Climate-mediated hybridization and the future of Andean forests

Running title: Hybridization in Andean forests

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ABSTRACT

The tropical Andes face unprecedented warming and shifting precipitation patterns due to climate change and land-use alteration, challenging the futures of Andean forests. During the Quaternary, many Andean trees responded to climate change through upslope migrations, but while there is evidence of such ongoing migrations in many species, they are at rates far below what is needed to remain in equilibrium with current climate. Similarly, given the number of generations required for adaptation and the long lifespans of many tropical trees, it is unlikely that most species will be able to adapt fast enough. This synthesis explores the role of migration induced secondary contact and hybridization as potential mechanisms for accelerating the adaptive response of Andean forests. Hybridization, historically underappreciated in tropical trees, is increasingly recognized as an important driver of speciation and ecological diversity. It may facilitate gene flow and introgression, providing novel genetic combinations that enhance species resilience to climate change. This process can generate new allelic diversity, allowing species to adapt more rapidly than through mutation or selection on standing variation alone. However, hybridization can also lead to negative outcomes like genetic swamping and outbreeding depression. Conservation strategies should consider the potential benefits and risks of hybridization in maintaining biodiversity under changing environmental conditions. As habitat fragmentation and deforestation exacerbate the challenges faced by these forests, preserving habitat connectivity will be crucial to facilitate migration and gene flow, potentially aiding the survival of many Andean tree species in the Anthropocene.

Keywords: climate change, Andes, hybridization, gene flow, biodiversity, adaptation, migration, introgression, conservation, tropical montane forests

1. INTRODUCTION

The tropical Andes are the most biodiverse region on Earth and one of the most threatened terrestrial environments, acutely vulnerable to both climate change and land-use change (Myers et al. 2000; Mittermeier et al. 2011; Rahbek et al. 2019). Andean forests are warming at rates faster than any in the historical record as well as experiencing shifts in precipitation regimes (Urrutia and Vuille 2009; Morales et al. 2023), requiring species to evolutionarily adapt or physiologically acclimate in situ to climates outside their current climatic niche, or migrate for populations to remain in equilibrium with climate and avoid extinction (Feeley and Silman 2010b). It has been widely argued that given the rapid pace of climate change and the generation times required for evolutionary change, it is unlikely that most tree species will be able to adapt fast enough (e.g., Smith and Donoghue 2008; Shaw and Etterson 2012), and the potential for acclimation is still unclear (e.g., Shaw and Etterson 2012; Feeley et al. 2023). Several studies have reported migration as evidenced by upslope shifts in population mean range (Feeley et al. 2011; Fadrique et al. 2018; Mamantov et al. 2021, among others), but few tree species have migration rates that keep pace with shifts in their preferred habitat (Farfan Ríos 2019). Still, species undergoing range shifts may increasingly overlap with close relatives both spatially and temporally, particularly those that replace each other along climatic gradients. A breakdown of these barriers to gene flow and increased hybridization and introgression may offer alternative eco-evolutionary mechanisms for species to respond to climate change.

Tropical montane forests, particularly the tropical Andes, are distinctly susceptible to climate-driven secondary contact and gene flow for several reasons. First, these systems comprise a high diversity of rare species and congeners that turn over rapidly with elevation (Terborgh 1971; Gentry 1982; Cadena et al. 2012; Freeman et al. 2022) resulting in the packing of many, closely related species along elevation gradients (e.g., Kitayama 1992, Lieberman et al. 1996, Jankowski et al. 2009). Rarity can facilitate hybridization, as individuals in small populations are more likely to hybridize when in contact with other closely related taxa (Rhymer and Simberloff 1996). Additionally, the relatively young evolutionary age of the tropical Andes may increase the likelihood of gene flow and hybridization, as irreversible ecological speciation is thought to require long, stable periods (millions of years) of the environmental conditions that initiated it in the first place (e.g. Seehausen 2006). The Andes are one of the youngest mountain ranges on earth, with mountain building beginning in the late Cretaceous (~65 Ma) and the most significant uplift occurring during the middle to late Miocene (~23-12 Ma) and early Pliocene (~4.5 Ma) in tropical zones (Hoorn et al. 2010; Boschman 2021). Diversification of montane plant and animal genera coincides with these events, beginning ~20 Ma and many events <5 Ma (Hoorn et al. 2010). While the crown ages of many mid-elevation Andean plant lineages are within the Miocene (Hoorn et al. 2010; Pérez-Escobar 2022), speciation events are often much younger, resulting from changing environmental conditions, habitat connectivity, and immigrations over the Pliocene and Pleistocene. Thus, the proportion of species amenable to hybridization resulting from modern climate-induced secondary contact is significant. It is therefore, important to understand the role gene flow has played in shaping Andean tree diversity in the past and the potential impact it may have on the persistence or extinction of these species in the future.

Range shifts will result in novel species assemblages, influencing both competitive and reproductive interactions. The evolutionary implications of such secondary contact are difficult to predict, as hybridization and introgression can increase extinction rates through mechanisms such as genetic swamping and outbreeding depression and be an important source of genomic and phenotypic diversity (Rhymer and Simberloff 1996; Todesco et al. 2016; Taylor and Larson 2019). The study of hybridization has a long history in plants (e.g., Linné and Haartman 1751), but only recently has it become clear how widespread and fundamental this process is in plant evolution (e.g. Soltis & Soltis 2009, Alix et al. 2017, Stull et al. 2023). In the British flora, it is estimated that hybridization has occurred in at least 25% of taxa (Mallet 2005; Stace et al. 2015), and in up to 40% of species in certain genera (Preston and Pearman 2015). Yet despite this propensity for plants to hybridize, there are proportionately few reported hybrid zones and it is unclear whether this is an artefact of underreporting, lack of data, and botanist biases or a mechanistic difference in plant and animal hybridization result in different evolutionary outcomes, or a combination of both (see Nieto Feliner et al. 2023 for a discussion of potential causes). Similarly, hybridization has historically been considered a rare occurrence in tropical trees, as hybrids were thought to be poor competitors in high-diversity tropical forests (Ashton 1969; Ehrendorfer 1970; Gentry 1982). Mounting genomic evidence now suggests that hybridization was not only common historically, but was a key driver of speciation in the Neotropical tree flora (reviewed by Schley et al. 2022). In addition, hybridization has been shown to play a central role in expanding the niche breadth of hybridizing tree species, which may enhance their resilience to future change (Karunarathne et al. 2024).

Prior reviews have examined the legacy of hybridization in vascular plant evolution (Stull et al. 2023) and historical plant evolution across the Neotropics (Schley et al. 2022), while others considered the implications of a warming world on hybridization globally and across all taxa (Chunco 2014). Still, hybridization is nonexistent in discussions about the future of Andean forests under climate change. Here we explore the potential for increased hybridization in Andean trees due to climate-mediated range shifts and the possible eco-evolutionary outcomes. Considering hybridization in climate change scenarios may thus reshape to the classic "adapt, acclimate, migrate or die" framework for Andean trees (Feeley et al. 2012), wherein even minor range shifts facilitate gene flow that allows some species to adapt and cope more quickly (Kulmuni et al. 2024).

2. HISTORICAL CLIMATE CHANGE AND GENE FLOW

The tropical Andes have a history of significant climatic change, and most modern plant lineages persisted through oscillations in temperature, precipitation, and CO_2 concentration over at least the last 2.5 million years (Bush, Silman, and Urrego 2004). Paleo-hydrological records show a gradual trend toward enhancement of the South American Summer Monsoon (SASM) throughout the Holocene, marked by abrupt shifts between intense rainfall and significant drought (Bustamante et al. 2016). During the Pleistocene-Holocene transition, tropical montane forests experienced ~6 ºC of warming, 2-3 ºC greater than what is expected for the current century (Bush et al. 2004). However, because the pace of this change was gradual, averaging less than 1 ºC Ky^{-1}, trees were able to migrate to keep pace with their climatic optimum (Bush et al. 2004). Current rates of temperature change are unprecedented in the Andean Quaternary record (by at least an order of magnitude) and it is unlikely that most species will be able to remain in equilibrium with climate through migration alone (Feeley and Silman 2010b). Additionally, future projections show regions of both increased and decreased precipitation across the Andes, with some of the greatest uncertainty dependent on the ultimate extent of deforestation and land cover change, as the Amazon Basin is the major source of moisture for Andean precipitation (Vizy and Cook 2007; Espinoza et al. 2020; Segura et al. 2020; Costa et al. 2021; Moraes et al. 2021). Still, it is important to understand the impact past climate change and resulting range shifts have had on Andean plant diversity and gene flow to establish baseline predictions for current change.

Much of the high plant diversity of the tropical Andes is thought to have accumulated through Quaternary species radiations, driven by repeated altitudinal migrations in response to mountain building and climatic oscillations (Flantua et al. 2019; Pérez-Escobar et al. 2022). Downslope migrations during cold glacial periods and upslope migrations during warmer interglacials provided repeated opportunities for secondary contact and interspecific gene flow. Many studies have shown evidence of such climate-mediated hybridization, particularly in hyper-diverse Páramo genera. For example, Nevado et al. (2018) detected several episodes of gene flow among *Lupinus* species, linked to changes in habitat connectivity and climate throughout the Pleistocene. However, even with ongoing gene flow, their results suggest that species are not immediately re-absorbed into parental forms. Instead, gene flow occurred heterogeneously, at different rates across the genome, with some regions protected from introgression, though the cause and function of these “genomic islands of divergence” remain unclear (Nevado et al. 2018). Similarly, Pouchon et al. (2018) found that in the Asteraceae subtribe Espeletiinae most diversification occurred through morphological adaptation and geographical isolation due to Pleistocene climatic oscillations. Hybridization was common among sympatric species and may be responsible for the morphological variation within this group (Pouchon et al. 2018). Historically, high rates of hybridization and introgression have also been shown to promote phenotypic variation and adaptation to novel environments in Andean plant lineages such as *Polylepis* (Schmidt-Lebuhn, Kessler & Kumar 2006), *Lachemilla* (Morales-Briones, Liston & Tank 2018), and *Solanum* (Cara et al. 2013; Pease et al. 2016) through generating novel genetic and epigenetic variation, gene duplications, and polyploidization.

3. POTENTIAL IMPACTS OF CLIMATE CHANGE ON GENE FLOW

Gene flow can be limited by premating and postmating barriers, driven by both ecological and evolutionary mechanisms (Arnold 1997; Riesberg and Willis 2007; Lowry et al. 2008). Premating isolation in trees includes spatial and temporal components, relying on geographic barriers, seasonality and phenology, and biotic interactions that are driven by the spatiotemporal structure of environments. Alternatively, postmating isolation may result from mechanical mechanisms such as pollen-pistil incompatibilities or decreased fitness of hybrid individuals due to developmental abnormality and/or reduced competitive ability. The ongoing breakdown of premating and postmating barriers due to climate change (reviewed below) may increase the likelihood of gene flow among closely related Andean trees through increased spatiotemporal overlap, or decrease the likelihood by shifting species further apart, both which have important implications for the future of these forests.

3.1 Collapse of spatial barriers

Recent range shifts in response to current climate change have been documented globally, across a wide range of taxa. However, these shifts rarely occur uniformly, and even closely related species do not respond in the same way or at the same rate (Tingley et al. 2009; Chunco 2014). In a recent meta-analysis of 987 species across sixteen global montane regions, Mamantov et al. (2021) found more than 600 species that have experienced some amount of elevational shift since 1850 (though the Neotropics were represented by only a single study of birds). Among these species, range shifts were not unidirectional—61% moved upslope and 28% shifted their ranges downslope (Mamantov et al. 2021), with the downslope shifts largely associated with changes in precipitation regimes resulting in population declines or local extirpations (Lenoir et al. 2010; Crimmins et al. 2011). Additionally, low-elevation species were found to be moving faster than the high-elevation species. Whereas tree-line may be artificially truncated due to anthropogenic land use for high-elevation species (Lutz et al. 2013), the disparity in the pace of the elevational shifts is also predicted by thermal tolerance theory. Janzen (1967) hypothesized that reduced seasonality and temperature variability select for narrower thermal niches in the tropics. As high elevations experience far greater daily temperature variation than lowland counterparts, high-elevation species should have wider thermal tolerances and a slower or delayed response to warming. Many empirical studies have supported Janzen's Climate Variation Hypothesis (CVH) across taxa (e.g., ectotherms—Sunday et al. 2010; terrestrial vertebrates—Chan et al. 2016; insects—Polato et al. 2018; and plants—Lancaster et al. 2020).

Tropical plants are particularly susceptible to climate warming due to their narrow thermal niches (Janzen 1967; Perez et al. 2016; Lancaster et al. 2020), and montane regions are warming faster than their lowland counterparts (Pepin et al. 2015). Several studies have documented widespread upslope shifts in tree community composition across the tropical Andes over the last two decades (Feeley et al. 2011; Morueta-Holme et al. 2015; Duque et al. 2015; Fadrique et al. 2018), with the rates of change varying across locations or elevations. This rate disparity has been attributed to variations in warming rates (Vuille et al. 2015) and specialized tree communities in ecotones (such as the transition from montane rain forest to cloud forest at cloud base). Conditions in cloud forests are biotically and abiotically distinct, reducing the establishment of lowland colonizers not adapted to those conditions (Hillyer and Silman 2010; Hillyer 2018; Fadrique et al. 2018). However, with climate change, cloud base is predicted to rise by 1000 m or more over the Amazon by 2100 (Cowling et al. 2008; Pinto et al. 2009), and thus future colonization of these elevations by lowland species is more likely (e.g. Pounds et al. 1999; Stone 2018). These range shifts combined with the general patterns of rarity, high turnover, and congeneric replacement across elevation gradients (Pitman et al. 1999; Gentry 1982; Terborgh 1971) make allopatric species barriers particularly fragile in Andean trees. In addition, the tendency for interspecific gene flow and hybridization among closely related sympatric trees has been widely documented in the Northern Hemisphere (e.g., oaks–Cavender-Bares 2019; spruce–De La Torre et al. 2015; birch–Tsuda et al. 2017; poplar–Chhatre et al. 2018; and pine–Menon et al. 2018). Thus, even a small elevational shift that results in spatial overlap among two previously allopatric tree species could increase the likelihood of gene flow. There are many examples of such hybrid zones developing from climate-induced range shifts across taxa in temperate zones including in mammals, birds, fish, insects, and plants (Table 1), though, to date, it has been poorly documented in tropical systems.

3.2 Collapse of temporal barriers

Temporal barriers also act as important barriers to gene flow, even when species occur in sympatry. Differentiation in breeding times maintains reproductive isolation in many species, and these barriers are particularly sensitive to climate change (Menzel et al. 2006; Cleland et al. 2007; Todesco et al. 2016). Whereas the actual effect of climate change on breeding is highly species- and location-specific (Parmesan 2007; Prevey et al. 2019), a slight shift in the timing of a species can result in increased or decreased temporal overlap, regardless of whether its sister species experiences a similar response (Chunco 2014).

Such phenological shifts have been documented widely, particularly across north-temperate and arctic plant communities in response to changes in both temperature and precipitation, resulting in shifts in flowering times and flower senescence (Table 2). Crimmins et al. (2010) reported shifts in the onset of spring flowering across a 1200 m semi-arid elevation gradient, but the climatic variables associated with these shifts and the direction of the response varied among the low and high-elevation communities.

Similarly, Prevéy et al. (2019) detected a community-wide shortening of flowering across tundra species in response to summer warming, although the size of the effect was greater among late-flowering species. These studies and others (i.e., Bradley et al. 1999, Høye et al. 2013, Bjorkman et al. 2015) demonstrate that whereas temporal patterns are highly sensitive to climate change in plants, these changes are complex and variable across species and environmental gradients.

In tropical systems, the partitioning of flowering times among close relatives is thought to be an important mechanism for maintaining species coexistence, by reducing competition for pollinators and other resources (i.e., Snow 1965; van Schaik et al. 1993). Most tropical trees are obligate out-crossers and have hermaphroditic flowers (Ashton 1969; Bawa 1974, 1979). Bawa et al. (1985) estimated that 98-99% of lowland tropical trees are pollinated by animals and up to 31% have generalist pollinators from an array of small insects. If non-specialized pollination systems are common in tropical trees, temporal isolation may be critical for maintaining species boundaries, particularly as some generalist pollinators are known to forage over kilometers (Bawa et al. 1985). Synchronized phenology is one mechanism thought to be common among species dependent on the seasonal presence of the same animal pollinators and/or dispersers, though fruiting is often much more synchronized than flowering among close relatives (Appanah 1985; van Schaik et al. 1993).

Temporal partitioning may be less sensitive to temperature and photoperiod, and more strongly correlated with rainfall in the tropics (Borchert 1983; van Schaik et al. 1993; Sakai 2001), as precipitation varies more significantly across seasons and latitudes and is an important axis for speciation (Ringelberg et al. 2023). Particularly in seasonally dry forests, leafing, flowering, and fruiting are all driven largely by moisture cycles, although other environmental factors, such as temperature and solar irradiance, have been shown to play a role (van Schaik et al. 1993; Wright and Calderón 2006; Alfaro-Sánchez et al. 2017). With climate change, patterns of precipitation are changing across South America. Many locations have experienced upward trends in total seasonal and extreme precipitation events (specifically the southern La Plata Basin and the eastern Andes), whereas generally drier conditions have become more frequent (reviewed by Carvalho 2020). In the Andes, these trends are more complex and difficult to predict due to the steep elevation gradients and microclimates, and projected changes show regions of both increased and decreased precipitation (Urrutia and Vuille 2009). Shifts in local precipitation regimes will likely affect the predictability of flowering cues for many species, leading to atypical flowering times and the breakdown of temporal species barriers.

The phenology of Neotropical forests, though long studied (e.g. Bawa 1983; Leigh 1985; van Schaik et al. 1993; Sakai 2001; Wright and Calderón 2006), is poorly known outside of a few well-studied lowland sites (e.g., La Selva, Costa Rica; Barro Colorado Island, Panama; Cocha Cashu, Peru). Even less is known about shifts in phenology, as aseasonality, complex abiotic factors, intraspecific and interannual variation, and high species diversity all make such studies more difficult than in temperate zones (Mendoza et al. 2017; Sheldon 2019). Mendoza et al. (2017) reviewed patterns of fruiting phenology across the Neotropics and found that phenological research is concentrated in Brazil and Costa Rica, while the vast majority of Central and South America remains entirely unstudied. Some of the best evidence for phenological shifts linked to climate change in tropical forests comes from southwest China, where Zhao et al. (2013) studied temporal trends in budburst, growing season, flowering time, and flowering duration among 21 deciduous trees from 1973–1999. Fourteen of these species showed consistent trends in phenological changes, such as budburst delays and shorter flowering periods, and those changes were correlated with increasing regional temperature. Dunham et al. (2018) tracked the fruiting phenology of 69 rain forest tree species in Madagascar over 12 years and found that increased rainfall was linked to an increase in the number of co-fruiting species, and drier dry seasons shifted the timing of peak fruiting later in the season. Climate change is predicted to increase the frequency and intensity of extreme rainfall and extreme drought events in Madagascar and will thus likely alter the timing and availability of fruits (Dunham et al. 2018). In the few studies that have recorded overlaps in flowering times among closely-related tropical trees, these overlaps have resulted in hybridization, although it is unclear whether these interactions are longstanding or novel (Scotti-Saintagne et al. 2013; Kenzo et al. 2019).

As flowering is complex and difficult to predict in tropical forests, research should first focus on establishing species-specific baseline data that can be used to monitor these changing systems into the future. Tropical field botanists typically prioritize collecting species in flower, and thus there is a wealth of historical data on flowering date for many species stored in herbaria, particularly from long-term forest plots where the same individuals have been monitored for many years (Borchert 1996; Ouédraogo et al. 2020). Large global databases such as the Global Biodiversity Information Facility (GBIF) that can be queried for flowering specimens make these collections more powerful. However, herbarium collections are biased due to non-random collecting efforts (i.e., Daru et al. 2017; Vargas et al. 2022) and, therefore, the distribution of fertile plant material across a region reflects the behavior of researchers as much or more than plant phenological patterns (future effort should be placed on the latter). Additionally, the advancement of high-resolution remote sensing technologies over the last several decades has made it possible to map and identify tree species flowering across a landscape regularly and cost-effectively (e.g., Park et al. 2019; Lee et al. 2023). Together, herbarium specimens and drone imagery offer high-resolution spatio-temporal data for monitoring phenological shifts in response to climate change and potential breakdowns of temporal barriers among tropical trees. Still, the establishment of useful "baseline" data in a rapidly changing system is difficult, particularly given the time it takes to establish such baselines, the variability among populations, species, and locations, and the complete paucity of data from most sites. Thus, global investment is urgently needed in establishing climate change observatories that can continuously monitor fine-scale changes at many sites not only in the Neotropics but across the globe.

3.3 Collapse of post-mating barriers

Hybridization is common in flowering plants, with at least 25% of species estimated to exchange genes with close relatives, nearly double that in animals (Mallet et al. 2016). In tropical trees, hybridization between closely related species may produce populations with novel genetic variation at a minimal fitness cost (Schley et al. 2022). As many tropical tree populations persist at low densities, this increased genetic variation may then reduce Allee effects and inbreeding depression (Cannon and Lerdau 2015; Schley et al. 2022). One example of this is in the dipterocarp genus *Shorea* Roxb. ex C.F. Gaertn. from southeast Asia, in which hybridization frequently occurs among four species with overlapping flowering periods (Kenzo et al. 2019). The resulting hybrid seedlings exhibit high growth performance, suggesting they have a fitness advantage relative to their parents.

Climate change may impact both the opportunities for hybridization to occur through altering spatial and temporal barriers and the outcomes of those events by influencing relative fitness (Chunco 2014). The fitness of hybrids is highly sensitive to the environment, as hybrids may be more successful than their parents in some environments but not others (Arnold 1997; Rieseberg et al. 2003, 2007; Taylor et al. 2009; Grant and Grant 1993, 2002; reviewed by Arnold and Martin 2010). As climate change is expected to result in novel combinations of environmental parameters, increased fitness of hybrids may be an important mechanism for species adaptation and persistence, particularly in contact zones at range margins, where both parent species may be less well adapted to local conditions (Cronk and Suarez-Gonzalez 2018). In this way, introgressed genetic variation can facilitate local adaptation (Suarez-Gonzalez et al. 2018) and even promote adaptive radiations and functional diversity (e.g., anoles–Wogan et al. 2023; cichlids–Irisarri et al. 2018).

Across montane gradients, and particularly in the Andes, upslope range shifts tracking temperature and precipitation optima will result in tree species encountering a suite of novel environmental conditions. In most cases, climate change will far outpace the upslope shifts of most trees, making it impossible for species to remain at equilibria with climate. For example, given the rate of temperature increase in the Andes since 1975 (0.03—0.04 ºC year^{-1}; Vuille and Bradley 2000) and adiabatic lapse rate (5.5 ºC km^{-1}; Bush et al. 2004), Feeley et al. (2011) argued that tree species would have to migrate upslope at a pace of 5.5–7.5 vertical m year^{-1} just to remain at equilibrium. As a result, upslope shifts in species' population means have been largely due to mortality at the warm end of their range (range retractions), rather than significant recruitment at the cooler end (Duque et al. 2015). These range retractions may result in higher extinction and decreased hybridization (at least initially), particularly in species with narrow thermal tolerances.

Elevation is known to play a significant role in shaping the gradients of other environmental variables in the Andes, including humidity, solar radiation, wind, cold-air intrusions, soil properties, and diurnal temperature variation (Grubb 1977; Vitousek 1998; Rapp and Silman 2012; Unger et al. 2012; Nottingham et al. 2015). Biotic gradients in the Andes can have as strong of an effect on plant performance (or even greater), than the abiotic factors (Hillyer and Silman 2010; Nottingham et al. 2018). As such, range shifts will also result in novel communities and thus a new suite of competitive interactions (Lurgi et al. 2012), as the distributions of individual species (Terborgh and Weske 1975; Callaway 1998), their pollinators (Simanonok and Burkle 2014; Lefebvre et al. 2018), dispersers (Dehling et al. 2014; Chapman et al. 2016), herbivores (Pellissier et al. 2012; Rasmann et al. 2014), and pathogens (Abbate and Antonovics 2014; Halliday et al. 2021) are highly structured across these gradients and have different responses to microclimatic changes (e.g., Rasmann et al. 2014; Halliday et al. 2021; McCabe and Cobb 2021). Hybrid offspring of historically high and low-elevation species (even when rare) may thus be more fit for these novel abiotic conditions and biotic interactions than either of their parents (e.g. Cronk and Suarez-Gonzalez 2018).

4. ECO-EVOLUTIONARY IMPLICATIONS

Evidence suggests that, historically, hybridization was common and played an important role in shaping Neotropical plant diversity (reviewed by Schley et al. 2022). Hybridization can facilitate both diversification and extinction, and these outcomes are determined by many factors including the divergence times between parental lineages (Comeault and Matute 2018), recombination (Martin et al. 2019), and selection (Suarez-Gonzalez et al. 2018; Schley et al. 2022). As current climate change is likely to modify opportunities for gene flow through spatial and temporal shifts in populations, it is important to understand the potential eco-evolutionary implications of hybridization in tropical Andean forests.

First, hybridization can be deleterious (especially initially) through maladaptive gene flow (Kirkpatrick and Barton 1997; Mallet 2005; Tavares et al. 2018). Often, this results in poorly fit hybrids and parent populations that are less well-adapted to the local environment due to backcrossing (Rhymer and Simberloff 1996). If selection does not quickly remove these hybrids, maladaptive alleles may become fixed or rise to high frequency (due to pleiotropy, hitchhiking, genetic drift, and other context-specific eco-evolutionary trade-offs) resulting in parent population homogenization and a decrease in niche specialization (Kirkpatrick and Barton 1997; Buggs and Pannell 2006). Alternatively, hybridization may result in offspring with low fitness that act as evolutionary “dead ends,” by producing genetic combinations that are a poor match for the environment or sterile due to chromosomal abnormalities, thus reducing their chances of survival and reproduction (e.g. Zhang et al. 2021). In extreme cases, extensive introgression and homogenization may lead to the collapse of two distinct evolutionary lineages back into a single lineage, termed “reverse speciation” (Rhymer and Simberloff 1996; Seehausen 2006). Reverse speciation is increasingly likely in response to significant environmental change, as such change can simultaneously increase the potential for gene flow and reduce selection against hybrids (Seehausen 2006). Additionally, reverse speciation and extinction are more likely when common species hybridize with rare ones, as a greater fraction of the rare species’ population will hybridize each generation leaving a smaller fraction with no genetic mixing (Rhymer and Simberloff 1996; Balao et al. 2015).

The classic and best-studied example of reverse speciation is the Enos Lake sympatric stickleback species. Though some baseline gene flow has likely always occurred among these species, they were phenotypically distinct and gene flow was strongly constrained by niche differentiation and selection against intermediate phenotypes. However, the rapid environmental change that followed the introduction of an invasive crayfish resulted in a hybrid swarm and the collapse of the two distinct lineages into a single lineage in less than two decades (Kraak et al. 2001; Taylor et al. 2006; Gow et al. 2006). Other theoretical work has shown that hybridization can lead to rapid extinction, in some cases in less than five generations (Wolf et al. 2001). Given the short divergence times and fragile spatio-temporal boundaries between many Andean trees, combined with climate change and the emergence of novel environments, reverse speciation and/or extinction may be possible—or even likely—among many Andean tree lineages. With hyperdominance and extreme rarity as the predominant community pattern in these forests, migrating species with broad elevational ranges and high population densities could quickly aggregate allelic diversity through introgression while the rare and narrowly distributed species are driven extinct. If instead of being a rare event, this asymmetric hybridization becomes increasingly common, it could result in the Andean "species-pump" (sensu Antonelli and Sanmartín 2011) shifting to a "species-sink" of diversity (Figure 1).

A less extreme outcome of hybridization is that gene flow is maintained over many generations with minimal impact on the evolutionary trajectories of the species involved. Due to differential selection and introgression rates across the genome, loci that confer differential fitness benefits between species may remain distinct, while unlinked, neutral loci are homogenized through gene flow (Gompert et al. 2012; Schley et al. 2022). This type of hybridization can maintain stable hybrid zones at species' range margins for generations. Examples of such stable hybrid zones from the Andes include parrots (Masello et al. 2011), flycatchers (Dubay and Witt 2014), *Heliconius* butterflies (Rosser et al. 2014), and lupines (Nevado et al. 2018) and given the high degree of sympatry and parapatry among congeneric species, stable hybrid zones may also be widespread in Andean trees, particularly at range margins.

Finally, hybridization can drive rapid evolutionary change by producing novel gene combinations (Rhymer and Simberloff 1996; Prentis et al. 2008). This change occurs more rapidly than evolution by mutation, as hybridization results in novel variation in multiple genes simultaneously, within a single generation (Rieseberg et al. 2003; Seehausen 2004; Chunco 2014). The introduction of new alleles may then increase the resilience of populations to environmental change and even rescue small populations at risk of extinction (Basket and Gomulkiewicz 2011). In novel, extreme, or rapidly changing environments, selection may favor hybrids whose novel gene combinations produce traits with higher fitness than either of their parents (Chunco 2014; Schley et al. 2022). For example, in sunflowers, species found in extreme habitats (*Helianthus anomalus, H. deserticola, and H. paradocus*) are of hybrid origin, and colonization of these habitats (e.g. sand dunes, deserts, salt marshes) is thought to have been facilitated by selection favoring the extreme phenotypes generated by hybridization (Rieseberg et al. 2003; Rieseberg et al. 2007). Simulations show that hybrids may even adapt faster to new environments compared to their parent populations by generating a fitness advantage that can offset other incompatibilities (Kulmuni et al. 2024). In this way, climate-change-mediated hybridization can trigger adaptive radiations, as is thought to have occurred in many Andean plant lineages throughout the Quaternary (e.g. Dušková et al. 2017, Vargas et al. 2017, Pouchon et al. 2018, Nevado et al. 2018; Figure 1).

The special case of polyploidization through hybridization (termed allopolyploidy) has long been recognized as a particularly important evolutionary mechanism in plants. Allopolyploidy can result in "instantaneous" speciation from the parental lineage due to chromosomal incompatibilities resulting in reproductive isolation (Stull et al. 2023). Stebbins (1959) suggested that allopolyploidy is one of the most common ways that plant species arise, and Wood et al. (2009) proposed that at least 15% of speciation events in angiosperms are accompanied by ploidy increase. Allopolyploidy results in greater genomic variation for selection to act upon through the merging of differentiated genomes (Alix et al. 2017), and provides "backup" copies of genes if one is rendered maladaptive or nonfunctional due to allele changes. Thus, hybridization resulting in changes in ploidy may further increase the pace at which species can respond to rapidly changing environments. Evidence from the Andes suggests that allopolyploidy has played a role in diversification and colonization of novel habitats in groups such as *Nicotiana* (Solanaceae; Clarkson et al. 2017), *Solanum* (Solanaceae; Hijmans et al. 2007), *Silenes* (Caryophyllaceae; Frajman et al. 2018), *Polylepis* (Rosaceae; Schmidt-Lebuhn et al. 2010), *Castilleja* (Orobanchaceae; Tank and Olmstead 2009), and *Lachemilla* (Rosaceae; Morales-Briones et al. 2018), though this remains largely uninvestigated for the majority of tree lineages in these high diversity forests.

5. CONSERVATION IMPLICATIONS

Increased gene flow within and hybridization and introgression among species can allow for greater flexibility in the responses of Andean trees to climate change through the formation of novel allelic combinations unlikely to occur in parental genomes alone (Cronk and Suarez-Gonzalez 2018). The potential for species to respond to environmental change through genomic mechanisms depends largely on the standing genetic diversity, which may underpin fitness, inbreeding depression, and niche breadth (DeWoody et al. 2021; Hoban et al. 2022). Population size also impacts adaptive potential and extinction probability, as selection is less effective in small populations and the effects of genetic drift are more pronounced (Wright 1932; Willi et al. 2006). As such, hybridization provides for evolutionary outcomes other than extinction (Pereira et al. 2016)—currently the most likely outcome for a high number of tree species in tropical Andean forests under future climate change scenarios (e.g. Feeley et al. 2012). If hybridization and adaptive introgression are indeed important for the persistence of these species in the Anthropocene (Hamilton and Miller 2015), it may even call into question what extinction really means, with much allelic diversity residing *within* interbreeding populations and species rather than segregated *among* them. Perhaps biodiversity conservation efforts should more strongly consider species complexes, and focus on maintaining interspecific gene flow rather than preventing it (Cronk and Suarez-Gonzalez 2018). This could be achieved through protecting and restoring the connectivity of ecosystems, one of the primary goals outlined in the Kunming-Montreal Biodiversity Framework to safeguard the genetic diversity of populations and their adaptive potential (United Nations Convention on Biological Diversity 2022).

Habitat connectivity is inextricably linked to the potential for species migrations, gene flow, and hybridization, but faces significant threat from climate change and deforestation. In the tropical Andes, anthropogenic land-cover change is rapidly reducing suitable habitat (e.g., Rodríguez Eraso et al. 2013, Curatola Fernández et al. 2015), which in turn decreases population sizes, fragments, and isolates populations, and increases distances they must migrate or adds "friction" to the landscape (Ricketts 2001; Zeller et al. 2012). Forest loss accelerates upslope range shifts in tropical regions, possibly due to population extirpation and microclimatic changes (Guo et al. 2018), while cattle grazing and anthropogenic fires in the Andes are reducing the upper elevational limits of forest growth (Lutz et al. 2013). In addition, defaunation reduces the potential for both migration and gene flow (Malhi et al. 2014; Mokany et al. 2014) as most tropical trees rely on animals for both pollination and dispersal (see Zjhra and Kaplin 2004). Without immediate action to better protect and expand protected areas in these regions and create habitat and, specifically, climate corridors, many species will be driven to extinction before climate change pushes them to the limits of their environmental tolerance (Silman and Feeley 2010a; Malhi et al. 2014).

6. CONCLUSIONS

The rapid pace of current climate change means that most Andean tree species cannot move fast enough to keep pace with their preferred climate. However, any migration that results in spatio-temporal overlap among previously allopatric species may result in hybridization, which can introduce new suites of allelic diversity and gene combinations. Although the evolutionary outcomes of hybridization can be both creative and destructive, and these outcomes are difficult to predict, increased genomic diversity provides a greater opportunity for selection to act upon. Traditional adaptation via natural selection upon standing genetic variation and new mutations can take many generations, rendering it an untenable response for long-lived tropical trees under current climate change scenarios (Smith and Donoghue 2008; Shaw and Etterson 2012). Hybridization with introgression can significantly speed up this process through the introduction of many new genes or whole genomes within a single generation (Rieseberg et al. 2003; Seehausen 2004; Chunco 2014). Whereas this may occur at a cost to biodiversity in some instances due to lineage collapse or reduced hybrid fitness (Rhymer and Simberloff 1996; Seehausen 2006; Todesco et al. 2016), there may still be an overall net biodiversity gain when considering the expected losses to the Andean tree flora under migration and adaptation alone (Feeley et al. 2012).

Though not as well characterized, increased genetic variation can also influence a population's ability to acclimate to changing environmental conditions by broadening the range of individual physiological responses. Further, Walter et al. (2023) showed that genetic variation underlying plasticity can increase adaptive potential in novel environments. However, Andean tree genera tend to show strong niche conservatism, with congeneric species often occupying similar elevations and clustering above or below the cloud forest ecotone (Griffiths et al. 2020). Though niche conservatism may constrain the range of environmental conditions to which a lineage is ultimately able to acclimate or adapt, some species and genera are able to escape this constraint and are not phylogenetically clustered (Griffiths et al. 2020). Others have even argued that clades whose species occupy similar habitats exhibit increased mutualism, niche expansion, and hybridization, resulting in reduced vulnerability to environmental change (Prinzing et al. 2016). Niche conservatism may also contribute to the lability of plant hybrid zones and thus the lack of hybrid zone reporting in plants compared to animals, by enabling them to track their ecological preferences through active dispersal, which can lead to disjunctions and the dynamic formation and dissolution of hybrid zones over time (Nieto Feliner et al. 2023).

Hybridization has been fundamental to the evolution of Neotropical trees historically (reviewed by Schley 2022), but the paleoecological record shows that species largely responded to past climate change by shifting geographically to remain in equilibrium with climate or went extinct (e.g. Jackson and Overpeck 2000; Bush et al. 2004; Williams et al. 2004). In the past, species shifting in equilibrium with climate likely had higher fitness and swamped hybrids and novel adaptations that allowed species to adapt to new climates. Here, the past may not be the key to understanding the future given the exceptional pace and directionality of temperature changes compared to the late Quaternary fossil record (Bush et al. 2004). Instead, population sizes may collapse with range retractions, reducing competition and swamping novel gene combinations generated by hybridization. Future work should focus on understanding how climate change and land cover change may affect opportunities for hybridization and its evolutionary outcomes across elevational gradients in Neotropical trees, as this is critical for predicting community-wide responses and understanding biodiversity responses to ongoing climate change.

Recent advances in genomics provide powerful tools to better characterize the complex outcomes and implications of climate-induced range shifts and hybridization. Next-generation sequencing has made the study of non-model organisms, such as tropical trees, not only possible but cost-effective (Andrews et al. 2016; Parchman et al. 2018). Genome-wide sequencing can identify allelic shifts and gene flow across gradients, and detect potential hybridization at range margins (e.g. Eaton et al. 2015 OR Nevado et al. 2018, Linan et al. 2021). When resources such as annotated genomes are available, genome-wide association (GWAS) and quantitative trait loci (QTL) mapping can identify gene variants linked to adaptive traits such as thermal tolerance and drought resilience to help researchers understand which hybrid combinations may enhance adaptive potential and under which conditions these adaptations arise (Santure and Garant 2018). Targeted enrichment sequencing even allows for the inclusion of historical plant material in such studies, and resources such as taxon-specific loci sets are rapidly being developed (e.g. Nicholls et al. 2015; Johnson et al. 2019). Finally, combining genomics with transcriptomics can help to disentangle the roles of adaptive evolution versus physiological plasticity in species responses to a changing environment (DeBiasse and Kelly 2016). Importantly, these next-generation technologies generate data for hundreds to thousands of loci for a single sample, an essential advance for the study of tropical trees which often occur at low densities (ter Steege et al. 2013).

Still, even in the presence of next-generation technologies, the greatest limit to our understanding of hybridization in Andean forests is the number of collections that remain unidentified – nearly a third of all trees in most tropical forest plot networks. Future work must also focus on collections-based research and using molecular tools to identify unknown morphospecies, and thereby better constrain species ranges, identify ongoing distributional shifts, and characterize the extent and consequences of hybridization in Andean forests.

TABLES

Table 1. Studies identifying recent hybrid zones among species or subspecies that developed after a range shift attributed to climate change.

Study	**Common name**	**Scientific name**	**Taxonomic group**	**Location**
Garroway et al. 2010	Northern & southern flying squirrels	*Glaucomys sabrinus x G. volans*	Mammal	Ontario, Canada
Cahill et al 2015, Pongracz et al. 2017	Polar bears x brown bears	*Ursus maritimus x U. arctos*	Mammal	ABC islands, Alaska, Canada, Europe
Garcia-Elfring et al. 2017	White-footed mouse x deer mouse	*Peromyscus leucopus x P. maniculatus*	Mammal	Quebec
Taylor et al. 2014	Black-capped chickadees x Carolina chickadees	*Poecile atricapillus x P. carolinensis*	Bird	Pennsylvania & New Jersey
Kersten et al. 2023	Atlantic puffins	*Fratercula arctica naumanni x F. a. arctica x F. a. grabae*	Bird	Norway
Muhlfeld et al. 2009 & 2014	Cutthroat trout x Rainbow trout	*Oncorhynchus clarkii lewisi x O. mykiss*	Fish	Flathead river basin (Montana, US & Alberta, Canada)
Walls 2009	Plethodon salamanders	*Plethodon teyahalee x P. shermani*	Amphibian	Southern Appalachians
Sequeira et al. 2011	Neotropical toads	*Rhinella marina x R. schneideri*	Amphibian	Amazonia
Pereira et al. 2016	Fire salamanders	*Salamandra salamandra* (9 subspecies)	Amphibian	Iberian Peninsula
Britch et al. 2008	Striped ground cricket x southern ground cricket	*Allonemobius fasciastus x A. socius*	Insect	Eastern United States
Mallet et al. 2011	Brown argus butterflies	*Polyommatus (Aricia) agestis x P. (A.) artaxerxes*	Insect	Britain
Sanchez-Guillen et al. 2011, Wellenreuther et al. 2018	Damselflies	*Ischnura elegans x I. graellsii*	Insect	Europe
Ryan et al. 2018	Tiger swallowtail butterflies	*Papilio glaucus x P. canadensis*	Insect	Illinois & Wisconsin
Stewart et al. 2012	Shortleaf x loblolly pine	*Pinus echinata x P. taeda*	Plant	Southeastern United States
Beatty et al. 2015	St. Patrick's cabbage x kidney saxifrage	*Saxifraga spathularis x S. hirsuta*	Plant	Ireland

Gomez et al. 2015	Alpine plants	Many species	Plant	Sierra-Nevada Mountains (south-eastern Spain)
Ortego et al. 2016	Californian oaks	*Quercus durata x Q. berberidifolia*	Plant	California
Leroy et al. 2017	European white oaks	*Quercus petraea x Q. robur x Q. pubescens x Q. pyrenaica*	Plant	France
Chhatre et al. 2018	Poplar trees	*Populus angustifolia x P. balsamifera x P. trichocarpa*	Plant	Rocky Mountains
Pfeilsticker et al. 2022, 2023	Tasmanian eucalyptus	*Eucalyptus risdonii x E. amygdalina*	Plant	Tasmania
Tsuda et al. 2016, Chen et al. 2019, Karunarathne et al. 2024	Norway spruce x Siberian spruce	*Picea abies x P. obovate*	Plant	Europe

Table 2. Studies of climate change-induced plant phenological shifts.

Study	**Type of phenological shift**	**Location**	**Time period of study**
Bradley et al. 1999	Early onset of spring flowering	Wisconsin	1936-1947 & 1976-1998
Menzel 2000	Early onset of spring leafing and flowering and delayed onset of autumn leaf coloring	Europe	1959-1996
Piao et al. 2006	Early onset of leafing	China	1982-1999
Crimmins et al. 2010	Early onset of spring flowering	Mt. Kimball, Arizona	1984-2003
Høye et al. 2013	Shortening of flowering	Greenland	1996-2009
Ovaskainen et al. 2013	Early onset of spring flowering	Russia	1960-2010
Zhao et al. 2013	Shortening of flowering and budburst delays	Southwest China	1973-1999
Bjorkman et al. 2015	Experimental warming – early onset flowering; Natural plots – constant or delayed flowering (hypothesized due to increased snowfall & delayed snowmelt)	Ellesmere Island, Canadian Arctic Archipelago	1992-2013
Panchen and Root 2015	Early onset flowering and fruiting in *Dryas integrifolia* but no change in *Saxifraga oppositifolia*	Ellesmere Island, Canadian Arctic Archipelago	1994-2014
Dunham et al. 2018	Shifts in fruiting timing	Madagascar	2005-2016
Prevéy et al. 2019	Early onset of flowering in late-flowering species; overall shorter flowering seasons	Tundra ecosystems across N America, Greenland, and Europe	
Rosbakh et al. 2021	Early onset of leaf out, flowering, and fruiting	Siberia	1976-2018

FIGURES

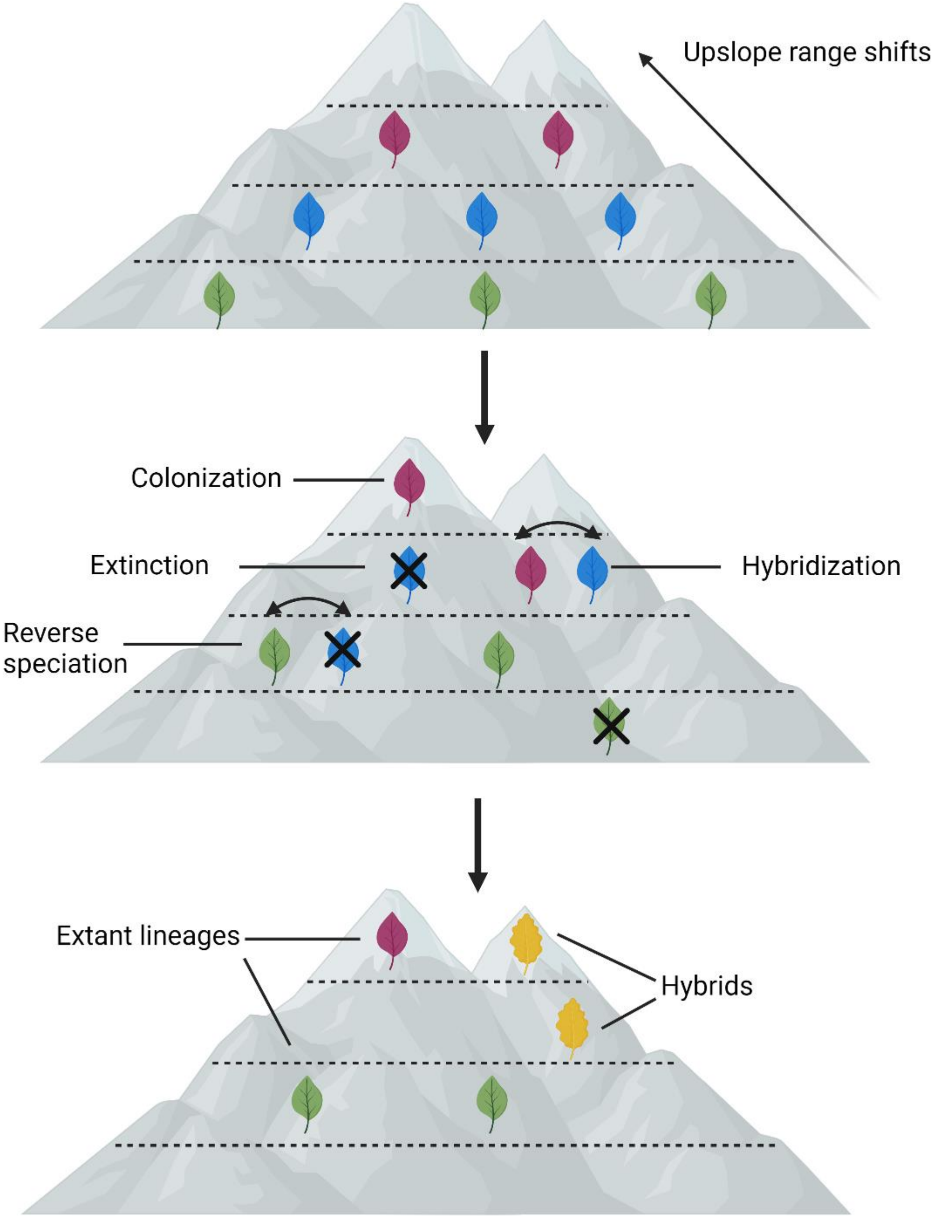

Figure 1. Under current climate change, species are shifting their ranges upslope to track their optimal environmental conditions, resulting in increased range overlap and gene flow. Some populations and species will go extinct, while other recently diverged lineages may collapse back into a single lineage, resulting in decreased species diversity. Alternatively, increased gene flow may result in hybrids that are more fit than their parents or backcrossing of novel allelic diversity via introgression, allowing for diversification and colonization of novel climate zones. Colors represent distinct lineages. Leaves with wavy margins represent hybrids.

DATA AVAILABILITY STATEMENT

Not applicable.

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APPENDICES

Not applicable.

SUPPORTING INFORMATION

Not applicable.