and for determining the evolutionary mechanisms shaping their evolution (see The genetics of RI). However, genomic information has proven to be more directly useful for elucidating the origins of genetic variation that contributes to adaptive divergence and speciation (see Sources of genetic variation underlying RI). A major conclusion is that standing variation plays an important role in the early stages of plant speciation and contributes importantly to the repeatability of speciation. However, later in the speciation process, new mutations rule. Last, demographic modeling of the speciation process based on large genomics datasets has been shown to hold enormous promise for reconstructing the demographic history of speciation (see The demography of speciation), although the possibility that confounding variables, such as inclusion of admixed populations, bias these estimates should be properly addressed (Filatov et al., 2016). Importantly, demographic modeling studies available to date offer little support for earlier theories promoting important roles for population bottlenecks and drift in plant speciation.

Our review of the literature also suggests several promising avenues of future study. So far, most of what we have learned about speciation from genomics studies comes from analyses of SNPs. However, such studies provide an incomplete picture of speciation because much of the action likely involves epigenetic and structural changes. Future studies of the landscape of genomic divergence would be most powerful if they included epigenetic and structural variation, although we note that additional theoretical, conceptual, and computational advances will be necessary to fully analyze and understand such data sets. Such studies hold particular promise for assessing the role of epigenetic changes, potentially driven by repression of TE activity, as recombination modifiers.

Another gap, which is rapidly being filled, is that most of what we currently know about plant speciation genomics comes from a handful of experimental systems. *Arabidopsis*, *Mimulus*, and *Oryza* stand out, but we also have learned a great deal from genomics studies of *Helianthus*, *Populus*, *Senecio*, and *Solanum*. An obvious next step, which will happen without any urging from this review, will be to extend such work to other systems. At the other end of the spectrum, there are surprisingly few examples where the genes underlying RI traits have been functionally validated, the evolutionary forces underlying their evolution elucidated, and their effects on RI in natural populations demonstrated. Such vertical studies arguably offer more to our understanding of speciation than the many horizontal studies seen in the literature. Population genomics analyses of the many hybrid incompatibilities that have been cloned and characterized in *Arabidopsis* and rice offer a sensible way forward, maximizing insights about the evolution of RI genes with minimal effort (at least in terms of gathering new data because large genomics datasets exist for both taxa).

Last, we note that an enormous amount of genomics data has been generated for many different plant species and is freely accessible on NCBI and other databases. Much of these data have not been fully analyzed with respect to patterns of genomic divergence, structural variation, selective sweeps, introgression, diploidization, sources of variation, demographic history, cryptic lineages, and so forth. Careful and comprehensive analyses of such existing data should be a priority, as well as connecting

the results from such analyses to gene flow and RI in natural populations.

FUNDING

Research on the genomics of plant speciation in the Rieseberg and Owens labs has been supported by Discovery grants from the Natural Sciences and Engineering Research Council of Canada.

ACKNOWLEDGMENTS

No conflict of interest is declared.

Received: January 26, 2023
Revised: March 21, 2023
Accepted: April 6, 2023
Published: April 11, 2023

REFERENCES

Abbott, R., Albach, D., Ansell, S., Arntzen, J.W., Baird, S.J.E., Bierne, N., Boughman, J., Brelsford, A., Buerkle, C.A., Buggs, R., et al. (2013). Hybridization and speciation. J. Evol. Biol. **26**:229–246.

Ament-Velásquez, S.L., Gilchrist, C., Rêgo, A., Bendixsen, D.P., Brice, C., Grosse-Sommer, J.M., Rafati, N., and Stelkens, R. (2022). The dynamics of adaptation to stress from standing genetic variation and de novo mutations. Mol. Biol. Evol. **39**:msac242.

Anacker, B.L., and Strauss, S.Y. (2014). The geography and ecology of plant speciation: range overlap and niche divergence in sister species. Proc. Biol. Sci. **281**:20132980.

Anderson, E. (1948). Hybridization of the habitat. Evolution **2**:1–9.

Anderson, E. (1949). Introgressive Hybridization (New York: John Wiley and Sons, Inc.).

Anderson, E., and Stebbins, G.L. (1954). Hybridization as an evolutionary stimulus. Evolution **8**:378–388.

Andrew, R.L., and Rieseberg, L.H. (2013). Divergence is focused on few genomic regions early in speciation: incipient speciation of sunflower ecotypes. Evolution **67**:2468–2482.

Andrew, R.L., Kane, N.C., Baute, G.J., Grassa, C.J., and Rieseberg, L.H. (2013). Recent nonhybrid origin of sunflower ecotypes in a novel habitat. Mol. Ecol. **22**:799–813.

Arnold, M.L. (1997). Natural Hybridization and Evolution (USA: Oxford University Press).

Baack, E., Melo, M.C., Rieseberg, L.H., and Ortiz-Barrientos, D. (2015). The origins of reproductive isolation in plants. New Phytol. **207**:968–984.

Badaeva, E.D., Dedkova, O.S., Gay, G., Pukhalskyi, V.A., Zelenin, A.V., Bernard, S., and Bernard, M. (2007). Chromosomal rearrangements in wheat: their types and distribution. Genome **50**:907–926.

Baird, S.J.E. (2015). Exploring linkage disequilibrium. Mol. Ecol. Resour. **15**:1017–1019.

Baniaga, A.E., Marx, H.E., Arrigo, N., and Barker, M.S. (2020). Polyploid plants have faster rates of multivariate niche differentiation than their diploid relatives. Ecol. Lett. **23**:68–78.

Barb, J.G., Bowers, J.E., Renaut, S., Rey, J.I., Knapp, S.J., Rieseberg, L.H., and Burke, J.M. (2014). Chromosomal evolution and patterns of introgression in *Helianthus*. Genetics **197**:969–979.

Barker, M.S., Arrigo, N., Baniaga, A.E., Li, Z., and Levin, D.A. (2016a). On the relative abundance of autopolyploids and allopolyploids. New Phytol. **210**:391–398.

Barker, M.S., Li, Z., Kidder, T.I., Reardon, C.R., Lai, Z., Oliveira, L.O., Scascitelli, M., and Rieseberg, L.H. (2016). Most Compositae (Asteraceae) are descendants of a paleohexaploid and all share a paleotetraploid ancestor with the Calyceraceae. Am. J. Bot. **103**:1203–1211.

Barraclough, T.G., and Vogler, A.P. (2000). Detecting the geographical pattern of speciation from species-level phylogenies. Am. Nat. **155**:419–434.

Barragan, A.C., Collenberg, M., Wang, J., Lee, R.R.Q., Cher, W.Y., Rabanal, F.A., Ashkenazy, H., Weigel, D., and Chae, E. (2021). A truncated singleton NLR causes hybrid necrosis in *Arabidopsis thaliana*. Mol. Biol. Evol. **38**:557–574.

Barrett, R.D.H., and Schluter, D. (2008). Adaptation from standing genetic variation. Trends Ecol. Evol. **23**:38–44.

Barton, N.H., and Charlesworth, B. (1984). Genetic revolutions, founder effects, and speciation. Annu. Rev. Ecol. Syst. **15**:133–164.

Barton, N.H., and Hewitt, G.M. (1985). Analysis of hybrid zones. Annu. Rev. Ecol. Syst. **16**:113–148.

Benoit, M., Drost, H.-G., Catoni, M., Gouil, Q., Lopez-Gomollon, S., Baulcombe, D., and Paszkowski, J. (2019). Environmental and epigenetic regulation of Rider retrotransposons in tomato. PLoS Genet. **15**:e1008370.

Blackman, B.K. (2016). Speciation genes. In Encyclopedia of Evolutionary Biology, R.M. Kliman, ed. (Oxford Academic Press), pp. 166–175.

Blanc, G., and Wolfe, K.H. (2004). Widespread paleopolyploidy in model plant species inferred from age distributions of duplicate genes. Plant Cell **16**:1667–1678.

Blanc, G., Hokamp, K., and Wolfe, K.H. (2003). A recent polyploidy superimposed on older large-scale duplications in the *Arabidopsis* genome. Genome Res. **13**:137–144.

Bohutínská, M., Alston, M., Monnahan, P., Mandáková, T., Bray, S., Paajanen, P., Kolář, F., and Yant, L. (2021a). Novelty and convergence in adaptation to whole genome duplication. Mol. Biol. Evol. **38**:3910–3924.

Bohutínská, M., Vlček, J., Yair, S., Laenen, B., Konečná, V., Fracassetti, M., Slotte, T., and Kolář, F. (2021). Genomic basis of parallel adaptation varies with divergence in *Arabidopsis* and its relatives. Proc. Natl. Acad. Sci. USA **118**. e2022713118.

Bomblies, K., Higgins, J.D., and Yant, L. (2015). Meiosis evolves: adaptation to external and internal environments. New Phytol. **208**:306–323.

Bomblies, K., and Weigel, D. (2007). Hybrid necrosis: autoimmunity as a potential gene-flow barrier in plant species. Nat. Rev. Genet. **8**:382–393.

Bowers, J.E., Chapman, B.A., Rong, J., and Paterson, A.H. (2003). Unravelling angiosperm genome evolution by phylogenetic analysis of chromosomal duplication events. Nature **422**:433–438.

Bradshaw, H.D., Wilbert, S.M., Otto, K.G., and Schemske, D.W. (1995). Genetic mapping of floral traits associated with reproductive isolation in monkeyflowers (*Mimulus*). Nature **376**:762–765.

Brandvain, Y., Kenney, A.M., Flagel, L., Coop, G., and Sweigart, A.L. (2014). Speciation and introgression between *Mimulus nasutus* and *Mimulus guttatus*. PLoS Genet. **10**:e1004410.

Brennan, A.C., Bridle, J.R., Wang, A.L., Hiscock, S.J., and Abbott, R.J. (2009). Adaptation and selection in the Senecio (Asteraceae) hybrid zone on mount etna, sicily. New Phytol. **183**:702–717.

Brennan, A.C., Hiscock, S.J., and Abbott, R.J. (2019). Completing the hybridization triangle: the inheritance of genetic incompatibilities during homoploid hybrid speciation in ragworts (*Senecio*). AoB Plants **11**:ply078.

Buckler, E.S., 4th, Phelps-Durr, T.L., Buckler, C.S., Dawe, R.K., Doebley, J.F., and Holtsford, T.P. (1999). Meiotic drive of chromosomal knobs reshaped the maize genome. Genetics **153**:415–426.

Buerkle, C.A., Morris, R.J., Asmussen, M.A., and Rieseberg, L.H. (2000). The likelihood of homoploid hybrid speciation. Heredity **84**:441–451.

Buerkle, C.A., Wolf, D.E., and Rieseberg, L.H. (2003). The origin and extinction of species through hybridization. In Population Viability in Plants: Conservation, Management, and Modelling of Rare Plants, C.A. Brigham and M.W. Schwartz, eds. (Heidelberg: Springer Verlag), pp. 117–141.

Buggs, R.J.A., Zhang, L., Miles, N., Tate, J.A., Gao, L., Wei, W., Schnable, P.S., Barbazuk, W.B., Soltis, P.S., and Soltis, D.E. (2011). Transcriptomic shock generates evolutionary novelty in a newly formed, natural allopolyploid plant. Curr. Biol. **21**:551–556.

Burri, R. (2017). Interpreting differentiation landscapes in the light of long-term linked selection. Evol. Lett. **1**:118–131.

Butelli, E., Licciardello, C., Zhang, Y., Liu, J., Mackay, S., Bailey, P., Reforgiato-Recupero, G., and Martin, C. (2012). Retrotransposons control fruit-specific, cold-dependent accumulation of anthocyanins in blood oranges. Plant Cell **24**:1242–1255.

Carlquist, S.J. (1965). Island Life; a Natural History of the Islands of the World (New York, New York: Natural History Press).

Carson, H.L. (1968). The population flush and its genetic consequences. In Population Biology and Evolution, R.C. Lewontin, ed.. 137 (Syracuse, New York: Syracuse University Press), p. 123.

Carson, H.L. (1975). The genetics of speciation at the diploid level. Am. Nat. **109**:83–92.

Carson, H.L. (1982). Speciation as a major reorganization of polygenic balances. In Mechanisms of Speciation, C. Baigozzi, ed. (New York, New York, USA: Alan R. Liss), pp. 411–433.

Case, A.L., and Willis, J.H. (2008). Hybrid male sterility in *Mimulus* (Phrymaceae) is associated with a geographically restricted mitochondrial rearrangement. Evolution **62**:1026–1039.

Castelletti, S., Tuberosa, R., Pindo, M., and Salvi, S. (2014). A MITE transposon insertion is associated with differential methylation at the maize flowering time QTL Vgt1. G3 **4**:805–812.

Cavrak, V.V., Lettner, N., Jamge, S., Kosarewicz, A., Bayer, L.M., and Mittelsten Scheid, O. (2014). How a retrotransposon exploits the plant's heat stress response for its activation. PLoS Genet. **10**:e1004115.

Chae, E., Bomblies, K., Kim, S.-T., Karelina, D., Zaidem, M., Ossowski, S., Martín-Pizarro, C., Laitinen, R.A.E., Rowan, B.A., Tenenboim, H., et al. (2014). Species-wide genetic incompatibility analysis identifies immune genes as hot spots of deleterious epistasis. Cell **159**:1341–1351.

Chandler, J.M., Jan, C.-C., and Beard, B.H. (1986). Chromosomal differentiation among the annual *Helianthus* species. Syst. Bot. **11**:354–371.

Chang, J.-T., Chao, C.-T., Nakamura, K., Liu, H.-L., Luo, M.-X., and Liao, P.-C. (2022). Divergence with gene flow and contrasting population size blur the species boundary in Cycas sect. Asiorientales, as inferred from morphology and RAD-seq data. Front. Plant Sci. **13**:824158.

Chapman, M.A., Hiscock, S.J., and Filatov, D.A. (2013). Genomic divergence during speciation driven by adaptation to altitude. Mol. Biol. Evol. **30**:2553–2567.

Charlesworth, B. (1995). Speciation: down the bottleneck? Curr. Biol. **5**:995–996.

Charlesworth, B., and Barton, N.H. (2018). The spread of an inversion with migration and selection. Genetics **208**:377–382.

Chmátal, L., Gabriel, S.I., Mitsainas, G.P., Martínez-Vargas, J., Ventura, J., Searle, J.B., Schultz, R.M., and Lampson, M.A. (2014). Centromere strength provides the cell biological basis for meiotic drive and karyotype evolution in mice. Curr. Biol. **24**:2295–2300.

Choi, J.Y., Purugganan, M., and Stacy, E.A. (2020). Divergent selection and primary gene flow shape incipient speciation of a riparian tree on Hawaii island. Mol. Biol. Evol. **37**:695–710.

Choi, J.Y., Dai, X., Alam, O., Peng, J.Z., Rughani, P., Hickey, S., Harrington, E., Juul, S., Ayroles, J.F., Purugganan, M.D., and Stacy, E.A. (2021). Ancestral polymorphisms shape the adaptive radiation of *Metrosideros* across the Hawaiian Islands. Proc. Natl. Acad. Sci. USA **118**. e2023801118.

Clark, F.E., and Akera, T. (2021). Unravelling the mystery of female meiotic drive: where we are. Open Biol. **11**:210074.

Clausen, J. (1951). Stages in the Evolution of Plant Species (Ithaca, New York: Cornell University Press).

Clausen, J., Keck, D.D., and Hiesey, W.M. (1945). Experimental Studies on the Nature of Species. II. Plant Evolution through Amphiploidy, with Examples from the Madiinae (Washington, D.C., USA: Carnegie Institute of Washington).

Coen, E.S., Carpenter, R., and Martin, C. (1986). Transposable elements generate novel spatial patterns of gene expression in *Antirrhinum majus*. Cell **47**:285–296.

Coughlan, J.M., and Willis, J.H. (2019). Dissecting the role of a large chromosomal inversion in life history divergence throughout the*Mimulus guttatus* species complex. Mol. Ecol. **28**:1343–1357.

Coyne, J.A., and Orr, H.A. (2004). Speciation (MA: Sinauer associates Sunderland).

Crawford, D.J. (2010). Progenitor-derivative species pairs and plant speciation. Taxon **59**:1413–1423.

Crowl, A.A., Myers, C., and Cellinese, N. (2017). Embracing discordance: phylogenomic analyses provide evidence for allopolyploidy leading to cryptic diversity in a Mediterranean *Campanula* (Campanulaceae) clade. Evolution **71**:913–922.

Cruickshank, T.,E., and Hahn, M.W. (2014). Reanalysis suggests that genomic islands of speciation are due to reduced diversity, not reduced gene flow. Mol. Ecol. **23**:3133–3157.

Dagilis, A.J., and Kirkpatrick, M. (2016). Prezygotic isolation, mating preferences, and the evolution of chromosomal inversions. Evolution **70**:1465–1472.

Dagilis, A.J., Peede, D., Coughlan, J.M., Jofre, G.I., D'Agostino, E.R.R., Mavengere, H., Tate, A.D., and Matute, D.R. (2021). 15 years of introgression studies: quantifying gene flow across Eukaryotes. Preprint at bioRxiv. https://doi.org/10.1101/2021.06.15.448399.

Darlington, C.D. (1937). Recent Advances in Cytology (Philadelphia: Blakiston).

Darlington, C.D. (1953). Polyploidy in animals. Nature **171**:191–194.

Darwin, C. (1859). On the Origin of Species (London: John Murray).

de Vos, J.M., Augustijnen, H., Bätscher, L., and Lucek, K. (2020). Speciation through chromosomal fusion and fission in lepidoptera. Philos. Trans. R. Soc. Lond. B Biol. Sci. **375**:20190539.

Dobzhansky, T. (1937). Genetics and the Origin of Species. Columbia Classics (New York: Columbia University Press).

Dobzhansky, T. (1940). Speciation as a stage in evolutionary divergence. Am. Nat. **74**:312–321.

Doyle, J.J., and Coate, J.E. (2019). Polyploidy, the nucleotype, and novelty: the impact of genome doubling on the biology of the cell. Int. J. Plant Sci. **180**:1–52.

Doyle, J.J., Flagel, L.E., Paterson, A.H., Rapp, R.A., Soltis, D.E., Soltis, P.S., and Wendel, J.F. (2008). Evolutionary genetics of genome merger and doubling in plants. Annu. Rev. Genet. **42**:443–461.

Eaton, D.A.R., and Ree, R.H. (2013). Inferring phylogeny and introgression using RADseq data: an example from flowering plants (*pedicularis*: orobanchaceae). Syst. Biol. **62**:689–706.

Fang, Z., Pyhäjärvi, T., Weber, A.L., Dawe, R.K., Glaubitz, J.C., de González, J.J.S., Ross-Ibarra, C., Doebley, J., Morrell, P.L., and Ross-Ibarra, J. (2012). Megabase-scale inversion polymorphism in the wild ancestor of maize. Genetics **191**:883–894.

Feder, J.L., Gejji, R., Powell, T.H.Q., and Nosil, P. (2011). Adaptive chromosomal divergence driven by mixed geographic mode of evolution. Evolution **65**:2157–2170.

Feng, L., Ruhsam, M., Wang, Y.H., Li, Z.H., and Wang, X.M. (2020). Using demographic model selection to untangle allopatric divergence and diversification mechanisms in the Rheum palmatum complex in the Eastern Asiatic Region. Mol. Ecol. **29**:1791–1805.

Filatov, D.A., Osborne, O.G., and Papadopulos, A.S.T. (2016). Demographic history of speciation in a Senecio altitudinal hybrid zone on Mt. Etna. Mol. Ecol. **25**:2467–2481.

Finseth, F.R., Nelson, T.C., and Fishman, L. (2021). Selfish chromosomal drive shapes recent centromeric histone evolution in monkeyflowers. PLoS Genet. **17**:e1009418.

Fishman, L., and Saunders, A. (2008). Centromere-associated female meiotic drive entails male fitness costs in monkeyflowers. Science **322**:1559–1562.

Fishman, L., and Sweigart, A.L. (2018). When two rights make a wrong: the evolutionary genetics of plant hybrid incompatibilities. Annu. Rev. Plant Biol. **69**:707–731.

Fishman, L., Stathos, A., Beardsley, P.M., Williams, C.F., and Hill, J.P. (2013). Chromosomal rearrangements and the genetics of reproductive barriers in *Mimulus* (monkey flowers). Evolution **67**:2547–2560.

Fitzpatrick, B.M., and Turelli, M. (2006). The geography of mammalian speciation: mixed signals from phylogenies and range maps. Evolution **60**:601–615.

Foxe, J.P., Slotte, T., Stahl, E.A., Neuffer, B., Hurka, H., and Wright, S.I. (2009). Recent speciation associated with the evolution of selfing in *Capsella*. Proc. Natl. Acad. Sci. USA **106**:5241–5245.

Fransz, P., Linc, G., Lee, C.-R., Aflitos, S.A., Lasky, J.R., Toomajian, C., Ali, H., Peters, J., van Dam, P., Ji, X., et al. (2016). Molecular, genetic and evolutionary analysis of a paracentric inversion in *Arabidopsis thaliana*. Plant J. **88**:159–178.

Garcia-Mas, J., Benjak, A., Sanseverino, W., Bourgeois, M., Mir, G., González, V.M., Hénaff, E., Câmara, F., Cozzuto, L., Lowy, E., et al. (2012). The genome of melon (*Cucumis melo* L.). Proc. Natl. Acad. Sci. USA **109**:11872–11877.

Gopinathan, M.C., and Babu, C.R. (1986). Meiotic studies of the F1 hybrid between rice bean (*Vigna umbellata*) and its wild relative *V. minima*. Genetica **71**:115–117.

Gottlieb, L.D. (1973). Enzyme differentiation and phylogeny in *Clarkia franciscana, C. rubicunda* and *C. amoena*. Evolution **27**:205–214.

Gottlieb, L.D. (1984). Genetics and morphological evolution in plants. Am. Nat. **123**:681–709.

Gottlieb, L.D. (2004). Rethinking classic examples of recent speciation in plants. New Phytol. **161**:71–82.

Goulet-Scott, B.E., Garner, A.G., and Hopkins, R. (2021). Genomic analyses overturn two long-standing homoploid hybrid speciation hypotheses. Evolution **75**:1699–1710.

Grant, V. (1981). Plant Speciation (New York, USA: Columbia University Press).

Griffiths, S., Sharp, R., Foote, T.N., Bertin, I., Wanous, M., Reader, S., Colas, I., and Moore, G. (2006). Molecular characterization of Ph1 as a major chromosome pairing locus in polyploid wheat. Nature **439**:749–752.

Grossenbacher, D.L., Veloz, S.D., and Sexton, J.P. (2014). Niche and range size patterns suggest that speciation begins in small, ecologically diverged populations in North American monkeyflowers (*Mimulus* spp.): niche and range size patterns. Evolution **68**:1270–1280.

Kato Yamakake, T.A. (1976). Cytological Studies of Maize [*Zea mays* L.] and Teosinte [*Zea mexicana* Schrader Kuntze] in Relation to Their Origin and Evolution (Amherst: Bulletin of the Massachusetts Agricultural Experimental Station).

Grünig, S., Fischer, M., and Parisod, C. (2021). Recent hybrid speciation at the origin of the narrow endemic *Pulmonaria helvetica*. Ann. Bot. **127**:21–31.

Guerrero, R.F., and Hahn, M.W. (2017). Speciation as a sieve for ancestral polymorphism. Mol. Ecol. **26**:5362–5368.

Guerrero, R.F., and Kirkpatrick, M. (2014). Local adaptation and the evolution of chromosome fusions. Evolution **68**:2747–2756.

Hahn, M.W. (2018). Molecular Population Genetics (New York : Sunderland, MA: Oxford University Press; Sinauer Associates).

He, Z., Li, X., Yang, M., Wang, X., Zhong, C., Duke, N.C., Wu, C.-I., and Shi, S. (2019). Speciation with gene flow via cycles of isolation and migration: insights from multiple mangrove taxa. Natl. Sci. Rev. **6**:275–288.

Hedrick, P.W. (2013). Adaptive introgression in animals: examples and comparison to new mutation and standing variation as sources of adaptive variation. Mol. Ecol. **22**:4606–4618.

Hermisson, J., and Pennings, P.S. (2005). Soft sweeps: molecular population genetics of adaptation from standing genetic variation. Genetics **169**:2335–2352.

Hibbins, M.S., and Hahn, M.W. (2022). Phylogenomic approaches to detecting and characterizing introgression. Genetics **220**:iyab173.

Hilu, K.W. (1983). The role of single-gene mutations in the evolution of flowering plants. In Evolutionary Biology, M.K. Hecht, B. Wallace, and G.T. Prance, eds. (Boston: Springer), pp. 97–128.

Hoban, S., Kelley, J.L., Lotterhos, K.E., Antolin, M.F., Bradburd, G., Lowry, D.B., Poss, M.L., Reed, L.K., Storfer, A., and Whitlock, M.C. (2016). Finding the genomic basis of local adaptation: pitfalls, practical solutions, and future directions. Am. Nat. **188**:379–397.

Hollister, J.D., Arnold, B.J., Svedin, E., Xue, K.S., Dilkes, B.P., and Bomblies, K. (2012). Genetic adaptation associated with genome-doubling in autotetraploid *Arabidopsis arenosa*. PLoS Genet. **8**:e1003093.

Hopkins, R. (2013). Reinforcement in plants. New Phytol. **197**:1095–1103.

Hu, T.T., Pattyn, P., Bakker, E.G., Cao, J., Cheng, J.-F., Clark, R.M., Fahlgren, N., Fawcett, J.A., Grimwood, J., Gundlach, H., et al. (2011). The *Arabidopsis lyrata* genome sequence and the basis of rapid genome size change. Nat. Genet. **43**:476–481.

Huang, S., Li, R., Zhang, Z., et al. (2009). The genome of the cucumber,*Cucumis sativus* L. Nat. Genet. **41**:1275–1281.

Huang, C.-H., Zhang, C., Liu, M., Hu, Y., Gao, T., Qi, J., and Ma, H. (2016). Multiple polyploidization events across Asteraceae with two nested events in the early history revealed by nuclear phylogenomics. Mol. Biol. Evol. **33**:2820–2835.

Huang, K., and Rieseberg, L.H. (2020). Frequency, origins, and evolutionary role of chromosomal inversions in plants. Front. Plant Sci. **11**:296.

Huang, K., Andrew, R.L., Owens, G.L., Ostevik, K.L., and Rieseberg, L.H. (2020). Multiple chromosomal inversions contribute to adaptive divergence of a dune sunflower ecotype. Mol. Ecol. **29**:2535–2549.

Igea, J., Bogarín, D., Papadopulos, A.S.T., and Savolainen, V. (2015). A comparative analysis of island floras challenges taxonomy-based biogeographical models of speciation. Evolution **69**:482–491.

Iida, S., Morita, Y., Choi, J.-D., Park, K.-I., and Hoshino, A. (2004). Genetics and epigenetics in flower pigmentation associated with transposable elements in morning glories. Adv. Biophys. **38**:141–159.

James, M.E., Arenas-Castro, H., Groh, J.S., Allen, S.L., Engelstädter, J., and Ortiz-Barrientos, D. (2021). Highly replicated evolution of parapatric ecotypes. Mol. Biol. Evol. **38**:4805–4821.

Jiao, W.-B., and Schneeberger, K. (2019). Chromosome-level assemblies of multiple *Arabidopsis* genomes reveal hotspots of rearrangements with altered evolutionary dynamics. Nat. Commun. **11**:1–10.

Jiao, Y., Wickett, N.J., Ayyampalayam, S., Chanderbali, A.S., Landherr, L., Ralph, P.E., Tomsho, L.P., Hu, Y., Liang, H., Soltis, P.S., et al. (2011). Ancestral polyploidy in seed plants and angiosperms. Nature **473**:97–100.

Jones, K. (1998). Robertsonian fusion and centric fission in karyotype evolution of higher plants. Bot. Rev. **64**:273–289.

Zeng, K., and Corcoran, P. (2015). The effects of background and interference selection on patterns of genetic variation in subdivided populations. Genetics **201**:1539–1554.

Kalendar, R., Tanskanen, J., Immonen, S., Nevo, E., and Schulman, A.H. (2000). Genome evolution of wild barley (*Hordeum spontaneum*) by BARE -1 retrotransposon dynamics in response to sharp microclimatic divergence. Proc. Natl. Acad. Sci. USA **97**:6603–6607.

Kantar, M.B., Sosa, C.C., Khoury, C.K., Castañeda-Álvarez, N.P., Achicanoy, H.A., Bernau, V., Kane, N.C., Marek, L., Seiler, G., and Rieseberg, L.H. (2015). Ecogeography and utility to plant breeding of the crop wild relatives of sunflower (*Helianthus annuus* L.). Front. Plant Sci. **6**:841.

Ke, F., Vasseur, L., Yi, H., Yang, L., Wei, X., Wang, B., and Kang, M. (2022). Gene flow, linked selection, and divergent sorting of ancient polymorphism shape genomic divergence landscape in a group of edaphic specialists. Mol. Ecol. **31**:104–118.

Kenney, A.M., and Sweigart, A.L. (2016). Reproductive isolation and introgression between sympatric *Mimulus* species. Mol. Ecol. **25**:2499–2517.

Kent, T.V., Uzunović, J., and Wright, S.I. (2017). Coevolution between transposable elements and recombination. Phil. Trans. R. Soc. B. **372**:20160458.

Kenton, A. (1981). Chromosome evolution in the *Gibasis linearis* alliance (Commelinaceae): 1. The Robertsonian differentiation of *G. venustula* and *G. speciosa*. Chromosoma **84**:291–304.

Kerwin, R.E., and Sweigart, A.L. (2017). Mechanisms of transmission ratio distortion at hybrid sterility loci within and between *Mimulus* species. G3 **7**:3719–3730.

Kianian, S.F., and Quiros, C.F. (1992). Generation of a *Brassica oleracea* composite RFLP map: linkage arrangements among various populations and evolutionary implications. Theor. Appl. Genet. **84**:544–554.

King, M. (1995). Species Evolution: The Role of Chromosome Change (Cambridge: Cambridge University Press).

Kirkpatrick, M., and Barton, N. (2006). Chromosome inversions, local adaptation and speciation. Genetics **173**:419–434.

Kisel, Y., and Barraclough, T.G. (2010). Speciation has a spatial scale that depends on levels of gene flow. Am. Nat. **175**:316–334.

Kuwada, Y. (1915). Ueber die Chromosomenzahl von *Zea Mays* L. Shokubutsugaku Zasshi **29**:69–91.

Lai, Z., Nakazato, T., Salmaso, M., Burke, J.M., Tang, S., Knapp, S.J., and Rieseberg, L.H. (2005). Extensive chromosomal repatterning and the evolution of sterility barriers in hybrid sunflower species. Genetics **171**:291–303.

Lande, R. (1979). Effective deme sizes during long-term evolution estimated from rates of chromosomal rearrangement. Evolution **33**:234–251.

Lee, C.R., Wang, B., Mojica, J.P., et al. (2017). Young inversion with multiple linked QTLs under selection in a hybrid zone. Nat. Ecol. Evol. **1**:119.

One Thousand Plant Transcriptomes Initiative, Barker, M.S., Carpenter, E.J., Deyholos, M.K., Gitzendanner, M.A., Graham, S.W., Grosse, I., Li, Z., Melkonian, M., Mirarab, S., et al. (2019). One thousand plant transcriptomes and the phylogenomics of green plants. Nature **574**:679–685.

Lei, L., Goltsman, E., Goodstein, D., Wu, G.A., Rokhsar, D.S., and Vogel, J.P. (2021). Plant pan-genomics comes of age. Annu. Rev. Plant Biol. **72**:411–435.

Leroy, T., Louvet, J.-M., Lalanne, C., Le Provost, G., Labadie, K., Aury, J.-M., Delzon, S., Plomion, C., and Kremer, A. (2020). Adaptive introgression as a driver of local adaptation to climate in European white oaks. New Phytol. **226**:1171–1182.

Lewis, H. (1962). Catastrophic selection as a factor in speciation. Evolution **16**:257–271.

Lewis, H., and Raven, P.H. (1958). Rapid evolution in *Clarkia*. Evolution **12**:319–336.

Li, L., and Weigel, D. (2021). One hundred years of hybrid necrosis: hybrid autoimmunity as a window into the mechanisms and evolution of plant-pathogen interactions. Annu. Rev. Phytopathol. **59**:213–237.

Li, Z., Baniaga, A.E., Sessa, E.B., Scascitelli, M., Graham, S.W., Rieseberg, L.H., and Barker, M.S. (2015). Early genome duplications in conifers and other seed plants. Sci. Adv. **1**:e1501084.

Li, J., Zhong, L., Wang, J., Ma, T., Mao, K., and Zhang, L. (2021). Genomic insights into speciation history and local adaptation of an alpine aspen in the Qinghai–Tibet Plateau and adjacent highlands. J. Syst. Evol. **59**:1220–1231.

Li, H., Wang, S., Chai, S., Yang, Z., Zhang, Q., Xin, H., Xu, Y., Lin, S., Chen, X., Yao, Z., et al. (2022a). Graph-based pan-genome reveals structural and sequence variations related to agronomic traits and domestication in cucumber. Nat. Commun. **13**:1–14.

Li, M., Zhang, H., Yang, Y., Wang, H., Xue, Z., Fan, Y., Sun, P., Zhang, H., Zhang, X., and Jin, W. (2022). Rosa1, a transposable element-like insertion, produces red petal coloration in rose through altering RcMYB114 transcription. Front. Plant Sci. **13**:857684.

Liu, J., and Dawe, R.K. (2022). Large haplotypes highlight a complex age structure within the maize pan-genome. Preprint at bioRxiv. https://doi.org/10.1101/2022.02.22.481510.

Liu, Y., Wang, S., Li, L., Yang, T., Dong, S., Wei, T., Wu, S., Liu, Y., Gong, Y., Feng, X., et al. (2022). The *Cycas* genome and the early evolution of seed plants. Nat. Plants **8**:389–401.

Liu, J., He, Y., Amasino, R., and Chen, X. (2004). siRNAs targeting an intronic transposon in the regulation of natural flowering behavior in *Arabidopsis*. Genes Dev. **18**:2873–2878.

Lotsy, J.P. (1925). Species or linneon. Genetica **7**:487–506.

Lowry, D.B. (2012). Ecotypes and the controversy over stages in the formation of new species. Biol. J. Linn. Soc. **106**:241–257.

Lowry, D.B., and Willis, J.H. (2010). A widespread chromosomal inversion polymorphism contributes to a major life-history transition, local adaptation, and reproductive isolation. PLoS Biol. **8**:e1000500.

Lowry, D.B., Modliszewski, J.L., Wright, K.M., Wu, C.A., and Willis, J.H. (2008). The strength and genetic basis of reproductive isolating barriers in flowering plants. Phil. Trans. R. Soc. B. **363**:3009–3021.

Lutz, A.M. (1907). A preliminary note on the chromosomes of oenothera lamarckiana and one of its mutants, O. Gigas. Science **26**:151–152.

Ma, T., Wang, K., Hu, Q., Xi, Z., Wan, D., Wang, Q., Feng, J., Jiang, D., Ahani, H., Abbott, R.J., et al. (2018). Ancient polymorphisms and divergence hitchhiking contribute to genomic islands of divergence within a poplar species complex. Proc. Natl. Acad. Sci. USA **115**:E236–E243.

Ma, Y., Wang, J., Hu, Q., Li, J., Sun, Y., Zhang, L., Abbott, R.J., Liu, J., and Mao, K. (2019). Ancient introgression drives adaptation to cooler and drier mountain habitats in a cypress species complex. Commun. Biol. **2**:213.

MacPherson, A., and Nuismer, S.L. (2017). The probability of parallel genetic evolution from standing genetic variation. J. Evol. Biol. **30**:326–337.

Maguilla, E., Escudero, M., Hipp, A.L., and Luceño, M. (2017). Allopatric speciation despite historical gene flow: divergence and hybridization in *Carex furva* and *C. lucennoiberica* (Cyperaceae) inferred from plastid and nuclear RAD -seq data. Mol. Ecol. **26**:5646–5662.

Mallet, J. (2005). Hybridization as an invasion of the genome. Trends Ecol. Evol. **20**:229–237.

Mandakova, T., Singh, V., Kraemer, U., and Lysak, M.A. (2015). Genome structure of the heavy metal hyperaccumulator *Noccaea caerulescens* and its stability on metalliferous and nonmetalliferous soils. Plant Physiol **169**:674–689.

Mandáková, T., Pouch, M., Harmanová, K., Zhan, S.H., Mayrose, I., and Lysak, M.A. (2017). Multispeed genome diploidization and diversification after an ancient allopolyploidization. Mol. Ecol. **26**:6445–6462.

Mandáková, T., and Lysak, M.A. (2018). Post-polyploid diploidization and diversification through dysploid changes. Curr. Opin. Plant Biol. **42**:55–65.

Marburger, S., Monnahan, P., Seear, P.J., Martin, S.H., Koch, J., Paajanen, P., Bohutínská, M., Higgins, J.D., Schmickl, R., and Yant, L. (2019). Interspecific introgression mediates adaptation to whole genome duplication. Nat. Commun. **10**:5218.

Martin, G., Baurens, F.C., Hervouet, C., Salmon, F., Delos, J.M., Labadie, K., Perdereau, A., Mournet, P., Blois, L., Dupouy, M., et al. (2020). Chromosome reciprocal translocations have accompanied subspecies evolution in bananas. Plant J. **104**:1698–1711.

Mason, A.S., and Wendel, J.F. (2020). Homoeologous exchanges, segmental allopolyploidy, and polyploid genome evolution. Front. Genet. **11**:1014.

Masterson, J. (1994). Stomatal size in fossil plants: evidence for polyploidy in majority of angiosperms. Science **264**:421–424.

Matthey-Doret, R., and Whitlock, M.C. (2019). Background selection and F_{ST}: consequences for detecting local adaptation. Mol. Ecol. **28**:3902–3914.

Mayr, E. (1942). Systematics and the Origin of Species (New York: Columbia University Press).

Mayr, E. (1954). Change of genetic environment and evolution (London: Allen & Unwin), pp. 157–180.

Mayr, E. (1963). Animal Species and Evolution (Cambridge, MA: Harvard University Press).

Mayrose, I., Zhan, S.H., Rothfels, C.J., Magnuson-Ford, K., Barker, M.S., Rieseberg, L.H., and Otto, S.P. (2011). Recently formed polyploid plants diversify at lower rates. Science **333**:1257.

Mayrose, I., Zhan, S.H., Rothfels, C.J., Arrigo, N., Barker, M.S., Rieseberg, L.H., and Otto, S.P. (2015). Methods for studying polyploid diversification and the dead end hypothesis: a reply to Soltis et al. (2014). New Phytol. **206**:27–35.

McClintock, B. (1950). The origin and behavior of mutable loci in maize. Proc. Natl. Acad. Sci. USA **36**:344–355.

Melo, M.C., James, M.E., Roda, F., Bernal-Franco, D., Wilkinson, M.J., Liu, H., Walter, G.M., and Ortiz-Barrientos, D. (2019). Evidence for mutation-order speciation in an Australian wildflower. Preprint at bioRxiv. https://doi.org/10.1101/692673.

Mendel, G. (1965). Experiments in Plant Hybridisation (Cambridge, MA: Harvard University Press).

Mérot, C., Oomen, R.A., Tigano, A., and Wellenreuther, M. (2020). A roadmap for understanding the evolutionary significance of structural genomic variation. Trends Ecol. Evol. **35**:561–572.

Momigliano, P., Florin, A.-B., and Merilä, J. (2021). Biases in demographic modeling affect our understanding of recent divergence. Mol. Biol. Evol. **38**:2967–2985.

Morgan, C., Zhang, H., Henry, C.E., Franklin, F.C.H., and Bomblies, K. (2020). Derived alleles of two axis proteins affect meiotic traits in autotetraploid *Arabidopsis arenosa*. Proc. Natl. Acad. Sci. USA **117**:8980–8988.

Morgan, C., White, M.A., Franklin, F.C.H., Zickler, D., Kleckner, N., and Bomblies, K. (2021). Evolution of crossover interference enables stable autopolyploidy by ensuring pairwise partner connections in *Arabidopsis arenosa*. Curr. Biol. **31**:4713–4726.e4.

Morin, P.A., Luikart, G., and Wayne, R.K.; the SNP Workshop Group (2004). SNPs in ecology, evolution and conservation. Trends Ecol. Evol. **19**:208–216.

Morjan, C.L., and Rieseberg, L.H. (2004). How species evolve collectively: implications of gene flow and selection for the spread of advantageous alleles. Mol. Ecol. **13**:1341–1356.

Moya, A., Galiana, A., and Ayala, F.J. (1995). Founder-effect speciation theory: failure of experimental corroboration. Proc. Natl. Acad. Sci. USA **92**:3983–3986.

Muir, C.D., and Hahn, M.W. (2015). The limited contribution of reciprocal gene loss to increased speciation rates following whole-genome duplication. Am. Nat. **185**:70–86.

Müntzing, A. (1936). The evolutionary significance of autopolyploidy. Hereditas **21**:363–378.

Nadachowska-Brzyska, K., Konczal, M., and Babik, W. (2022). Navigating the temporal continuum of effective population size. Methods Ecol. Evol. **13**:22–41.

Nakazato, T., Rieseberg, L.H., and Wood, T.E. (2013). The genetic basis of speciation in the Giliopsis lineage of *Ipomopsis* (Polemoniaceae). Heredity **111**:227–237.

Navarro, A., and Barton, N.H. (2003). Accumulating postzygotic isolation genes in parapatry: a new twist on chromosomal speciation. Evolution **57**:447–459.

Nevado, B., Harris, S.A., Beaumont, M.A., and Hiscock, S.J. (2020). Rapid homoploid hybrid speciation in British gardens: the origin of Oxford ragwort (*Senecio squalidus*). Mol. Ecol. **29**:4221–4233.

Nieto Feliner, G., Álvarez, I., Fuertes-Aguilar, J., Heuertz, M., Marques, I., Moharrek, F., Piñeiro, R., Riina, R., Rosselló, J.A., Soltis, P.S., and Villa-Machío, I. (2017). Is homoploid hybrid speciation that rare? An empiricist's view. Heredity **118**:513–516.

Noor, M.A., Grams, K.L., Bertucci, L.A., and Reiland, J. (2001). Chromosomal inversions and the reproductive isolation of species. Proc. Natl. Acad. Sci. USA **98**:12084–12088.

Nosil, P. (2012). Ecological Speciation (Oxford: Oxford University Press).

Nosil, P., and Feder, J.L. (2012). Genomic divergence during speciation: causes and consequences. Phil. Trans. R. Soc. B. **367**:332–342.

Nosil, P., Funk, D.J., and Ortiz-Barrientos, D. (2009). Divergent selection and heterogeneous genomic divergence. Mol. Ecol. **18**:375–402.

Okamoto, M. (1957). Asynaptic effect of chromosome V. Wheat Inf. Serv. **5**:6.

Ortiz-Barrientos, D., Engelstädter, J., and Rieseberg, L.H. (2016). Recombination rate evolution and the origin of species. Trends Ecol. Evol. **31**:226–236.

Osborne, O.G., Batstone, T.E., Hiscock, S.J., and Filatov, D.A. (2013). Rapid speciation with gene flow following the formation of Mt. Etna. Genome Biol. Evol. **5**:1704–1715.

Ostevik, K.L., Andrew, R.L., Otto, S.P., and Rieseberg, L.H. (2016). Multiple reproductive barriers separate recently diverged sunflower ecotypes: reproductive barriers between sunflower ecotypes. Evolution **70**:2322–2335.

Ostevik, K.L., Samuk, K., and Rieseberg, L.H. (2020). Ancestral reconstruction of karyotypes reveals an exceptional rate of nonrandom chromosomal evolution in sunflower. Genetics **214**:1031–1045.

Otto, S.P., and Whitton, J. (2000). Polyploid incidence and evolution. Annu. Rev. Genet. **34**:401–437.

Ouyang, Y., and Zhang, Q. (2018). The molecular and evolutionary basis of reproductive isolation in plants. J. Genet. Genomics **45**:613–620.

Owens, G.L., Todesco, M., Bercovich, N., Légaré, J.S., Mitchell, N., Whitney, K.D., and Rieseberg, L.H. (2021). Standing variation rather than recent adaptive introgression probably underlies differentiation of the texanus subspecies of *Helianthus annuus*. Mol. Ecol. **30**:6229–6245.

Owens, G.L., Huang, K., Todesco, M., and Rieseberg, L.H. (2023). Re-evaluating Homoploid Reticulate Evolution in Helianthus Sunflowers. Molecular biology and evolution **40**:msad013. https://doi.org/10.1093/molbev/msad013.

Papadopulos, A.S.T., Baker, W.J., Crayn, D., Butlin, R.K., Kynast, R.G., Hutton, I., and Savolainen, V. (2011). Speciation with gene flow on lord howe island. Proc. Natl. Acad. Sci. USA **108**:13188–13193.

Papadopulos, A.S.T., Kaye, M., Devaux, C., Hipperson, H., Lighten, J., Dunning, L.T., Hutton, I., Baker, W.J., Butlin, R.K., and Savolainen, V. (2014). Evaluation of genetic isolation within an island flora reveals unusually widespread local adaptation and supports sympatric speciation. Phil. Trans. R. Soc. B. **369**:20130342.

Payseur, B.A., and Rieseberg, L.H. (2016). A genomic perspective on hybridization and speciation. Mol. Ecol. **25**:2337–2360.

Pease, J.B., Haak, D.C., Hahn, M.W., and Moyle, L.C. (2016). Phylogenomics reveals three sources of adaptive variation during a rapid radiation. PLoS Biol. **14**:e1002379.

Peter, B.M., Huerta-Sanchez, E., and Nielsen, R. (2012). Distinguishing between selective sweeps from standing variation and from a de novo mutation. PLoS Genet. **8**:e1003011.

Poland, J.A., and Rife, T.W. (2012). Genotyping-by-Sequencing for plant breeding and genetics. Plant Genome **5**, plantgenome2012.05.0005.

Powell, D.L., García-Olazábal, M., Keegan, M., Reilly, P., Du, K., Díaz-Loyo, A.P., Banerjee, S., Blakkan, D., Reich, D., Andolfatto, P., et al. (2020). Natural hybridization reveals incompatible alleles that cause melanoma in swordtail fish. Science **368**:731–736.

Price, T. (2007). Speciation in Birds (Greenwood Village, Colorado: Roberts and Company Publishers).

Qin, P., Lu, H., Du, H., Wang, H., Chen, W., Chen, Z., He, Q., Ou, S., Zhang, H., Li, X., et al. (2021). Pan-genome analysis of 33 genetically diverse rice accessions reveals hidden genomic variations. Cell **184**:3542–3558.e16.

Quattrocchio, F., Wing, J., van der Woude, K., Souer, E., de Vetten, N., Mol, J., and Koes, R. (1999). Molecular analysis of the anthocyanin2 gene of Petunia and its role in the evolution of flower color. Plant Cell **11**:1433–1444.

Racimo, F., Kuhlwilm, M., and Slatkin, M. (2014). A test for ancient selective sweeps and an application to candidate sites in modern humans. Mol. Biol. Evol. **31**:3344–3358.

Ramsey, J. (2011). Polyploidy and ecological adaptation in wild yarrow. Proc. Natl. Acad. Sci. USA **108**:7096–7101.

Rendón-Anaya, M., Wilson, J., Sveinsson, S., Fedorkov, A., Cottrell, J., Bailey, M.E.S., Ruņis, D., Lexer, C., Jansson, S., Robinson, K.M., et al. (2021). Adaptive introgression facilitates adaptation to high latitudes in European aspen (*Populus tremula* L.). Mol. Biol. Evol. **38**:5034–5050.

Rieseberg, L.H. (1997). Hybrid origins of plant species. Annu. Rev. Ecol. Syst. **28**:359–389.

Rieseberg, L.H. (2001). Chromosomal rearrangements and speciation. Trends Ecol. Evol. **16**:351–358.

Rieseberg, L.H., and Blackman, B.K. (2010). Speciation genes in plants. Ann. Bot. **106**:439–455.

Rieseberg, L.H., and Willis, J.H. (2007). Plant speciation. Science **317**:910–914.

Rothfels, C.J. (2021). Polyploid phylogenetics. New Phytol. **230**:66–72.

Roux, C., Fraïsse, C., Romiguier, J., Anciaux, Y., Galtier, N., and Bierne, N. (2016). Shedding light on the grey zone of speciation along a continuum of genomic divergence. PLoS Biol. **14**. e2000234.

Ru, D., Sun, Y., Wang, D., Chen, Y., Wang, T., Hu, Q., Abbott, R.J., and Liu, J. (2018). Population genomic analysis reveals that homoploid hybrid speciation can be a lengthy process. Mol. Ecol. **27**:4875–4887.

Rundle, H.D., Mooers, A.Ø., and Whitlock, M.C. (1998). Single founder-flush events and the evolution of reproductive isolation. Evolution **52**:1850–1855.

Rutherford, S., van der Merwe, M., Wilson, P.G., Kooyman, R.M., and Rossetto, M. (2019). Managing the risk of genetic swamping of a rare and restricted tree. Conserv. Genet. **20**:1113–1131.

Savolainen, V., Anstett, M.-C., Lexer, C., Hutton, I., Clarkson, J.J., Norup, M.V., Powell, M.P., Springate, D., Salamin, N., and Baker, W.J. (2006). Sympatric speciation in palms on an oceanic island. Nature **441**:210–213.

Scannell, D.R., Byrne, K.P., Gordon, J.L., Wong, S., and Wolfe, K.H. (2006). Multiple rounds of speciation associated with reciprocal gene loss in polyploid yeasts. Nature **440**:341–345.

Schaal, S.M., Haller, B.C., and Lotterhos, K.E. (2022). Inversion invasions: when the genetic basis of local adaptation is concentrated within inversions in the face of gene flow. Phil. Trans. R. Soc. B. **377**:20210200.

Schluter, D. (2009). Evidence for ecological speciation and its alternative. Science **323**:737–741.

Schluter, D., and Rieseberg, L.H. (2022). Three problems in the genetics of speciation by selection. Proc. Natl. Acad. Sci. USA **119**. e2122153119.

Schranz, M.E., Lysak, M.A., and Mitchell-Olds, T. (2006). The ABC's of comparative genomics in the Brassicaceae: building blocks of crucifer genomes. Trends Plant Sci. **11**:535–542.

Schumer, M., Rosenthal, G.G., and Andolfatto, P. (2014). How common in homoploid hybrid speciation? Evolution **68**:1553–1560.

Seear, P.J., France, M.G., Gregory, C.L., Heavens, D., Schmickl, R., Yant, L., and Higgins, J.D. (2020). A novel allele of ASY3 is associated with greater meiotic stability in autotetraploid *Arabidopsis lyrata*. PLoS Genet. **16**:e1008900.

Seehausen, O., Butlin, R.K., Keller, I., Wagner, C.E., Boughman, J.W., Hohenlohe, P.A., Peichel, C.L., Saetre, G.P., Bank, C., Brännström, A., et al. (2014). Genomics and the origin of species. Nat. Rev. Genet. **15**:176–192.

Shang, H., Rendón-Anaya, M., Paun, O., Field, D.L., Hess, J., Vogl, C., Liu, J., Ingvarsson, P.K., Lexer, C., and Leroy, T. (2022). Drivers of genomic landscapes of differentiation across *Populus* divergence gradient. Preprint at bioRxiv. https://doi.org/10.1101/2021.08.26.457771.

Shapiro, B. (2017). Pathways to de-extinction: how close can we get to resurrection of an extinct species? Funct. Ecol. **31**:996–1002.

Sianta, S.A., and Kay, K.M. (2022). Phylogenomic analysis does not support a classic but controversial hypothesis of progenitor-derivative origins for the serpentine endemic Clarkia franciscana. Evolution **76**:1246–1259.

Sicard, A., Kappel, C., Josephs, E.B., Lee, Y.W., Marona, C., Stinchcombe, J.R., Wright, S.I., and Lenhard, M. (2015). Divergent sorting of a balanced ancestral polymorphism underlies the establishment of gene-flow barriers in Capsella. Nat. Commun. **6**:1–10.

Slotkin, R.K., and Martienssen, R. (2007). Transposable elements and the epigenetic regulation of the genome. Nat. Rev. Genet. **8**:272–285.

Sobel, J.M., Chen, G.F., Watt, L.R., and Schemske, D.W. (2010). The biology of speciation. Evolution **64**:295–315.

Soltis, D.E., Soltis, P.S., Schemske, D.W., Hancock, J.F., Thompson, J.N., Husband, B.C., and Judd, W.S. (2007). Autopolyploidy in angiosperms: have we grossly underestimated the number of species? Taxon **56**:13–30.

Soltis, D.E., Albert, V.A., Leebens-Mack, J., Bell, C.D., Paterson, A.H., Zheng, C., Sankoff, D., de Pamphilis, C.W., Wall, P.K., and Soltis, P.S. (2009). Polyploidy and angiosperm diversification. Am. J. Bot. **96**:336–348.

Soltis, D.E., Buggs, R.J., Doyle, J.J., and Soltis, P.S. (2010). What we still don't know about polyploidy. Taxon **59**:1387–1403.

Soltis, D.E., Segovia-Salcedo, M.C., Jordon-Thaden, I., Majure, L., Miles, N.M., Mavrodiev, E.V., Mei, W., Cortez, M.B., Soltis, P.S., and Gitzendanner, M.A. (2014). Are polyploids really evolutionary dead-ends (again)? A critical reappraisal of Mayrose et al. (2011). New Phytol. **202**:1105–1117.

Stankowski, S., Chase, M.A., Fuiten, A.M., Rodrigues, M.F., Ralph, P.L., and Streisfeld, M.A. (2019). Widespread selection and gene flow shape the genomic landscape during a radiation of monkeyflowers. PLoS Biol. **17**:e3000391.

Stathos, A., and Fishman, L. (2014). Chromosomal rearrangements directly cause underdominant F1 pollen sterility in *Mimulus lewisii–Mimulus cardinalis* hybrids. Evolution **68**:3109–3119.

Stebbins, G.L. (1947). Types of polyploids: their classification and significance. In Advances in Genetics, M. Demerec, ed. (Cambridge Massachusetts, MA: Academic Press), pp. 403–429.

Stebbins, G.L. (1950). Variation and Evolution in Plants (New York: Columbia University Press).

Stebbins, G.L. (1959). The role of hybridization in evolution. Proc. Am. Philos. Soc. **103**:231–251.

Stebbins, G.L. (1971). Chromosomal Evolution in Higher Plants (London: Edward Arnold).

Stein, J., Quarin, C.L., Martínez, E.J., Pessino, S.C., and Ortiz, J.P.A. (2004). Tetraploid races of *Paspalum notatum* show polysomic inheritance and preferential chromosome pairing around the apospory-controlling locus. Theor. Appl. Genet. **109**:186–191.

Strasburg, J.L., and Rieseberg, L.H. (2011). Interpreting the estimated timing of migration events between hybridizing species. Mol. Ecol. **20**:2353–2366.

Strasburg, J.L., Kane, N.C., Raduski, A.R., Bonin, A., Michelmore, R., and Rieseberg, L.H. (2011). Effective population size is positively correlated with levels of adaptive divergence among annual sunflowers. Mol. Biol. Evol. **28**:1569–1580.

Streisfeld, M.A., Young, W.N., and Sobel, J.M. (2013). Divergent selection drives genetic differentiation in an R2R3-MYB transcription factor that contributes to incipient speciation in Mimulus aurantiacus. PLoS Genet. **9**:e1003385.

Suarez-Gonzalez, A., Hefer, C.A., Christe, C., Corea, O., Lexer, C., Cronk, Q.C.B., and Douglas, C.J. (2016). Genomic and functional approaches reveal a case of adaptive introgression from *Populus balsamifera* (balsam poplar) in *P. trichocarpa* (black cottonwood). Mol. Ecol. **25**:2427–2442.

Suarez-Gonzalez, A., Lexer, C., and Cronk, Q.C.B. (2018). Adaptive introgression: a plant perspective. Biol. Lett. **14**:20170688.

Sweigart, A.L., and Flagel, L.E. (2015). Evidence of natural selection acting on a polymorphic hybrid incompatibility locus in Mimulus. Genetics **199**:543–554.

Tavares, M.M., Ferro, M., Leal, B.S.S., and Palma-Silva, C. (2022). Speciation with gene flow between two Neotropical sympatric species (*Pitcairnia* spp.: bromeliaceae). Ecol. Evol. **12**:e8834.

Templeton, A.R. (1980). The theory of speciation via the founder principle. Genetics **94**:1011–1038.

Templeton, A.R. (1982). Genetic architectures of speciation. In Mechanisms of Speciation, C. Baigozzi, ed.. 121 (New York, New York, USA: Alan R. Liss), p. 105.

Thompson, K.A., Osmond, M.M., and Schluter, D. (2019). Parallel genetic evolution and speciation from standing variation. Evol. Lett. **3**:129–141.

Ting, Y.C. (1964). Chromosomes of Maize-Teosinte Hybrids (Cambridge, Massachusetts: The Bussey Institute of Harvard University).

Todesco, M., Pascual, M.A., Owens, G.L., Ostevik, K.L., Moyers, B.T., Hübner, S., Heredia, S.M., Hahn, M.A., Caseys, C., Bock, D.G., and Rieseberg, L.H. (2016). Hybridization and extinction. Evol. Appl. **9**:892–908.

Todesco, M., Owens, G.L., Bercovich, N., Légaré, J.S., Soudi, S., Burge, D.O., Huang, K., Ostevik, K.L., Drummond, E.B.M., Imerovski, I., et al. (2020). Massive haplotypes underlie ecotypic differentiation in sunflowers. Nature **584**:602–607.

Trickett, A.J., and Butlin, R.K. (1994). Recombination suppressors and the evolution of new species. Heredity **73**:339–345.

Turesson, G. (1922). The species and the variety as ecological units. Hereditas **3**:100–113.

Vaid, N., and Laitinen, R.A.E. (2019). Diverse paths to hybrid incompatibility in Arabidopsis. Plant J. **97**:199–213.

Via, S. (2009). Natural selection in action during speciation. Proc. Natl. Acad. Sci. USA **106**:9939–9946.

Via, S. (2012). Divergence hitchhiking and the spread of genomic isolation during ecological speciation-with-gene-flow. Phil. Trans. R. Soc. B. **367**:451–460.

Wallace, A.R. (1889). Darwinism: An Exposition of the Theory of Natural Selection with Some of its Applications (New York: Macmillan and Company).

Wang, J., Ding, J., Tan, B., Robinson, K.M., Michelson, I.H., Johansson, A., Nystedt, B., Scofield, D.G., Nilsson, O., Jansson, S., et al. (2018). A major locus controls local adaptation and adaptive life history variation in a perennial plant. Genome Biol. **19**:1–17.

Wang, B., Mojica, J.P., Perera, N., Lee, C.-R., Lovell, J.T., Sharma, A., Adam, C., Lipzen, A., Barry, K., Rokhsar, D.S., et al. (2019). Ancient polymorphisms contribute to genome-wide variation by long-term balancing selection and divergent sorting in *Boechera stricta*. Genome Biol. **20**:1–15.

Wang, J., Yu, J., Sun, P., Li, C., Song, X., Lei, T., Li, Y., Yuan, J., Sun, S., Ding, H., et al. (2020a). Paleo-polyploidization in lycophytes. Genom. Proteom. Bioinform. **18**:333–340.

Wang, H., Yin, H., Jiao, C., Fang, X., Wang, G., Li, G., Ni, F., Li, P., Su, P., Ge, W., et al. (2020b). Sympatric speciation of wild emmer wheat driven by ecology and chromosomal rearrangements. Proc. Natl. Acad. Sci. USA **117**:5955–5963.

Wang, X., Liu, S., Zuo, H., Zheng, W., Zhang, S., Huang, Y., Pingcuo, G., Ying, H., Zhao, F., Li, Y., et al. (2021a). Genomic basis of high-altitude adaptation in Tibetan Prunus fruit trees. Curr. Biol. **31**:3848–3860.e8.

Wang, Z., Jiang, Y., Bi, H., Lu, Z., Ma, Y., Yang, X., Chen, N., Tian, B., Liu, B., Mao, X., et al. (2021b). Hybrid speciation via inheritance of alternate alleles of parental isolating genes. Mol. Plant **14**:208–222.

Wang, Z., Kang, M., Li, J., Zhang, Z., Wang, Y., Chen, C., Yang, Y., and Liu, J. (2022). Genomic evidence for homoploid hybrid speciation between ancestors of two different genera. Nat. Commun. **13**:1–9.

Wellenreuther, M., Mérot, C., Berdan, E., and Bernatchez, L. (2019). Going beyond SNPs: the role of structural genomic variants in adaptive evolution and species diversification. Mol. Ecol. **28**:1203–1209.

Wendel, J.F. (2015). The wondrous cycles of polyploidy in plants. Am. J. Bot. **102**:1753–1756.

White, M.J.D. (1973). Animal Cytology and Evolution (Cambridge: Cambridge University Press).

Wilkes, H.G. (1967). Teosinte: The Closest Relative of Maize (Cambridge, Massachusetts: The Bussey Institute of Harvard University).

Wilkinson, M.J., Roda, F., Walter, G.M., James, M.E., Nipper, R., Walsh, J., Allen, S.L., North, H.L., Beveridge, C.A., and Ortiz-Barrientos, D. (2021). Adaptive divergence in shoot gravitropism creates hybrid sterility in an Australian wildflower. Proc. Natl. Acad. Sci. USA **118**. e2004901118.

Wong, E.L.Y., Nevado, B., Osborne, O.G., Papadopulos, A.S.T., Bridle, J.R., Hiscock, S.J., and Filatov, D.A. (2020). Strong divergent selection at multiple loci in two closely related species of ragworts adapted to high and low elevations on Mount Etna. Mol. Ecol. **29**:394–412.

Wood, T.E., Takebayashi, N., Barker, M.S., Mayrose, I., Greenspoon, P.B., and Rieseberg, L.H. (2009). The frequency of polyploid speciation in vascular plants. Proc. Natl. Acad. Sci. USA **106**:13875–13879.

Wright, K.M., Lloyd, D., Lowry, D.B., Macnair, M.R., and Willis, J.H. (2013). Indirect evolution of hybrid lethality due to linkage with selected locus in *Mimulus guttatus*. PLoS Biol. **11**:e1001497.

Wu, C.-I. (2001). The genic view of the process of speciation. J. Evol. Biol. **14**:851–865.

Wu, C.A., Lowry, D.B., Cooley, A.M., Wright, K.M., Lee, Y.W., and Willis, J.H. (2008). Mimulus is an emerging model system for the integration of ecological and genomic studies. Heredity **100**:220–230.

Yant, L., Hollister, J.D., Wright, K.M., Arnold, B.J., Higgins, J.D., Franklin, F.C.H., and Bomblies, K. (2013). Meiotic adaptation to genome duplication in *Arabidopsis arenosa*. Curr. Biol. **23**:2151–2156.

Yelina, N.E., Lambing, C., Hardcastle, T.J., Zhao, X., Santos, B., and Henderson, I.R. (2015). DNA methylation epigenetically silences crossover hot spots and controls chromosomal domains of meiotic recombination in *Arabidopsis*. Genes Dev. **29**:2183–2202.

Yuan, Y., Bayer, P.E., Batley, J., and Edwards, D. (2021). Current status of structural variation studies in plants. Plant Biotechnol. J. **19**:2153–2163.

Zalmat, A.S., Sotola, V.A., Nice, C.C., and Martin, N.H. (2021). Genetic structure in Louisiana Iris species reveals patterns of recent and historical admixture. Am. J. Bot. **108**:2257–2268.

Zhang, Q.-J., and Gao, L.-Z. (2017). Rapid and recent evolution of LTR retrotransposons drives rice genome evolution during the speciation of AA-genome *Oryza* species. G3 **7**:1875–1885.

Zhou, Y., Minio, A., Massonnet, M., Solares, E., Lv, Y., Beridze, T., Cantu, D., and Gaut, B.S. (2019). The population genetics of structural variants in grapevine domestication. Nat. Plants **5**:965–979.

Zielinski, M.-L., and Mittelsten Scheid, O. (2012). Meiosis in polyploid plants. In Polyploidy and Genome Evolution, P.S. Soltis and D.E. Soltis, eds. (Berlin, Heidelberg: Springer), pp. 33–55.

Zuellig, M.P., and Sweigart, A.L. (2018). Gene duplicates cause hybrid lethality between sympatric species of Mimulus. PLoS Genet. **14**:e1007130.