

Review

# Mixing It Up: The Role of Hybridization in Forest Management and Conservation under Climate Change

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**Abstract:** Forest tree hybrid zones provide a wealth of novel genetic variation that can be harnessed to safeguard populations in changing climates. In the past 30 years, natural and artificial forest hybrid zones have facilitated significant contributions to selective breeding programs, conservation, and our understanding of the evolutionary processes and mechanisms that influence the maintenance of species and community interactions. This review highlights advances in these areas using forest hybrid zones. Taking examples from well-known genera, including eucalypt, poplar, oak and spruce, this review details the important role hybrid zones play in managing conservation of genetic variation, the environmental and non-environmental factors that influence barriers to reproduction, and the impact that genetic ancestry may have on community biodiversity. Given increasing concern surrounding species adaptability under rapidly changing conditions, we describe how the study of forest hybrid zones, using quantitative and genomic approaches, can facilitate conservation of genetic diversity and long-term species management.

**Keywords:** hybridization; introgression; climate change; eucalypt; spruce; poplar; genomics

## 1. Introduction

Hybridization is an important component of the evolution of modern plants and animals [1–4]. With up to 25% of plant species thought to be of hybrid origin, hybridization is increasingly recognized as an important mechanism involved in generating novel genetic recombinants [5–7]. These new recombinant types are important components of evolutionary change, providing natural systems that are involved in the creation or maintenance of species differences. Indeed, where ecological differences exist between hybridizing species, evaluation of the fine-scale transfer of genetic material between species provides useful insight into the genetic architecture of important traits involved in adaptation [8]. Thus, exploring novel genetic variation in natural hybrid zones provides a better appreciation of the processes involved in speciation and adaptation.

Interspecific hybridization may be particularly valuable in long-lived forest species, where generation length and reduced mutation rates limit accumulation of novel genetic variation [9–11]. Given the pace of global environmental change, the ability of plants to adapt to changing pressures is crucial for long-term species persistence. Populations must either be phenotypically plastic, undergo rapid adaptive evolution or migrate to permissive environments to ensure continued survival [12,13]. However, populations may not have sufficient genetic variation for an adaptive response if reduced migration limits a species' ability to track fitness optima or increased geographic isolation limits migration across heterogeneous environments [14,15]. Thus, interspecific gene flow via natural hybrid zones may generate the necessary genetic variation to adapt to changing selective pressures.

The maintenance of genetic diversity provides the basis for future adaptation, thus natural hybrid zones offer a valuable tool for exploring the genetic and phenotypic consequences of interspecific recombination. Traditionally, forest managers and researchers alike have explored genetic variation within 'pure' species to understand the mechanisms that contribute to local adaptation [16,17]. To this end, traditional provenance trials and genomic data, alongside environmental data, have been used to better understand the molecular basis of phenotypic variation within species and identify genetic variation that may be managed for adaptation [18–22]. However, natural hybrid zones may circumvent the time required to develop and test experimental crosses not feasible in many forest species.

The goal of this review is to outline factors that influence the formation and maintenance of natural hybrid zones and consider their implications in forest breeding, conservation, and adaptation under changing climates. Given current rates of climate change and predicted shifts in community composition and function, we suggest that an understanding of hybrid zone dynamics is essential to managing increasingly heterogeneous landscapes. Using examples from some of the world's key forest genera (i.e., eucalypt, oak, poplar and spruce), we show that studies of hybrid zones have influenced tree breeding, community ecology, species predictions under climate change, and conservation. These examples illustrate that species' persistence in the face of changing climate will be impacted by their capacity to adapt to these new conditions, and potentially altered interactions with other species as they too respond to changing climate. Finally, we draw attention to gaps in our current methodology and understanding that could benefit from further study, and highlight ways in which new genomic technologies could be used to advance these study areas.

## 2. What Is a Hybrid Zone?

Hybridization is broadly defined as the successful mating between individuals from two populations, or groups of populations, that are differentiated on the basis of one or more heritable traits [23,24]. Thus, the term 'hybrid' is applied to offspring of an initial cross between parental lineages (i.e., F1s), as well as subsequent crosses (e.g., backcrosses, F2s, etc.) within populations. Artificial hybridization beyond the F1-generation is a major component of plant breeding programs, and both artificial and natural hybridization result in progeny of varying degrees of admixture. A hybrid zone refers to an area in which genetically distinct parental individuals form hybrids of mixed ancestry, often resulting in genetic clines from one parental genotype to the other across a variety of spatial contexts [23,25]. Zones of mixed ancestry are important sources of novel recombinant genotypes, in which hybrids are considered the raw material of evolution and a source of functional novelty [24,26]. Thus, hybrid zones are important sources of genetic variation for examining the mechanisms that underlie evolution in natural environments [27].

Introgression is the permanent infiltration of the genes of one species into the genome of another through repeated backcrossing [28,29]. Natural introgression may act to extend a species' gene pool, where new adaptations are more likely to be developed by modifying existing adaptations than being produced *de novo*. This produces a wide array of variation on which natural selection may act [28,30]. Hybrid zone theory predicts that where parental species have different adaptive norms, hybrids may be intermediate to the parental species. However, early-generation F1 recombinants may have hybrid vigor (i.e., heterosis) resulting from dominant allelic effects [31]. Natural hybrids, particularly advanced generation introgressants, exhibit a range of fitness characteristics, displaying lesser, equal or greater fitness of adaptive phenotypic traits relative to either parental species [32,33]. Some hybrids exhibit transgressive segregation resulting from the generation of extreme phenotypes relative to parental phenotypes [34]. Transgressive segregation is distinguished from heterosis as phenotypes that exceed parental phenotypes in either a positive or negative direction across a range of recombinant classes [31,35]. These heritable transgressive traits result from complementary gene action following hybridization and may contribute to adaptive evolution, including rapid niche or habitat divergence across hybrid lineages [31,36]. This may have direct implications in terms of conserving species'

evolutionary potential and influence populations' ability to adapt to climate change and increasing environmental stochasticity [30].

### 3. Models of Hybrid Zone Maintenance

Natural hybrid zones are maintained through a combination of selection and gene flow, where natural selection is broadly classified into two categories: (i) endogenous selection (environment-independent), and (ii) exogenous selection (environment-dependent) [37]. Three models of hybrid zone maintenance are widely recognized. Barton and Hewitt [38] first introduced the tension zone model describing a hybrid zone shaped by intrinsic genetic factors independent of the environment. Tension zones are maintained by a combination of gene flow into the hybrid zone and selection against hybrid formation, contributing to steep clines across contact zones [39]. The bounded hybrid superiority model of hybrid zone maintenance is environmentally-dependent. It assumes parental genotypes are most fit in their respective habitats, but hybrids would be more fit in intermediate habitats that represent an ecological transition between parental adaptive norms [40,41]. In contrast, the mosaic model implies that suitable habitat is patchy in space, with each parent locally adapted to particular patches and hybrid offspring occurring at the intersect of suitable parental patches, resulting in a mosaic pattern on the landscape [42–44]. The mosaic model integrates both environmental and non-environmental selection in the maintenance of the hybrid zone. Teasing apart the influence of both environmental- and non-environmental selection on the maintenance of hybrid zones, particularly in changing climates, can have important implications for production (e.g., identification of novel traits), managing for abiotic (e.g., temperature) and biotic (e.g., herbivory resistance) stresses, and conservation of evolutionary potential.

Poplars (*Populus* spp.) are often described as exhibiting weak barriers to reproduction [45–48] based on their propensity to form natural hybrids, suggesting that ecological or geographic separation may provide important pre-zygotic barriers [45,49]. As such, they are model systems to examine the formation and maintenance of hybrid zones. *Populus* × *canescens* occupies floodplain forest habitats adjacent to *P. alba*, typically several kilometers away from the more upland *P. tremula* [50]. The result is a mosaic of hybrid individuals with increased genetic variation that can take advantage of ecological niches distinct from either parental species. This pattern appears to be maintained largely by the environment, particularly floodplain disturbance regimes [50]. In addition, given their propensity to clonally propagate, hybrids may be maintained in regions where parental genotypes are no longer present [51]. More recently, non-environmental barriers to reproduction have been observed within this complex [52,53], suggesting a combination of environmental and non-environmental factors contributes to the maintenance of this hybrid zone. Understanding the impact environmental and non-environmental barriers may have on reproduction is critical, particularly where a combination of factors influences the maintenance of species barriers.

### 4. Dynamics of Hybrid Zones

Hybrid zones are spatially and temporally dynamic. The presence and geographic distribution of hybrid zones, and abundance of hybrid individuals, change in response to various abiotic (e.g., nutrients, climate) and biotic (e.g., competitive interactions, herbivory) factors. While a number of studies have reported a general trend for hybrid zones to shift toward higher latitudes or elevations in response to changing climates (e.g., [51,54]), the processes leading to range shifts, and individual responses to climate change, are still relatively unknown in many systems [55].

*Quercus engelmannii* × *Quercus* species complex [56] provides an interesting example of a complex that is impacted by abiotic factors. In this system, hybrids between *Q. engelmannii* and members of the scrub oak complex occupy a different ecological niche relative to parent species [56]. However, as *Q. engelmannii* is endangered, it is unclear how shifts in abiotic factors may impact the hybrid zone. Currently, the hybrid zone is considered valuable, as introgression facilitates exchange of beneficial scrub oak alleles into *Q. engelmannii*, while selection pressures appears to favor pure genotypes [56].

With climate change, the ranges of parental species may shift. Following this, hybrid zones may track the range of one parental species over the other, especially where environmental gradients are correlated with ecological or reproductive character displacement [57]. In this example, there are three possible outcomes: (1) *Q. engelmannii* and hybrids, which more closely resemble *Q. engelmannii* genotypes, may persist or expand their range given potential adaptive introgression from scrub oaks; (2) climatic conditions will favor scrub oaks, and hybrids may have sufficient scrub oak alleles to follow scrub oak expansion, thereby maintaining a small number of *Q. engelmannii* alleles in the 'new' range; or (3) selection will act against hybrids and one of the parental species, in which case further sources of adaptive introgression are removed.

The formation and maintenance of hybrid zones may be substantially impacted by global climate change, particularly where abiotic and biotic factors impact species interactions. *Picea glauca* × *P. engelmannii* provides an example of hybrid superiority in which interspecific competition and climate interact to determine species ranges [58]. *Picea glauca*, which has a high growth rate, outcompetes *P. engelmannii* at low altitudes, whereas *P. engelmannii* displays increased tolerance of cold at high altitudes relative to white spruce [58]. In contrast, hybrids appear adapted to intermediate altitudes as a consequence of intermediate traits [58]. Based on climate change predictions for species ranges [51,54], it could be expected that the range of *P. engelmannii* would be greatly reduced in response to warming temperatures. However, response models suggest that the hybrid zone will be greatly reduced as *P. glauca* will be better suited to low and intermediate altitude climates, but *P. engelmannii* will retain its advantage at high altitudes [54,58]. These results suggest that broad generalizations regarding species distributions under climate change may not be appropriate.

The relative abundance of a species plays an important role in determining the direction of introgression. As noted, species distributions are likely to shift in response to changing climates, and these shifts will impact population sizes. These demographic shifts could have important implications for rate of hybridization and species persistence. For example, Lepais et al. [59] showed that oak species with small population sizes can effectively be 'swamped' by pollen from a more abundant oak species as a result of increased mate-recognition (pre-zygotic) errors. It has also been suggested that some species colonize new areas through pollen swamping rather than seed dispersal (e.g., eucalypts [60], oaks [61]). Within oaks this process has been important, as it has shaped the current distributions of *Q. petraea*, *Q. robur* and their hybrids following post-glacial recolonization [62].

## 5. Major Barriers to Hybridization

Forest tree hybrid zones provide particularly interesting systems to examine the evolution of barriers to reproduction. As forest trees often exhibit weak barriers to reproduction they represent a segment of diversity that has challenged the biological species concept [63,64]. This is especially true for oak and conifer species, where weak barriers to reproduction impact species determination and management as a result of admixture and often-observed asymmetries in gene flow between ecotypes or sister species [65–70]. Barriers to reproduction may span either prezygotic life history stages, which may include habitat, temporal, and mechanical isolation among others, or post-zygotic life history stages, which may include either ecological inviability or hybrid inviability and sterility [71]. Within each of these stages the barrier to reproduction may be mediated by the environment or independent of the environment [72]. One of the most common barriers observed between ecotypes adapted to different environments is phenology [73–75]. Timing of reproductive phenology in conifers may contribute substantially to reproductive isolation [64,76]. In addition, pre-zygotic barriers may include unilateral incompatibility or conspecific pollen preference [62], whereas post-zygotic barriers may result from genetic incompatibilities leading to decreased fitness of hybrid offspring [77,78]. Where reproductive barriers have evolved, the genomic signature of those barriers may result in regions of differentiation throughout the genome [79,80]. Identification of those regions, or candidate genes associated with those regions, are necessary for genetic conservation and inclusion into breeding programs, particularly if asymmetries have evolved [63,81]. Where genetic signatures of introgression

are observed they may result from neutral introgression following contact or selection for different genetic regions in distinct genetic backgrounds [82]. Combining a mechanistic understanding of barriers to reproduction with genome-wide scans will transform our understanding of the genetic basis of reproductive isolation, particularly for genes important to the maintenance of species in these long-lived species [83].

Genomic tools have furthered our understanding of reproductive barriers between hybridizing species [84–86]. Genome-wide DArT (Diversity Arrays Technology) markers in artificial crosses of eucalypts (*Eucalyptus*) have provided insights into endogenous factors, in particular genetic incompatibilities that limit interspecific recombination. Larcombe et al. [87] showed that intrinsic incompatibilities (e.g., pre- and post-zygotic) result from increased genetic distances between eucalypt species leading to a complete barrier to reproduction among subgenera [87]. Interestingly, these incompatibilities broke down within subgenera, leading to gene flow within and among the taxonomic designation of series. The number of genetic incompatibilities among species is yet to be determined, but the high number of allelic differences identified from genome-wide scans between *E. grandis* and *E. globulus* suggests there could be a large number of genic incompatibilities even among closely related species [88].

The introgression zone between Sitka spruce (*Picea sitchensis*) and white spruce (*P. glauca*) along the Nass and Skeena river valleys in northern British Columbia offers an excellent system for examining the genetic consequences of hybridization. This introgression zone follows a transition from a maritime climate characteristic of Sitka spruce to continental climates characteristic of white spruce, and has been characterized for morphological variation [89], phenology [90], physiology [91–93] and molecular genetic markers and genomic tools [64,70,94–96]. Collectively, these data show strong associations between geographic and climatic variables suggesting that the environment plays an important role in maintaining the hybrid zone. For example, replicate transects from Sitka (*Picea sitchensis*) to white (*P. glauca*) spruce indicate genetic ancestry is influenced by drainage distance from the coast and mean annual precipitation [64,70]. In addition, weak barriers to reproduction suggest that long-term and persistent introgression has likely contributed to the evolution of recombinant genotypes adapted to the transitional environment between the two species. Interestingly, some genetic recombinants may be under selection within divergent genomic backgrounds or climates [96]. Similar observations have been made in the model herbaceous species *Arabidopsis thaliana*, in which particular gene regions may be targets of selection in different environments or genomic backgrounds, indicating that an adaptive polymorphism in one environment may be neutral in another [97,98]. These signatures of conditional neutrality may have a role in the maintenance of the hybrid zone, particularly given the close association between genetic ancestry and environmental factors. Increased resolution of genetic maps, combined with identifying the functional influence candidate genes may have in different environments and different genomic backgrounds will be valuable to predicting the impact genetic ancestry may have within this system.

## 6. Facilitating Breeding Programs

Interspecific hybridization figures prominently in the history of most agricultural species, including many woody species such as *Populus*, which has a long-history of incorporating hybrid crosses into breeding programs [99]. Beyond being a source for traditional wood products, *Populus* and their hybrids are often viewed as the premier woody perennial for bioenergy feedstock [100]. Increased biomass yields associated with hybrid ancestry have contributed to the development of early-generation hybrids for long-term biofuel production. The combination of rapid juvenile growth, ease with which *Populus* clones may be propagated vegetatively, weak barriers to reproduction, and small genomes make *Populus* a model system for applied hybrid breeding [99,101,102]. Interestingly, current breeding programs in *Populus* typically focus on the generation of F1 hybrids, as heterosis is an important mechanism associated with increased productivity. For example, some genetically improved hybrid clones can reach saw log size in just 15 years [103] and numerous other



breeding programs focusing on form, adaptability and disease resistance suggest early-generation hybrids exhibit heterosis [104]. F2 hybrids may also contain sufficient genetic variation and heritability for traits important to increased fitness, including winter survival and frost tolerance, making them good candidates for breeding programs [105]. However, while some more distantly related (i.e., intersectional) crosses have demonstrated breeding improvements [44,106,107], advanced generation hybrids often exhibit greater variability in performance, presumably due to the break-up of co-adapted gene complexes or genetic incompatibilities [99,108]. This variation in performance may explain why long-term, advanced hybrid breeding programs are not well-represented in forest tree species.

## 7. Hybrid Zone Impacts on Ecological Communities

Hybrid zones play an important role in community dynamics, evidenced by the rapidly expanding field of community genetics. Community genetics refers to the study of genetic interactions among species and their abiotic environment [109]. Community genetics aims to understand the influence that heritable trait variation within one species can have on the genetic variation across levels of biodiversity. Community genetics integrates community ecology, and population and quantitative genetics, expanding each theoretical construct for application within complex, multi-species communities. Within this field, *Populus* and their hybrids, alongside their broader communities have become model systems. Two key factors have advanced our understanding of the influence a genotype may have on community assemblages and interactions across scales of biodiversity. First, Whitham et al. [110] showed that heritable genetic traits for one species may influence other species' traits, including phytochemical traits, community structure, and ecosystem processes. Second, the development of the first tree genome—*Populus trichocarpa*, the black cottonwood [111]—provided the means to more accurately identify and characterize genetic regions associated with community responses. Early research on poplar community ecology demonstrated that phenotypes within a poplar population can effectively be considered part of the environment for another species, influencing the fitness of the broader ecological community [109,112]. This has been exemplified in natural hybrid zones as genetic ancestry of keystone individuals within a community may impact community interactions across trophic scales. Indeed, a natural hybrid zone between *Populus fremontii* and *Populus angustifolia* in Utah, USA revealed marked differences in the tannin content of leaf litter, with hybrids exhibiting reduced leaf decomposition rates relative to parents [47]. Further investigation of this system indicated that the high tannin phenotype of hybrids was significantly correlated with differences in community, from arthropod and fungal assemblages in the trees to aquatic invertebrate assemblages in nearby streams [110,113,114]. However, the impact of individual genotypes on community phenotypes went beyond these lower trophic levels. At a higher trophic level, beavers preferentially fell individuals with lower tannin concentrations, influencing the frequency of community genotypes at the forest stand level [115]. The removal of low tannin genotypes by beavers contributes to a community shift in which high tannin genotypes become more common, which in turn alters the community composition of arthropod and fungal species. These community genetic studies highlight the importance of ecological and genetic interactions at both the species- and genotype-level in understanding the mechanisms contributing to co-evolution.

Similar insights have been obtained from eucalypts and oaks (*Quercus*). Hybrids appeared more susceptible to insect herbivores than pure parental types within the *E. amygdalina* and *E. risdonii* system [116]. Theory suggests that the breakdown of co-adapted gene complexes will contribute to a decrease in insect resistance in recombinant genotypes, based on Bateson-Dobzhansky-Muller incompatibilities. However, using both natural and artificial hybrid zones, studies have shown that each of the parental species (*E. amygdalina* and *E. risdonii*), and the hybrid offspring, supported significantly different insect communities [117–119]. In fact, Dungey et al. [119] demonstrated that insect species richness was greatest on F1 hybrids as a result of typical resistance traits being diluted through complex evolutionary inheritance mechanisms, such as additive inheritance [120]. A similar pattern was observed among hybrids of red oak (*Q. crassifolia* × *Q. crassipes*). In this study, hybrids were

phenotypically intermediate relative to parents, but instead of supporting higher insect species richness they supported intermediate levels of species richness [121]. Thus, the hybrids had greater diversity of insect species than pure *Q. crassipes*, but lower diversity than *Q. crassifolia* illustrating that increased genetic diversity following hybridization may impact associated species richness [121]. Managing for this level of diversity may be desirable in natural forest stands to mitigate losses associated with maintaining critical ecosystem services under changing climates accumulate.

## 8. Predicting Adaptation to Changing Climates

Global warming is having significant impacts on many biological systems, with changes associated with community and ecosystem composition and functioning, temporal shifts in development, and spatial shifts in species' distributions predicted [122–124]. Climate modeling forecasts extensive changes in population reproductive biology, phenology, and geographic ranges, as well as extensive community and ecosystem-level changes [122,125]. Under these scenarios, many populations may not have the necessary genetic variation to adapt based on the magnitude and rate of climate change [126,127]. Within this context, hybrids, and the consequent admixture of two distinct gene pools, may offer greater adaptive evolutionary potential than intraspecific variation alone [35,127]. This includes an increased capacity to respond adaptively to a changing climate, increased capacity for range expansion, and in extreme cases where loss of parental species may be imminent, the persistence of locally adapted alleles at risk of extinction [128,129].

Identifying those genotypes suitable for replanting in areas where climatic conditions have, or are predicted to change, will influence both the future economic value and conservation status of the species. A combined approach integrating genomic, phenotypic and environmental data will provide increased opportunity to investigate the consequences of hybridization, particularly teasing apart cases where introgression may facilitate adaptation or contribute to maladaptation [127,130,131]. However, few studies have associated genomic, phenotypic and climatic data within a hybrid zone to assess the fitness consequences of introgression of genetic variation in different genomic backgrounds (but see [11,96]). *Populus* may provide a good model for future investigation of these effects, particularly as combinations of genomic ancestry and functional studies have begun to identify regions of the genome that contribute to functional differentiation under varying genomic backgrounds [132]. Assessing fine-scale analysis of the fitness consequences of introgression of individual candidate gene loci across different genomic backgrounds remains an exciting research area for the future.

In light of changing global temperatures, important life history transitions, including the development of dormancy and cold hardiness in the fall and bud burst in the spring have received particular attention as they are mediated by distinct environmental cues [133,134]. Under changing climate conditions there is an expectation that a mismatch between those environmental cues that shift under climate change (i.e., temperature), and those that remain unchanged (i.e., photoperiod), will contribute to increased maladaptation [134]. One of the traits impacted by this mismatch, cold hardiness, is considered to be increasingly salient for adaptation under climate change scenarios [135,136]. Representing a trade-off between growth and the development of dormancy in the fall, the acquisition of cold tolerance is critical for the health and survival of northern boreal tree species [134,137]. In a recent study, cold tolerance was compared between Sitka spruce (*Picea sitchensis*), adapted to maritime climates, and white spruce (*P. glauca*), adapted to continental climates, alongside a range of recombinant hybrid genotypes grown in a common environment [70]. Interestingly, at moderately cold temperatures ( $-8\text{ }^{\circ}\text{C}$ ) recombinant hybrid genotypes were more cold tolerant than either parental species, suggesting this phenotypic extreme may be transgressive among hybrid genotypes. However, at colder temperatures ( $-18\text{ }^{\circ}\text{C}$ ) the transgressive pattern was not maintained. Thus, hybrid genotypes in this system may exhibit a selective advantage at moderately cold temperatures, contributing to the maintenance of the hybrid zone within a specific temperature range [70]. Given climate predictions for the hybrid zone between Sitka and white spruce, and their well-differentiated climatic norms, these data identify critical factors that may contribute to the maintenance of natural hybrid zones and

underline the impact climatic shifts in the region may have on these important traits associated with plant fitness. Particularly where hybrid zone dynamics are strongly impacted by environmental factors, managing genetic diversity in these regions may be increasingly challenging. Under changing climates, one goal may be to speculate on an optimal hybrid index for warmer or drier climates, and within this scenario design appropriate seed transfer guidelines [70]. However, given the dynamic nature of hybrid zone formation and their maintenance, composite provenancing may be most appropriate to buffer against changing conditions [10,55].

## 9. Genetic Conservation and Hybridization

Under rapidly changing conditions, hybrid zones may provide a mechanism to conserve genetic diversity. This may be especially important in rare species at risk due to demographic stochasticity associated with environmental and non-environmental disturbance. Under changing conditions, natural hybrid zones provide a means to preserve evolutionary potential of a species, especially where parental species are at risk [7,35]. Genetic rescue via managed introduction of genetic variation through hybridization, or evolutionary rescue via natural introgression may provide a mechanism to conserve a species under changed conditions [6,35,138,139]. This strategy can provide several potential benefits, including increased fecundity and reduced inbreeding depression. However, hybridization may also pose a risk where the long-term fitness consequences of recombination are unknown. Thus, studies that combine phenotypic evaluation of various genotypic classes under different environmental conditions are necessary [70,140]. These datasets will be essential for evaluating whether hybridization or introgression is adaptive long-term, and answer the question as to whether hybridization should be considered a conservation strategy to maintain diversity and evolutionary potential in rare populations [139]. Quantifying the degree of hybridization between natural populations, and genetic variation associated with increased fitness in different genomic backgrounds will be valuable for predicting future forest health, productivity, and ecosystem services within these natural zones of introgression.

## 10. Conclusions

Hybrid zones are valuable sources of genetic variation across a shifting landscape. This review demonstrates the important role forest hybrid zones have had in advancing our understanding of the ecological and evolutionary processes influencing the structure of these natural or artificial systems. With the increasing availability of genomic tools, high-throughput phenotyping, and association with a wealth of climatic data; forest hybrid zones are primed to address fundamental questions in speciation, conservation, and community ecology under changing environments. The mechanisms influencing species divergence, particularly the relative contribution of environmental and non-environmental barriers to reproduction remains an area that has not garnered much attention in forest trees. However, integrating genomic tools, provenance tests, and experimental crosses holds great promise for teasing apart the mechanisms contributing to species barriers, their frequency and the extent of the incompatibilities.

Hybrid zones clearly have a role to play in conservation, particularly under rapidly changing environmental conditions where hybridization may result in a genetic rescue for species at risk. However, additional studies examining the fitness consequences of interspecific gene flow that span multiple generations across different environments is necessary. Artificial hybrid zones may provide an appealing way of 'speeding up' evolutionary rescue as they have already proven beneficial within a selective breeding context (e.g., *Populus × canadensis* [141]). However, the risks of introduction must be weighed against potential benefits, particularly in situations where the native parental species is considered rare [142]. The risks of hybridization and introgression may include genetic assimilation or spread of an invasive genotype. In the case of the native North American red mulberry (*Morus rubra*), an endangered species, hybridization with introduced white mulberry (*Morus alba*) and reduced fitness of native genotypes relative to non-native and admixed genotypes may contribute to local



extinctions of the native genotype [143]. Additional risks may include outbreeding depression or migration load where the introduction of non-native alleles results in reduced fitness of the native species [131,144]. However, although outbreeding depression has shown to impact short-term fitness, simulations and long-term experiments indicate that populations rebound in the long-term and the effects of outbreeding depression are temporary [131,145,146]. The impact of genetic swamping following the spread and fixation of allelic diversity that contribute to mean population fitness at a cost to locally adapted allelic diversity also remains a concern. This is particularly true where environmental heterogeneity impacts the migration-selection balance contributing to the loss of rare diversity important to local adaptation [144,147].

Forest tree hybrid zones are model systems for the field of community genomics, demonstrating that community phenotypes are heritable. However, additional research is required to identify the causal and correlational effects of genetic ancestry on community biodiversity. Gene knockout experiments may provide a means forward [110], as the influence of removing putative ‘community genes’ from one species could aid in determining the impact individual genes may have within a community. However, as the magnitude and complexity of data generated under community genomics increases, the theoretical and statistical framework behind it will need to keep pace. Additional computational resources are needed to correlate thousands of genomic markers across multiple species and trophic levels, while controlling for intraspecific differences requires a refined approach [148–150]. Accommodating a truly community-based approach will present further opportunities moving beyond solely plant-insect and plant-fungal interactions, considering multiple levels of trophic interactions.

Genomic studies continue to provide unprecedented precision and power, allowing increased association between genetic and trait variation across environments. Expansion of reference genomes and comparative analyses will be pivotal. For example, exceptionally long reads (e.g., Single Molecule Real-Time sequencing [151], nanopore technology [152]), and Hi-C chromosome conformation capture sequencing show great promise for species, such as trees, with large genomes [153]. It is likely that these technologies will have an increased role in streamlining and improving genome assemblies. Generating these high-quality genomic resources will facilitate even greater gains with increased opportunities for comparative approaches across species [79]. Thus, expanding these resources using natural and managed forest tree hybrid zones will provide a greater understanding of the mechanisms that contribute to speciation, conservation of evolutionary potential, and the extent and complexity of community interactions.

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