Rules of Plant Species Ranges: Applications for Conservation Strategies

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Earth is changing rapidly and so are many plant species' ranges. Here, we synthesize eco-evolutionary patterns found in plant range studies and how knowledge of species ranges can inform our understanding of species conservation in the face of global change. We discuss whether general biogeographic "rules" are reliable and how they can be used to develop adaptive conservation strategies of native plant species across their ranges. Rules considered include (1) factors that set species range limits and promote range shifts; (2) the impact of biotic interactions on species range limits; (3) patterns of abundance and adaptive properties across species ranges; (4) patterns of gene flow and their implications for genetic rescue, and (5) the relationship between range size and conservation risk. We conclude by summarizing and evaluating potential species range rules to inform future conservation and management decisions. We also outline areas of research to better understand the adaptive capacity of plants under environmental change and the properties that govern species ranges. We advise conservationists to extend their work to specifically consider peripheral and novel populations, with a particular emphasis on small ranges. Finally, we call for a global effort to identify, synthesize, and analyze prevailing patterns or rules in ecology to help speed conservation efforts.

Keywords: species range limits, biotic interactions, local adaptation, gene flow, range size, management, climate change

Sustained by previous discoveries, we can go forth into the future, and by foreseeing the consequences of phenomena, we can understand once and for all the laws to which nature subjected itself.

– Alexander von Humboldt and Aimé Bonpland (1807)

INTRODUCTION

A core component of ecology is to recognize and understand patterns in nature (MacArthur, 1972). Since the early studies of biogeography (e.g., von Humboldt and Bonpland, 1807), scientists have put forward a variety of ecological hypotheses, some of which have become entrenched or taken for granted enough to be considered paradigms or "rules," and these efforts continue today (Sagarin and Gaines, 2002; Connallon and Sgrò, 2018; Liu et al., 2020). For example, there is recent interest in establishing "rules of life" to understand and predict how properties of living systems (i.e., environment, phenotype, evolution, etc.) interact (National Science Foundation, 2016; Midlands Integrative Biosciences Training Partnership, 2019) and how these rules can inform

conservation (Kindsvater et al., 2016). A central issue is predicting how species will respond to climate change. Accelerated biodiversity loss (Urban, 2015) and disruptions to global patterns of community assembly (Trisos et al., 2020) are already underway. Thus, we urgently need to understand how species respond to rapid change at the geographic scale, and whether there are broad geographic patterns or phenomena that may lead to enhanced conservation and ecosystem management. Although many species are likely to become endangered or go extinct, targeted conservation measures can save many species from this fate. Every species has a story to tell, and its geographic range (e.g., range size, gene flow patterns, etc.) can provide important insights as to how it can be conserved, managed, and restored.

Whether or not ecological or evolutionary patterns can serve as reliable rules is debatable since few strict laws exist in ecology, but many general ones may (Lawton, 1999; Temperton et al., 2004; Dickey et al., 2021). **Broadly, we consider rules to be effective, predictive hypotheses with strong empirical support**. Like any good rule, they will be broken due to the idiosyncrasies among species and the vast variation life represents. Nevertheless, knowing whether species ranges provide generalizable ecological rules, such as in patterns of abundance, distribution, and interactions, or evolutionary rules, such as in patterns of selection, drift, and gene flow, would allow more informed management decisions at large geographic scales (Pelletier et al., 2018).

In this article, we evaluate various paradigms as potential "rules" within five eco-evolutionary realms of species ranges— some long-held—that are important for species conservation and biogeography. We highlight new and emerging findings throughout, including needed areas of future research, and we include conservation recommendations within each section. Although this topic applies to all forms of life, we focus our examples and conservation prescriptions primarily on plants. As primary producers, all ecosystems depend on their plant communities to influence a suite of essential ecological processes, including resource use efficiency, biomass production, and nutrient recycling (Cardinale et al., 2011). Therefore, managing for healthy, resilient plant communities is of primary concern for ecosystem conservation and restoration. We end the paper by summarizing our general findings for each rule and its associated conservation implications (**Table 1**).

HOW ARE SPECIES RANGES DEFINED AND TRACKED?

The Essence of Plant Species Ranges

Plants respond to stress and rapid environmental change through several mechanisms. As sessile organisms in terrestrial ecosystems, plants greatly employ a local scale of adaptation (Alpert and Simms, 2002; Palacio-López et al., 2015). However, there is also a large geographic scale at which plant populations vary in their attributes, environments, modes of communication among populations (i.e., gene flow), and interactions with abiotic and biotic factors (Darwin, 1859; Griggs, 1914; MacArthur, 1972;

Brown, 1984). This scale is commonly known as the species range (Gaston, 2003), which is assumed to be a projection of niche availability in geographic space (Sexton et al., 2009). In this vein, a classic paradigm that has garnered enough support to be considered a rule is that range limits are niche limits, beyond which populations tend to decline along with their available niche attributes. Nevertheless, some edges are limited more by dispersal. Recent and current work has sought to identify the relative importance of niche vs. dispersal limitation for focal species, mainly through the use of transplant experiments and species distribution models (SDMs) (Hargreaves et al., 2014; Lee-Yaw et al., 2016; Connallon and Sgrò, 2018; Bayly and Angert, 2019; Ackerly et al., 2020). From these studies, we can form generalizations about what types of edges are most likely to fall into each of these two categories, or both. Transplant and modeling approaches have strengths and weaknesses (reviewed in Araújo and Peterson, 2012; Ehrlén and Morris, 2015; Greiser et al., 2020). Moreover, with respect to species ranges, climate edges may not always correlate with geographic edges due to climate heterogeneity and geographic scale effects on climate properties (Oldfather et al., 2020). Thus, range limits are perceptible and approximate niche limits at particular scales, but also shift as climates change (Sexton et al., 2009; Halbritter et al., 2018).

Plant Species Ranges on the Move in a Changing Climate

In response to global warming, plant species ranges are shifting, contracting, and expanding into new territories and into refugia characterized by milder climate conditions and greater water availability (Hampe and Petit, 2005; Lenoir et al., 2008(Feeley, 2012; de Lafontaine et al., 2018; Freeman et al., 2018; Meng et al., 2019; Miller et al., 2020; Mamantov et al., 2021; Reed et al., 2021; Zu et al., 2021). In most cases, plant species range limits are moving quickly. The general pattern for plant species ranges is to move to higher latitudes, elevations, and cooler environments with higher precipitation to escape rising temperatures and drought, often resulting in range contraction (Kelly and Goulden, 2008). This pattern of uphill range shifts is documented in many ecosystems, including deserts, such as the Newberry mountains of the Mojave Desert (NV, United States) (Guida et al., 2014), the tropical Andes mountains (Peru, South America) (Feeley et al., 2011; Feeley, 2012), the subtropical mountains of Mt. Gongga (Sichuan, China) (Zu et al., 2021), and other montane systems worldwide (Mamantov et al., 2021). However, tracking of climate change in montane species may be more pronounced in the tropics, where seasonality is reduced (Ghalambor et al., 2006), than in temperate zones (Freeman et al., 2018). Rapid plant community change is also a symptom of climate change. In coastal ecosystems, as sea levels rise, the globally distributed mangrove, *Avicennia* sp. (Acanthaceae), is replacing existing habitats (e.g., salt marsh ecosystems) as their distributions expand (Saintilan et al., 2014). Nevertheless, there are plant species with static ranges that are so far resilient to climate change, such as with some heat-adapted desert shrubs (Tielbörger and Salguero-Gómez, 2014).

TABLE 1 | Rules of plant species ranges, their open research questions, conservation applications, and supporting literature.

Research directions: unanswered questions	*Conservation suggestions: well-supported applications*	*References*
Range limits often coincide with niche limits. (Section 2)		
1. What are the best strategies to facilitate colonization at the leading edge of a species range? What strategies conserve the rear edge? 2. What attributes best increase a plant species' capacity to move its range? 3. Does a species' capacity to track changing climate vary across ecosystems (e.g., tropical vs. temperate conditions)?	1. Future habitat for ranges predicted to move should be considered for conservation. 2. Assume most areas of a species range are limited by suitable habitat, except for leading edges, which are likely dispersal-limited. 3. Assume that species ranges are moving poleward or higher in elevation. Plan to conserve trailing edge populations, which are at risk for range contraction.	Hampe and Petit, 2005; Sexton et al., 2009; Stanton-Geddes et al., 2012; Hargreaves et al., 2014; Lee-Yaw et al., 2016; Sexton and Dickman, 2016; Halbritter et al., 2018; de Lafontaine et al., 2018; Cross and Eckert, 2020; Reed et al., 2021
Biotic interactions set range limits in both warm and cold climates. (Section 3)		
1. How do biotic interactions vary across a plant species' range? How do biotic interactions vary by time (e.g., by season or year) or by climate (e.g., at warm limits versus cold limits)? 2. Are there specific species or communities of species required for populations to establish in new territories? 3. What types of biotic interactions and how many are necessary to include in species distribution models (SDMs) to maximize accuracy?	1. Assume there are myriad biotic interactions important across a plant's species range. 2. Biotic interactions are important for overall ecosystem health and should be considered in conservation activities (e.g., assisted migration). 3. Soil microbial communities are important for successful plant habitat restoration. 4. During field surveys, note species that are co-occurring with target species. Sample for environmental data (eDNA) when possible, to produce a database of potential interacting species, including microbes.	Hille Ris Lambers et al., 2013; Afkhami et al., 2014; Louthan et al., 2015; Bueno de Mesquita et al., 2016; Freeman et al., 2018; Koziol et al., 2018; Benning and Moeller, 2019; Hargreaves et al., 2019a; Phillips et al., 2020; Rolshausen et al., 2020
Local adaptation is widespread across species ranges. (Section 4)		
1. Will rapid adaptation allow species to adapt to changing conditions rather than shifting their ranges? 2. How does adaptive potential and/or local adaptation vary across species ranges and affect the capacity for species range limits to expand or contract under climate change? 3. To what extend do small, peripheral populations harbor unique, adaptive genotypes? 4. What proportions of plant populations' adaptive potential are held within their seed banks, relative to the adaptive potential expressed above-ground in a given year? 5. Does plant population genetic variation (adaptive potential) decline at species niche or geographic margins?	1. Assume genetic variation is high in large populations and variable across the species range. 2. Assume that unique (e.g., having distinct phenotypes or occurring on rare soils) or old populations (e.g., refugia) harbor important genetic variants and are locally adapted, even if these populations are small. 3. Collect seeds widely across species ranges, from central to peripheral areas, to conserve important genetic variation (e.g., Project Baseline; Etterson et al., 2016).	Ellstrand and Elam, 1993; Lesica and Allendorf, 1995; Channell and Lomolino, 2000; Sagarin and Gaines, 2002; Hampe and Petit, 2005; Sexton et al., 2009; Moeller et al., 2011; Etterson et al., 2016; Dallas et al., 2017; Hoffmann et al., 2017; Pironon et al., 2017; Papuga et al., 2018; Hargreaves and Eckert, 2019; Anderson and Wadgymar, 2020; Angert et al., 2020; Pennington et al., 2021
Ranges are largely genetically structured by isolation by distance (IBD), isolation by environment (IBE), or both. (Section 5)		
1. How do gene flow rates and dispersal capability of different plant life forms compare with current and projected rates of climate change? 2. Do patterns of genetic isolation across species ranges differ at different spatial and environmental scales? By plant life form or taxon age? 3. Do outcomes of genetic rescue depend on the plant life stages examined? 4. How can seed mixes, representing different genetic distances, affect climate-related range shifts? 5. How do climate change-related phenological shifts impact adaptation and adaptive potential? 6. How does assisted migration affect genetic differentiation of populations?	1. Assume that among-population genetic variation and gene flow is geographically structured, regardless of the size of the range. 2. Assume that gene flow will be beneficial to small or declining populations but choose source populations with beneficial traits for target populations. 3. In plants under climate-related conservation concern, prescriptive gene flow or genetic rescue from distant (for IBD) and environmentally different (e.g., warmer; for IBE) populations may be warranted. Use adaptive management frameworks. 4. Utilize seed-saving and rescue gene flow for populations with low adaptive potential. 5. Practice experimental gene flow in non-model and understudied taxa, and at a wide variety of spatial and ecological scales 6. Assume IBD is present across large spatial extents and IBE is in play across heterogenous environments and landscapes. 7. Species suffering from habitat fragmentation will benefit from employing genetic rescue to restore disrupted gene flow.	Hirao and Kudo, 2004; Moyle, 2006; Eckert et al., 2008; Sgrò et al., 2011; Williams, 2011; Temunović et al., 2012; Aitken and Whitlock, 2013; Sexton et al., 2014; Wang and Bradburd, 2014; Haddad et al., 2015; Whiteley et al., 2015; Bell et al., 2019; Torres-Martínez et al., 2019; Twyford et al., 2020; Fitzpatrick and Funk, 2019; Kottler et al., 2021; Lien et al., 2021; Morente-López et al., 2021

(Continued)

TABLE 1 | (Continued)

Research directions: unanswered questions	Conservation suggestions: well-supported applications	References
Smaller ranges tend to be more vulnerable to global change. (Section 6)		
1. What are the relative effects of factors such as niche breadth, species' age, niche availability, mating system, ploidy, dispersal ability, and range position on the size of a species range?	1. Assume small ranges are most vulnerable to climate change.	Lyons et al., 2005; Slatyer et al., 2013; Baniaga et al., 2020; Grant and Kalisz, 2020; Leão et al., 2020; Sheth et al., 2020; Tanentzap et al., 2019; Bisbing et al., 2021; Vázquez-García et al., 2021
2. Are rare plant species more limited by genetic variation?	2. Assume range size is influenced by myriad factors, including niche-breadth, species' age, niche availability, range position, and mating system.	
3. How does the size of a species range predict the vulnerability of an individual plant (e.g., adaptive phenotypic plasticity) versus a population (e.g., genetic variation) to conservation risk?	3. Promote strong protection and conservation status for endemic, rare, and small-ranged species.	
4. Do small-ranged species show greater signals of extinction dept?	4. Promote connectivity and gene flow for large-range species. Engage relevant stakeholders in the discussion.	

For each rule, the article section discussing that rule is given in parentheses.

Conclusions, Future Directions, and Conservation Applications

A general rule is that species range limits often coincide with niche limits and as a consequence, are shifting in response to climate change (Reed et al., 2021). Dispersal limitation can cause discordance between shifting niche limits and range limits (Stanton-Geddes et al., 2012; Lee-Yaw et al., 2016; Sexton and Dickman, 2016; Cross and Eckert, 2020). Range limits continue to offer a compelling spatial context for conservation research (Serra-Diaz and Franklin, 2019). Research on how to best facilitate new colonizations at the leading edges and conserve rear edges of species ranges is needed (Kottler et al., 2021; **Table 1**). Through the use of transplant experiments and robust SDMs, key drivers and patterns across species ranges can be uncovered (Franklin et al., 2017). Studies that identify and distinguish between the capacity for ranges to move, versus rapid adaptation that stabilizes range limits, will be useful in predicting future range shifts or lack of shifts, respectively. Further research into whether a species' capacity to track climate varies across ecosystems (e.g., tropical vs. temperate conditions), or why some plant ranges (e.g., annuals, perennials, trees, etc.) are better than others at tracking conditions, is greatly needed.

Conservationists and managers should assume most areas outside of a species range are limited by suitable habitat, except for the leading edges, which are likely to be more limited by dispersal. The trailing edges of species ranges are, in many cases, at risk for contraction and should be another priority for conservation by saving seeds from warm-adapted regions to facilitate and enable genetic rescue (see section 5.5). Regions that represent future habitat for ranges that are moving should also be conserved and protected. In general, more research and protection are needed in tropical systems where biodiversity loss will be greatest and in the Southern Hemisphere where ecosystems are understudied.

HOW DO BIOTIC INTERACTIONS INFLUENCE SPECIES RANGES?

Evidence for the Importance of Biological Interactions on Species Ranges

Biotic interactions are an integral component of a species' realized niche (Peay, 2016; Phillips et al., 2020) and are essential to consider in range limit contexts (Hargreaves et al., 2014; Freeman et al., 2018) and species distributions (Hille Ris Lambers et al., 2013). For millennia, natural climate change events have altered the dynamic of these important interactions (Blois et al., 2013; Hamann et al., 2021), affecting their co-evolution (Parmesan, 2006), and influencing their role in facilitating range shifts (Hille Ris Lambers et al., 2013). Darwin (1859) predicted that negative biotic interactions (i.e., competition, predation, herbivory, and parasitism) establish range limits at warm edges where species diversity is higher. Since then, this paradigm has received extensive support (MacArthur, 1972; Brown et al., 1996; Gaston, 2003; Normand et al., 2009; Paquette and Hargreaves, 2021) and

is the leading hypothesis for how biotic interactions influence species ranges (Barton, 1993; Bullock et al., 2000; Scheidel and Bruelheide, 2001; Holt and Barfield, 2009; Louthan et al., 2015).

Over time, Darwin's theory has been expanded to acknowledge that both positive (i.e., pollination, facilitation, and mutualism) and negative interactions influence plant species range limits at both warm and cold climate limits (Afkhami et al., 2014; Louthan et al., 2015; Benning et al., 2019; Benning and Moeller, 2021a). For example, in *Clarkia xantiana* ssp. x*antiana* (Onagraceae) fitness decreased beyond its cold limit due to a lack of positive interactions (e.g., pollinators) and the presence of negative interactions (e.g., herbivores) (Benning and Moeller, 2019). When pollen was supplemented and herbivores were removed, fitness beyond the range tripled, demonstrating the importance of these positive and negative interactions for range shifts and expansions. In a second example, Ettinger and Hille Ris Lambers (2017) found that competition between neighboring trees limited performance within ranges, whereas facilitative interactions between adults and juveniles demonstrated the potential to accelerate upward range expansion. Most studies focus on one or a limited set of interactions, often due to logistical constraints, and rarely have multiple interactions been studied simultaneously in range-limit contexts. Given their clear ecological importance, identifying and including an array of biotic interactions will increase accuracy when predicting species range shifts under climate change (Van der Putten et al., 2010).

Both Positive and Negative Interactions Matter in Setting Warm and Cold Range Limits

From the above, the prevailing paradigm is that negative interactions, particularly competition, drive warm-edge range limits (Schemske et al., 2009; Sexton et al., 2009; Louthan et al., 2015; Paquette and Hargreaves, 2021). Although this is often true, there are examples in which other negative interactions affect plant distributions. For example, seed predation is known to influence cold-edge expansion (Brown and Vellend, 2014; Hargreaves et al., 2019b) and herbivory-induced delays in phenology and subsequent reductions in fitness (e.g., biomass or height) limit the species range of susceptible plants (Louda, 1982; Lau et al., 2008; Benning et al., 2019). In California serpentine environments, Lau et al. (2008) found that increased herbivory was one factor that reduced survival and persistence in the native herb *Collinsia sparsiflora* (Plantaginaceae), restricting the species, realized niche to serpentine habitats (Lau et al., 2008). Depending on which species is under consideration, negative biotic interactions can limit or facilitate expansion of a plant species range; in some cases, herbivory of one plant is beneficial to another plant. For instance, in tundra experiencing climate warming, herbivory of competing species protected native plant populations (Eskelinen et al., 2017), allowing range expansion of the tundra community (Kaarlejärvi et al., 2017).

More recently, positive interactions have emerged as relevant and important for consideration in climate-range research. Mutualisms are abundant in stressful conditions (Callaway et al., 2002), affect plant fitness (Lau and Lennon,

2012), mitigate climate stress on species distributions (Bulleri et al., 2016), and influence local adaptation (Pickles et al., 2015). Facultative mutualisms can facilitate expansion of species ranges into stressful habitats (Afkhami et al., 2014; Millar and Bennett, 2016; Benning and Moeller, 2021b) in addition to novel environments (Crotty and Bertness, 2015; Bueno de Mesquita et al., 2020). A key example of a mutualism that expands the plant realized niche is pollination (Phillips et al., 2020). In general, pollinator species distributions are strongly linked to their visiting plant geographic ranges (Duffy and Johnson, 2017). In a four-year study of *Clarkia xantiana* ssp. x*antiana* (Onagraceae), pollinator availability declined with distance from the center of the plant range, contributing to the maintenance of the species range limit (Moeller et al., 2012). Climate change continues to reduce the quantity and quality of pollination services globally (Burkle et al., 2013; Gérard et al., 2020), leading to contractions and reductions of plant species ranges (Chalcoff et al., 2012; Moeller et al., 2012).

Microbes are also important plant mutualists. As such, microbes are an integral part of a plant's habitat (Peay, 2016) and their absence contributes to defining suitable limits as well as hindering expansion (Benning and Moeller, 2019). In the endangered *Hypericum cumulicola* (Hypericaceae), soil microbes boosted population growth and persistence and allowed the plant to expand into previously uninhabitable environments (David et al., 2019). Similarly, soil microbes in the Rocky Mountains interacted with alpine bunchgrass, *Deschampsia cespitosa* (Poaceae), to allow establishment and growth in new, unvegetated areas beyond the range, suggesting the significance of microbes in climate-induced range expansions (Bueno de Mesquita et al., 2020). In the absence of mutualistic soil microbes beyond the species range edge, host plants experienced reduced fitness, limiting this expansion capacity (Benning and Moeller, 2021a). Climate change can alter plant-microbe interactions in a variety of ways, including changing microbial species ranges, community composition, functionality, fitness, and occurrence of host plant species (Rudgers et al., 2020). Plant genotype and root exudates affect microbial community composition (Bulgarelli et al., 2012), allowing plants to counter the impacts of climate-induced stress (Liu et al., 2015; Rodriguez and Durán, 2020). In turn, the spatial variation in microbial communities affects patterns of plant local adaptation (Pickles et al., 2015) and influences the location of a plant's species range (Van der Putten et al., 2010). Understanding microbial community structure across species ranges will provide a better view of mutualist-mediated niche dynamics, especially as it relates to expansion in response to environmental pressures from climate (Rolshausen et al., 2020).

Conclusions, Future Directions, and Conservation Applications

From the above evidence, it is still difficult to say whether biotic interactions are more limiting at warm versus cold limits, but a general rule that can be gleaned is that *biotic interactions often set range limits* in both warm and cold climate extremes. More studies are needed to identify and

understand important biotic interactions across plant species ranges (Wisz et al., 2013). Mutualisms are more important than classically appreciated for range limits in a changing climate, especially when introducing a plant to a new habitat or predicting future range shifts (Hille Ris Lambers et al., 2013; Freeman et al., 2018; Benning and Moeller, 2021a). Range limit research should aim at understanding interactions through species co-occurrence data (e.g., presence/absence data, field observations, etc.) to effectively model distributions and predict range shifts under climate change (Araújo and Luoto, 2007; Kissling et al., 2012; Bueno de Mesquita et al., 2016; Miele et al., 2021). To help track ecosystem biodiversity and change in biota over time, environmental samples from sediment, soil, air, or surfaces can be analyzed using metabarcoding and metagenomics and characterized through reference databases to more completely identify interacting taxa and communities (Moore et al., 2021). This process employs environmental DNA (eDNA) techniques and is known as ecological forensics, and this field has broad implications for conservation, especially for identifying associated soil microbial communities that confer ecosystem resistance and resilience to climate disruption (Koziol et al., 2018; Rudgers et al., 2020). Overall, species interactions are largely under-researched, especially across large biogeographic scales or in remote or unique habitats (**Table 1**).

Restoration efforts should consider the presence and significance of biotic interactions, including soil microbes. Assisted migration efforts are an important conservation strategy and can help plants occupy novel, habitable regions (Hällfors et al., 2017), but traditionally ignore biotic interactions and how they might influence transplanted populations (Bucharova, 2017). When protecting predicted range regions for transplantation or seeding, it is important to assess whether key biotic interactions can persist in these new territories, with special attention given to native soil communities. As we gain more perspective into positive and negative biotic interactions of conservation-targeted species, we can incorporate these occurrence data of interacting species into models (Giannini et al., 2013). For example, a recent model developed by Miele et al. (2021) combines species interaction data, environmental data, and species occurrences to disentangle the effects of abiotic and biotic interactions on species distributions (see ELGRIN model, Miele et al., 2021).

DO DIFFERENT REGIONS OF SPECIES RANGES HOLD PREDICTABLE ADAPTIVE OR RESILIENCE PROPERTIES?

The Abundant Center Hypothesis Is Not a General Rule

Whether specific regions of species ranges (e.g., peripheral, central, warmer, older, etc.) differ in ecological and evolutionary properties is an essential question for guiding management of plant populations under global change. As discussed earlier, range limits are generally niche limits when ranges are in

climate equilibrium, and the dynamics between and within different regions of plant species' ranges have evoked several hypotheses to consider. For example, Lesica and Allendorf (1995) proposed that peripheral regions of species ranges should harbor genetically unique and isolated genotypes that are useful for conservation purposes. In agreement with this hypothesis, peripheral populations in shrinking species ranges are just as likely as central populations to serve as refugia (Channell and Lomolino, 2000).

A handful of paradigms have developed regarding the center of the species range. One classic paradigm is the abundant center hypothesis (ACH), which posits that populations are most abundant at the center of their *range* and will decrease in both size and density towards range margins (Brown, 1984); nevertheless, this does not appear to hold as a general rule (Sagarin and Gaines, 2002; Sexton et al., 2009; Dallas et al., 2017; Pironon et al., 2017). Another paradigm is the niche-distance-abundance (NDA) hypothesis, which proposes that species will be most abundant at the center of their *niche* (Dallas and Hastings, 2018; Osorio-Olvera et al., 2019); however, this has also received mixed support (Dallas et al., 2017; Weber et al., 2017; Dallas and Hastings, 2018; Jiménez-Valverde et al., 2021). A recent study of the endemic Iberian Peninsula snapdragon, *Antirrhinum lopesianum* (Plantaginaceae), found a negative relationship with abundance and distance from the species' niche center (Hernández-Lambraño et al., 2020). Similarly, an analysis of European vascular plants found evidence of a negative niche distance-abundance relationship, but the relationship was weak and highly variable (Sporbert et al., 2020). There are many examples where range position, niche position, and abundance do not correlate (Sagarin and Gaines, 2002; Eckert et al., 2008; Sexton et al., 2009, 2016; Dallas et al., 2017; Pironon et al., 2017; Kennedy et al., 2020), and in some cases, plant population density actually increases towards range limits (e.g., Sexton et al., 2016). A growing body of research suggests that the history of a population is more indicative of its patterns of abundance and genetic variation than contemporary measures of the population's size, its range position, or the species' range size (Abeli et al., 2014; Koski et al., 2019; Cruz-Nicolás et al., 2020).

Genetic Variation Determines Adaptive Potential of Populations

To conserve threatened species, it is useful to identify populations that are most vulnerable and those that have the potential to help other populations of the species adapt to changing climate conditions. Adaptive potential is determined by genetic variation, which allows a population's traits to change in response to changes in the environment (Pennington et al., 2021). Quantitative genetic variation (QGV) is a measure of genetically based phenotypic variation and, ultimately, the evolutionary adaptive potential of populations (Rice and Emery, 2003; Conner and Hartl, 2004). Populations with larger effective population sizes tend to be higher in QGV (Hoffmann et al., 2017), and so are important for conservation. Nevertheless, small populations, especially those in adverse conditions (e.g., stressful soils), may harbor unique variation that is also important for conservation

(Ellstrand and Elam, 1993). Furthermore, older populations and populations that may have been glacial refugia may also retain important variation (Hampe and Petit, 2005), but may not have large numbers of individuals in their populations. Evidence suggests that larger, older, and unique populations are more likely to be important sources of QGV, and these may occur anywhere within species ranges, centrally or peripherally. Given that the ACH is not supported as a general rule, QGV, and therefore adaptability, may not be highest in central regions of species ranges. Overall, more research is needed in this area, including replicated sampling and comparison of peripheral and central regions within species ranges (Pennington et al., 2021).

Local Adaptation Follows Adaptive Potential

Local adaptation occurs throughout species ranges and is often driven by climate (Anderson and Song, 2020; Anderson and Wadgymar, 2020; Bontrager et al., 2021). Local adaptation has been observed in myriad species and results in differential responses to climate change across species ranges (Hargreaves et al., 2014; Harrison et al., 2019; Peterson et al., 2019; Torres-Martínez et al., 2019; Anderson and Wadgymar, 2020; Patsiou et al., 2020). Peripheral populations are critical when considering climate-driven fitness variation and conservation (Lesica and Allendorf, 1995; Channell and Lomolino, 2000; Macdonald et al., 2017; Papuga et al., 2018) because they are often locally adapted to more extreme habitats and are home to phenotypes that are not expressed in other areas of the range (Moeller et al., 2011; Papuga et al., 2018; Hargreaves and Eckert, 2019; Angert et al., 2020; Morente-López et al., 2021). For example, in a reciprocal transplant of the ʻōhiʻa lehua tree (*Metrosideros polymorpha*) from tropical Hawaii, seedlings that are locally adapted to historically wet regions germinated less than seedlings adapted to drought in contemporary dry regions (Barton et al., 2020).

Further such studies are needed, including more studies that reveal patterns of population genetic variation and size across plant species ranges (Pennington et al., 2021). As climate change alters local adaptation (Anderson and Wadgymar, 2020), patterns of adaptive variation and abundance may change. Besides directly measuring QGV across species ranges, other methods to quantify differences in adaptive potential such as artificial selection and resurrection studies—in which prior generations are compared to contemporary populations for their trait values—are useful for contrasting historical patterns with contemporary patterns to understand how populations are responding to climate change. Recent plant resurrection studies have captured varying phenological change in response to climate change and illustrate that some degree of rapid adaptation is possible for many plant species (Franks et al., 2018; Dickman et al., 2019; Vtipil and Sheth, 2020; Wooliver et al., 2020; Anstett et al., 2021; Kooyers et al., 2021).

Conclusions, Future Directions, and Conservation Applications

Patterns of adaptive potential and local adaptation are in need of better understanding, especially at range edges where

potential expansion or contraction may occur in response to rapidly changing climate. Nevertheless, peripheral populations are understudied and, as a result, underprotected (Caissy et al., 2020). *A general rule is that local adaptation is widespread across species ranges.* SDMs that incorporate local adaptation, such as ΔTraitSDMs (Garzón et al., 2019), should be considered when predicting species' range responses to climate change. Small populations in unique environments and older populations may harbor important, but underexplored, genetic variation. The abundant center-hypothesis, although supported in some species, is not a rule and, instead, a niche-abundance relationship deserves further study. Both central and peripheral populations are equally important to consider in research and conservation contexts. Deeper explorations of the relationship between niche, range, and abundance patterns across plant species ranges will provide better predictions of important populations for conservation. Overall, these questions need to be explored in more systems as these patterns vary widely by species (Angert et al., 2020; Reed et al., 2021).

To avoid losing unknown adaptive potential, plant conservationists should first assume that local adaptation is widespread, and that adaptive potential is equal across study species ranges, until shown otherwise. Populations with high adaptive potential and populations with unique genotypes are of particular interest to conservation. Small, young populations are likely to have lower adaptive potential and are, therefore, more vulnerable. Wherever possible, populations should be evaluated for their adaptive potential, especially in areas that are at risk to climate change. Small populations with high genetic variation or unique adaptations can be as important for a species' conservation as large populations. Conservationists should collect seeds widely across species ranges, including edge populations to conserve genetic variation and adaptive potential (see Project Baseline, Etterson et al., 2016). Additionally, to our knowledge, it is an open question what proportions of plant populations' adaptive potential are held within their seed banks, relative to the adaptive potential expressed above-ground in a given year. The proportion of genetic variation of a population contained within its soil seed bank should vary greatly by plant life form. Finally, measuring and mapping genetic variation and using approaches that estimate responses to selection such as resurrection studies are useful to assist in conservation and management of plant populations. These strategies can inform managers about which populations are most vulnerable to change, and whether certain areas of a species' range should be prioritized for conservation.

ARE THERE PREDICTABLE PATTERNS AND EFFECTS OF GENE FLOW ON ADAPTATION ACROSS SPECIES RANGES?

Gene Flow Across Species Ranges

Gene flow is widely recognized for both its enhancement and inhibition of adaptation, and it is one of the best evolutionary

tools for managing species range responses to climate change (Aitken and Whitlock, 2013; Sexton et al., 2014; Smith et al., 2014; Bontrager and Angert, 2019; Kottler et al., 2021). Thus, understanding rules of gene flow across plant species ranges is key for a conservation biologist. Prescribing gene flow is also a game of chance, of course (Bell et al., 2019), but it can be successful with good planning and strategy (Sgrò et al., 2011). Environmental, geographical (spatial), or temporal patterns of gene flow are prevalent across species ranges (Sexton et al., 2014; Peters and Weis, 2019). At species range limits, gene flow is theorized to enhance genetic variation to expand a species' niche (Holt and Gomulkiewicz, 1997), or gene flow may potentially limit or collapse a range (Kirkpatrick and Barton, 1997). The lack of gene flow is also theorized to set range limits in marginal populations that have small population sizes and high rates of inbreeding depression (Antonovics, 1976; Hoffmann and Blows, 1994; Morente-López et al., 2021). Finally, different patterns of gene flow occur simultaneously and interact with each other to influence eco-evolutionary outcomes across species ranges (Sexton et al., 2014; Bontrager and Angert, 2019; Nadeau and Urban, 2019).

Isolation by Distance Is Prevalent in Plants

Dispersal and dispersal limitation are key features influencing plant ecology, evolution, and distributions. Selection or habitat adaptation notwithstanding, limited dispersal of both pollen or seeds can lead to decreased gene flow and increased genetic drift, resulting in increased genetic isolation with increased geographic distance across the species range, known as genetic isolation by distance (IBD) (Dobzhansky, 1937; Wright, 1943). IBD is the most prevalent pattern of gene flow observed in plants to date, likely due to their sessile nature (Moyle, 2006; Eckert et al., 2008; Orsini et al., 2013; Sexton et al., 2014; Torres-Martínez et al., 2019; Twyford et al., 2020). In this vein, high dispersal ability usually promotes high genetic variation in plants (Hamrick and Godt, 1996; Lander et al., 2021); nevertheless, this variation can affect evolutionary processes among populations differently. For example, in one plant family (Fagaceae), there are examples of little to no adaptive effects of gene flow from long-distance dispersal (Moracho et al., 2016) and large adaptive effects from short distances (Gauzere et al., 2020).

Habitat fragmentation (e.g., agriculture, urbanization, or harvesting of natural resources) can disrupt gene flow among contiguous populations and erode genetic diversity by decreasing the effective population size and increasing the spatial isolation of populations. This can result in genetically depauperate populations subject to increased genetic drift, inbreeding depression and reduced gene flow (Young et al., 1996; Couvet, 2002; Aguilar et al., 2019). IBD increases with habitat fragmentation. Where IBD is detected, even at small spatial scales (Gauzere et al., 2020), genetic variation necessary to respond to rapid environmental change may be limiting, requiring prescriptive or rescue gene flow (see section 5.5) from distant sources (Willi et al., 2007).

Isolation by Environment Is Also Common in Plants

The movement of alleles between populations from similar habitats or environments creates a pattern known as isolation by environment (IBE) or "ecological isolation" (Dobzhansky, 1937; Wang, 2013). IBE scenarios are driven by environmental heterogeneity across species ranges and are caused by natural selection or non-random mating among similar environments (Hirao and Kudo, 2004; Temunović et al., 2012); IBE and IBD are often correlated (Wang and Bradburd, 2014; Shafer and Wolf, 2013). IBE is the prevalent pattern of gene flow in the majority of non-plant species examined, and is nearly as prevalent as patterns of IBD in plants (Sexton et al., 2014; Wang and Bradburd, 2014; Morente-López et al., 2021). Recently, an IBE pattern was found in Asian temperate deserts across the range of the broad-leaved evergreen shrub, *Ammopiptanthus mongolicus* (Fabaceae). In this example, landscape heterogeneity in precipitation was associated with IBE (Jiang et al., 2019). Similar to scenarios with IBD, if plants under conservation consideration exhibit local adaptation and IBE, genetic variation necessary to respond to rapid environmental change may require prescriptive or rescue gene flow from different (i.e., warmer) environments (Sexton et al., 2014; Kottler et al., 2021).

Climate warming has, in most cases, led to an earlier shift in plant flowering phenology (Menzel et al., 2006; Wolkovich et al., 2012; Dai et al., 2014; Leinonen et al., 2020), which influences both plant distribution (Parmesan and Yohe, 2003; Chuine, 2010; Song et al., 2021) and gene flow patterns (Schuster et al., 1989; Wadgymar et al., 2015). Isolation by phenology (IBP) is a form of IBE and occurs when phenology differences (e.g., flowering time) divide populations into different mating pools (Peters and Weis, 2019). Climate warming is leading to more uniformity in phenology, reducing IBP (Franks and Weis, 2009; Chen et al., 2018; Vitasse et al., 2018). Unfortunately, genetically-based evolution of phenology may happen too slowly to rescue populations from rapid climate change (Vtipil and Sheth, 2020). Future work is needed to examine the impact of climate shifts on phenology across large geographic gradients and in assisted migration conservation efforts.

Currently, most studies find that plant genetic variation is explained by a combination of IBE and IBD (Sexton et al., 2014; Moran et al., 2017; Nadeau and Urban, 2019; Da Silva et al., 2021). For example, long distance seed dispersal prevented snowmelt-driven isolation in *Salix herbacea* (Salicaceae) in the Swiss Alps (Cortés et al., 2014). Future studies of gene flow patterns should combine and parse the effects of environment and distance and sample a wide range of environmental variables (biotic and abiotic) across species ranges to isolate drivers of IBE.

The Myth of Gene Swamping in the Creation of Range Limits

Maladaptive gene flow as a mechanism for stalling or degrading adaptation is known as gene swamping and has been invoked as a mechanism for creating range limits (Haldane and Ford, 1956; Kirkpatrick and Barton, 1997). This long-standing paradigm assumes that gene swamping reduces fitness and limits local

adaptation at the range edge by flooding the region with genes adapted to different conditions in central populations, suppressing locally beneficial genes (Antonovics, 1976; García-Ramos and Kirkpatrick, 1997; Kirkpatrick and Barton, 1997; Kawecki, 2008; Lopez et al., 2008). Reduction in fitness from mating genetically divergent populations (i.e., outbreeding depression) has been observed in several plant species (Fenster and Galloway, 2000; Montalvo and Ellstrand, 2001; Oakley et al., 2015). For example, Montalvo and Ellstrand (2001) documented outbreeding depression as a result of crossing deerweed varieties (*Lotus scoparius* var. *scoparius* and *L. s.* var. *brevialatus;* Fabaceae) and recommended caution when crossing plants from very genetically divergent lines for restoration.

Although gene swamping can certainly stall adaptation, it does not appear to be a reliable rule for explaining range limits. A recent review found little evidence to support gene swamping in the evolution of range limits for two reasons (Kottler et al., 2021). First, gene flow is not universally asymmetrical from the center of a range to its peripheries, likely because the abundant center hypothesis is not a universal rule (see section 4), an assumption that range-wide gene swamping relies on. Second, in the few empirical cases where gene flow has been experimentally introduced to plant populations at the edge of a species range, the results are overwhelmingly positive for edge populations (Kottler et al., 2021). This is likely due to the fact that edge populations may suffer from reduced effective population sizes (drift) brought about by increased isolation and strong selection (Hoffmann and Blows, 1994; Eckert et al., 2008; Kottler et al., 2021; Pennington et al., 2021).

The Potential of Genetic Rescue in Conservation

An alternate hypothesis to gene swamping stalling adaptation is genetic rescue, where genetic variation from outside populations is beneficial to populations suffering from inbreeding depression (Tallmon et al., 2004; Hedrick et al., 2011). Gene flow can benefit depauperate populations through the introduction of environment-specific alleles that improve fitness (Sexton et al., 2011; Bontrager and Angert, 2019). When crossing monkeyflower plants (*Mimulus laciniatus*, Phrymaceae) between warm-limit edge populations, Sexton et al. (2011) found that plant fitness increased at the warm-limit. Similarly, Bontrager and Angert (2018) investigated gene flow effects across the *Clarkia pulchella* (Onagraceae) species range in the Pacific Northwest and found a fitness boost in cold-limit edge populations from central gene flow due to rescue effects of warm-adapted populations in a warm, dry climate year.

Small populations are particularly threatened by habitat fragmentation (Haddad et al., 2015) and restoring gene flow through genetic rescue is a viable option for protecting fragmented species ranges (Bell et al., 2019). Genetic rescue is an underappreciated and useful tool for conservation of endangered species (Whiteley et al., 2015). Nevertheless, although discussed often in the literature, genetic rescue is rarely used as a conservation strategy (Frankham et al., 2017;

Robinson et al., 2020). The exploration and use of genetic rescue as a conservation and management tool is still in its infancy (Bell et al., 2019). Yet, this strategy shows great promise (Fitzpatrick and Funk, 2019) and should be used more often in range-wide contexts.

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Gene flow is important for adaptation across species ranges, and range limits can be positively influenced by gene flow events in plant systems. *A general rule is that plant species ranges are largely genetically structured by IBD (driven by dispersal limitation and drift), IBE (driven by selection and non-random mating), or both.* Because of the preponderance of some form of genetic isolation across plant species ranges, assisted gene flow is an important tool for increasing the adaptive potential of populations. IBP, as a form of IBE, is likely to be a common phenomenon in plants, however, it is still poorly understood for its ramifications under climate change. Gene swamping as a creator of range limits is not a rule, since gene flow often has beneficial effects on local adaptation in marginal populations. To better understand beneficial and harmful effects of gene flow in plant conservation contexts, more research is needed at different plant life stages, in non-model and understudied taxa, and at a wide variety of spatial and ecological scales (**Table 1**). Key areas of focus should include controlled cases of gene flow, measuring the effects of different types of gene flow (i.e., IBD and IBE) across ranges, and studying gene flow effects on rapid adaptation (Rehfeldt et al., 1999; Montalvo and Ellstrand, 2001; Sexton et al., 2011; Bontrager and Angert, 2018). Lastly, restoring gene flow through genetic rescue is a proven technique for combating habitat fragmentation and needs more focused application and research (Bell et al., 2019).

Assisted gene flow can be used as a strategy to facilitate local adaptation to climate change (Aitken and Whitlock, 2013). Plant conservation and restoration managers are encouraged to experiment with gene flow and to use prescriptive gene flow more often, employing adaptive management (e.g., Williams, 2011; Lien et al., 2021) with respect to gene flow levels and prescriptive population mixes (Sgrò et al., 2011). Collecting seeds and experimenting with seed mixes that represent different gene flow "distances" are important and sorely needed actions and are especially important to test now that range shifts related to climate are prominent.

DOES RANGE SIZE PREDICT VULNERABILITY UNDER GLOBAL CHANGE?

Range Size Matters

The question of why some plant species are widespread, with large ranges, and others are rare or have restricted ranges, has intrigued botanists for ages. For instance, the niche breadth-range size hypothesis (Brown, 1984; Slatyer et al., 2013) predicts that a species' range size is a manifestation ultimately of

its niche breadth and thus represents its ability to persist in more or fewer environments. Besides potentially having reduced niche breadth, small-ranged species may also have fewer individuals and thus lower effective population sizes. As a result, species with small ranges may be at greater risk under global change. We refer to this phenomenon as the *range size vulnerability* hypothesis.

Explanations for restricted distributions range from a lack of genetic variation, to species being newly evolved taxa, to species being very old and consisting of remnants of a past range (Stebbins, 1942, 1980; Leão et al., 2020). Recent research has supported the case that plant species generally begin small, "budding" from parental species, often sympatrically within the parent species range, and then expanding over time through niche evolution and/or dispersing more widely over time (Grossenbacher et al., 2014; Anacker and Strauss, 2014). Recent literature mainly sustains this view (Gastauer et al., 2015; Heydel et al., 2017; Skeels and Cardillo, 2018), but there is important variation, nuance, and exception, and a variety of forms of speciation and specialization in plants (Boucher et al., 2016; Rajakaruna, 2018; Salariato and Zuloaga, 2021). For example, a species may evolve through adaptation to a niche that is very widespread (e.g., ruderal plants), and so it has the potential to fill this niche quickly and will appear, geologically, as if it expanded its niche rapidly and exploded. Alternatively, clade radiations may fill unused habitats, creating sudden bursts of diversification, followed by gradual broadening of ecological niches and range sizes (Tanentzap et al., 2015; Folk et al., 2019). More diverse plant lineages may typically be comprised of species with smaller ranges (Leão et al., 2020).

What ultimately determines plant species range size can be determined by myriad factors. Sheth et al. (2020) performed a meta-analysis and review on this topic and found that niche breadth, species' age, niche availability (i.e., how common a niche is), and range position (i.e., range characteristics such as latitudinal breadth) were consistently strong factors associated with range size, but concluded that much more research is needed to confirm these effects on plant range sizes plus other potentially important effects such as mating system, ploidy, and dispersal ability. Grossenbacher et al. (2015) found strong support that more highly selfing plants have larger range sizes, and Grant and Kalisz (2020) recently confirmed that selfing plants indeed generally possess greater niche breadth than more outcrossing plant species. Moreover, polyploid plants with higher numbers of chromosomes tend to differentiate their niches faster (Baniaga et al., 2020). Finally, although logistically challenging, very few studies exist testing whether rare plant species are limited by genetic variation, but research thus far suggests that they are (Sheth et al., 2020).

No Range Should Be Left Behind in Conservation

There are clear cases finding strong support for rarity predicting increased vulnerability or conservation risk for plants under climate change. For example, Zettlemoyer et al. (2019) found that rare, more specialized plants are more likely to go extinct

in a study in Michigan, United States. Aspinwall et al. (2019) demonstrated experimentally that *Eucalyptus* (Myrtaceae) trees with smaller range sizes were more susceptible to experimental heat waves. Many studies have found positive associations between niche breadth and species range sizes based on SDMs (see Slatyer et al., 2013). Such correlative species distribution models (cSDMs) show potentially causal relationships between range size and species performance. Nevertheless, an important caveat is that spatial autocorrelation between the number of possible environments sampled and larger geographic extents can mask or overemphasize causal relationships (Moore et al., 2018; Journé et al., 2020).

Another caveat is that such observational studies base patterns on the observed, or realized niche, rather than the fundamental niche, which is of primary interest for understanding environmental tolerances (Sexton et al., 2017; Liu et al., 2020), but see above discussions on biotic interactions and the realized niche. Nevertheless, experimental data can confirm true relationships between vulnerability and range size. Historical considerations may also be quite strong. For example, Rapoport's Rule states that species at higher latitudes should have larger ranges due to the greater stress and variability of those environments (Brown et al., 1996). Thus, more tropical species may be driven or boxed into smaller ranges than their higher-latitude relatives due to evolutionary history. Huang et al. (2021) recently presented evidence supporting this hypothesis in plants: greater climate variability has a large potential effect on the evolution of large range sizes.

There are also clear cases and considerations in contrast to the range size vulnerability hypothesis, or cases with mixed findings (Lacher and Schwartz, 2016; Hirst et al., 2017; Cai et al., 2021). Micro-habitats, local, or sub-surface factors can buffer plants under climate change stress (Franklin et al., 2013; Gremer et al., 2015; Denney et al., 2020), and so small-ranged species that occupy highly heterogeneous landscapes may be able to weather rapid global change through more accessible escape environments. For example, rarity does not appear to limit genetic variation or preclude subpopulation structure in the geographically restricted desert forb, *Astragalus lentiginosus* var. *piscinensis* (Fabaceae) (Harrison et al., 2019). Indeed, adaptation and diversification in rare, stressful environments can cause cradles or hotspots of diversity of taxa with smaller range sizes (Buira et al., 2021). Moreover, microhabitat variation may buffer populations via "portfolio effects," but such effects may not be enough to save rare species from extirpation under rapid climate change (Abbott et al., 2017). In this vein, a species' realized niche may be vastly smaller than their fundamental niche. In such cases, a plant with a very small range may be able to weather a great variety of climates experienced outside of its current realized niche. Finally, a complex and nuanced reality likely exists for many species regarding this question. For example, Hirst et al. (2017) found only mixed results in support of the niche-breadth range size hypothesis in Australian alpine daisies; rarer daisy species showed evidence of increased tolerance of stressful, specialized environments at the cost of lower growth rates in low-stress environments, but their seeds were also resilient to a wider range of germination environments. Thus, species may have

reduced performance in a critical stage only and such limiting stages may take a fair amount of experimentation to confirm.

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Generally, the range size vulnerability hypothesis holds as a rule: smaller ranges tend to be more vulnerable to global change, but exceptions and patterns can vary greatly by taxon. For example, Tanentzap et al. (2019) found range size to be more strongly associated with extinction risk in conifers than in palms. Thus, we recommend that special status species with smaller geographic ranges receive high conservation priority, including reserve establishment in regions having many restricted endemics plants. Rare species are also important for conservation and evolutionary study for a variety of reasons (Stebbins, 1979) and should be assumed to be of high value, including for ecosystem function and services (Lyons et al., 2005). Nevertheless, larger-ranged species are no less important as conservation targets and can be vulnerable from falling through the cracks of political boundaries (Bisbing et al., 2021; Vázquez-García et al., 2021). For such species, we recommend greater focus on connectivity, dispersal habitat corridors, and multi-stakeholder and intergovernmental conservation plans. In this vein, local adaptation is likely to be a mechanism by which widespread species maintain their distributions (see section 4) and thus population conservation of populations in unique environments is critical.

Regarding future research, several avenues can be explored to uncover the conservation risk associated with range size (**Table 1**). More experimental assessments of plant performance at different life stages, under variable conditions, and between different taxa with varying range sizes are required to better assess the range size vulnerability hypothesis. Although a challenging area of research, tests of plant species range size vulnerability at the population and individual level are lacking (Slatyer et al., 2013). For example, metrics such as heat shock protein response can be used to assess the vulnerability of rare versus common plant taxa to predicted climate change stress (Al-Whaibi, 2011; Aspinwall et al., 2019). In order to determine if smaller ranges are indeed more at-risk from modern habitat alterations, extinction debt (Kuussaari et al., 2009) should be assessed in taxa varying in range size (Jamin et al., 2020; Makishima et al., 2021). Questions concerning the relationship between range size and particular plant groups, or life histories, should be investigated. For example, as stated earlier, highly selfing species are expected to have larger geographic ranges and greater niche breadth, but this was not found for *Epipactis* (Orchidaceae) species in Europe (Evans and Jacquemyn, 2020).

CONCLUDING REMARKS

Our world is in a constant state of flux, exacerbated by rapid climate change, and researchers, managers, and stakeholders would benefit from adopting goals that attend to the impact of these changes and develop methods that can accommodate uncertainty (Rollinson et al., 2021). We have rejected some long-standing paradigms as plant species range rules, provided an initial list of rules for consideration, identified gaps in the research, and outlined tasks to enhance our understanding of how ranges are governed and how they will change (**Table 1**). We strongly encourage researchers to create eco-evolutionary projects that focus on native plant taxa that have not been studied or have been traditionally understudied. Whenever possible, citizen science efforts can support these initiatives and provide educational opportunities to excite the next generation of botanists and plant conservation biologists. We want to acknowledge that many patterns observed among species ranges are not independent of each other and can overlap. We also acknowledge that there may be additional rules of species ranges not considered in this review, and we encourage the field to shine light on them, especially as they relate to conservation. Finally, we encourage the scientific community at large to continue to evaluate patterns and potential rules across disciplines in order to inform effective conservation and ecosystem management. In the case of ecological or biogeographical patterns, rules can be judged or weighted by importance factors, such as phylogenetic, geographical, or environmental parameters, etc. We trust that future ecologists will finish uncovering the laws by which nature can be conserved.

AUTHOR CONTRIBUTIONS

All authors contributed to the development, writing, and approval of the final version of the manuscript.

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