PREDICTING AND MANAGING CLIMATE-DRIVEN RANGE SHIFTS IN PLANTS

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PREDICTING AND MANAGING CLIMATE-DRIVEN RANGE SHIFTS IN PLANTS

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EDITORIAL
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Editorial: Predicting and Managing Climate-Driven Range Shifts in Plants

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Editorial on the Research Topic

Predicting and Managing Climate-Driven Range Shifts in Plants

Plants' geographic ranges will shift in response to climate change; already some shifts have been documented (Lenoir et al., 2008; Parmesan and Hanley, 2015; Zu et al., 2021). Plants face a number of challenges to tracking climate, including dispersal (e.g., seed number, dispersal distance, etc.) and establishment limitations (i.e., unsuitable soil or competition from existing vegetation) (Van Grunsven et al., 2010; Svenning et al., 2014; Lustenhouwer et al., 2017; Thuiller et al., 2019; Sharma et al., 2022). It is also challenging to predict where suitable future habitats will be, given uncertainties in biodiversity models (Thuiller et al., 2019) and climate projections (IPCC, 2013). Inter- and intra-specific variation in climate sensitivity (Angert et al., 2011; Benito Garzón et al., 2019; DeMarche et al., 2019) and the possibility of evolutionary responses (Bush et al., 2016; Cotto et al., 2017; Moran, 2020) particularly complicate the latter. The goal of this Research Topic was to highlight the importance of understanding plant range shifts, to review what is known, and to identify key knowledge gaps.

Several studies used species distribution modeling (SDM) to examine potential range shifts. Zhang et al. found that while suitable area worldwide for the vine *Akebia quinata* might increase up to 50% by 2080, this was mostly driven by increased suitability where the species is introduced; suitable native habitat in Asia was projected to decline. Brodie et al. modeled the range of the succulent tree *Aloidendron dichotomum*. The species likely expanded poleward after the last glacial maximum, consistent with observed genetic variation. Suitable habitat could shift eastward toward the summer-rainfall areas of South Africa by 2070, but range shift rates needed to track habitat were substantial and many species are dispersal-limited. Moeller et al. found that there is a 100–150 km gap in suitable habitat between the Appalachian and Allegheny mountains both for four species endemic to the Southern Appalachians and for four more widely-distributed species. However, the endemic species never crossed this gap and thus have unfilled suitable habitat to the north. Since these endemics are projected to have declining habitat suitability in their native range, assisted migration across the gap might be necessary to conserve them. Similarly, Semenchuck et al. found that the representation of Austrian endemic plant species in protected areas was projected to decline to 1/3 by 2080 in both RCP 4.5 and RCP 8.5 scenarios, with 20–30% of the species studied having zero range representation in protected areas by that date.

While SDMs are relatively simple to implement, concerns have been raised regarding the inherent assumption that species are well-adapted to current conditions (Ibanez et al., 2006; Browne et al., 2019), omission of species interactions (Davis et al., 1998), and ability to project habitat suitability outside the current range of conditions (Williams and Jackson, 2007; Merow et al., 2014). Charney et al. tested 11 algorithms using subsets of forest inventory data for 108 North American tree species. When extrapolating from one region to another, a substantial proportion of algorithms performed worse than random. Data integration approaches that draw from the full

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species range often improve performance of SDMs (Chevalier et al., 2021) but novel future climate space or climate-edaphic combinations cannot be included in the initial model fitting. As Charney et al. noted, the use of more process-based or hybrid models might help to address this issue.

Petit et al. used a process-based model simulating physiological climate responses in five European tree species to estimate mortality risk. They found that, despite positive effects of higher CO_2 on carbon assimilation and water use efficiency, risks of extinction for "genetic conservation units" are similar to or higher than those calculated from SDMs. Qiu et al. used a combination of forest inventory data and demographic data from the MASTIF network to examine demographic sensitivity to climatic factors and forest structure. They found that many life stages, especially fecundity, were sensitive to temperature, but that responses to other factors varied substantially. The niche estimated from adult distributions likely reflects past recruitment conditions rather than current ones. A shift in the distribution of life stages was also observed by White et al. who found that reduced stream-flow in an Australian watershed was linked to fewer juveniles relative to adult riparian trees in low-rainfall areas but more juveniles in high-rainfall areas, where more exposed sediment may have allowed more seedling recruitment.

Experiments that measure growth responses to different climate conditions can also provide important information regarding the sensitivity of locally adapted populations to climate change (Angert et al., 2011; Leites et al., 2012; Moran et al., 2017b; Arnold et al., 2019). Hallingbäck et al. used Scots pine provenance experiments to examine sensitivity of growth to climate at its northern and southern range limits. They found that factors strongly affecting growth differ and that, while moderate transfer distances have little effect on growth, local seed-sources can exhibit lower growth than non-local sources. Growth was predicted to increase at Nordic sites and in northern Spain, but decrease in southern Spain. However, a shorter tree is not necessarily less fit, as conservative growth strategies can be adaptive (Moran et al., 2017a).

The two final papers in the collection synthesized broad-scale patterns. Zettlemoyer and Peterson examined how plasticity in phenology is likely to affect species' adjustment to climate change. They found that plasticity is usually adaptive, and that while plasticity did not generally differ with range position, when it did edge populations tended to be more plastic. This suggests that plasticity is more likely to promote than hinder range shifts, though direct tests are needed. Shay et al. reviewed rules governing plant species ranges and what this might tell us about climate responses. Five potential rules were supported by multiple studies, including "range limits often coincide with [abiotic] niche limits," "biotic interactions often set range limits," and "smaller ranges tend to be more vulnerable." These rules suggested corresponding conservation actions.

While much attention has been paid to direct climate impacts on species ranges, these papers and others indicate other important factors. Biotic interactions will likely affect both local persistence and colonization, as will physical barriers to dispersal. Life-stages may also be affected differently by climate shifts. A particularly important issue in research evident both in this collection and overall is the northern temperate zone bias; highly biodiverse equatorial regions including tropical rainforests have received much less attention regarding how climate change impacts on species' ranges (Feeley et al., 2017; Sheldon, 2019). Non-seed plants are also seldom studied. All these topics are deserving of further research effort, and studies integrating approaches to test impacts of multiple factors are particularly needed.

AUTHOR CONTRIBUTIONS

EVM wrote the initial draft of this manuscript. All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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REVIEW
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Does Phenological Plasticity Help or Hinder Range Shifts Under Climate Change?

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Climate warming is predicted to shift species' ranges as previously uninhabitable environments just beyond the leading range edges become suitable habitat and trailing range edges become increasingly unsuitable. Understanding which aspects of the environment and species traits mediate these range shifts is critical for understanding species' possible redistributions under global change, yet we have a limited understanding of the ecological and evolutionary responses underlying population spread or extinction at species' range edges. Within plant populations, shifts in flowering phenology have been one of the strongest and most consistent responses to climate change, and are likely to play an important role in mediating population dynamics within and beyond species' ranges. However, the role of phenological shifts, and particularly phenological plasticity, in species' range shifts remains relatively unstudied. Here, we synthesize literature on phenology, plasticity, and adaptation to suggest ways in which phenological responses to climate may vary across species' ranges and review the empirical evidence for and against these hypotheses. We then outline how phenological plasticity could facilitate or hinder persistence and potential consequences of phenological plasticity in range expansions, including phenological cues, shifts in correlated traits, altered species interactions, and effects on gene flow. Finally, we suggest future avenues for research, such as characterizing reaction norms for phenology across a species' range and in beyond-the-range transplant experiments. Given the prevalence and magnitude of phenological shifts, future work should carefully dissect its costs and benefits for population persistence, and incorporate phenological plasticity into models predicting species' persistence and geographic range shifts under climate change.

Keywords: phenology, adaptive plasticity, co-gradient variation, geographic cline, range shift, counter-gradient variation, genetic cline, range expansion

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INTRODUCTION

Species' geographic distributions are shifting due to climate change, but we often do not know the mechanisms underlying species' **range shifts** (Gaston, 2009) (see **Glossary** for bolded terms). Species may initially respond to novel environmental conditions via plastic responses (Ghalambor et al., 2007), either due to shifting climate conditions *in situ* or by encountering novel environmental conditions during range expansion. Distributional limits and range contractions should then occur where plasticity fails to enable establishment and/or long-term persistence (Pigliucci, 2001). One of the most commonly observed plastic responses to climate change is shifts in phenology, or the timing of life-cycle events. Given its prevalence, **phenological plasticity** is likely to play a critical role in shaping species' responses to ongoing climate change (Münzbergová et al., 2017). Therefore, phenological plasticity will likely influence spatial dynamics of persistence, range expansion, or local extirpation, but the consequences of phenological plasticity at species' range limits and beyond the range edge are relatively unstudied (Ensing and Eckert, 2019).

A fundamental question in range shifts is whether phenological plasticity can facilitate population spread and contribute to population persistence under novel environmental conditions (Richter et al., 2012; Urban et al., 2016). Most studies assume that phenological plasticity will promote establishment, population persistence, and population growth, but phenological plasticity could either facilitate or hinder population persistence in novel conditions. Specifically, phenological plasticity could "pre-adapt" populations to conditions beyond the **leading range edge** (i.e., the expanding or colonizing margin of a species' distribution) or act to stabilize populations at the **trailing range edge** if plasticity shifts the phenotype in the same direction that would be favored in the novel environment (i.e., **adaptive phenotypic plasticity** (Ghalambor et al., 2007; Soularue and Kremer, 2012). This is most often considered with respect to changes in mean climate conditions, but adaptive plasticity may also serve a critical role in enabling population persistence under increasingly variable environmental conditions with climate change (IPCC, 2014). Alternatively, phenological plasticity could be maladaptive, such as advancing flowering that risks damage from exposure to frost (Cooper et al., 2019). **Maladaptive phenological plasticity** would reduce fitness in novel environments and contribute to range contractions (Ghalambor et al., 2007; Ensing and Eckert, 2019). Maladaptive plasticity may be particularly likely in the context of climate change if environmental cues or species interactions become disrupted. For example, mismatches with chilling requirements or mutualists during range expansions could cause historically adaptive patterns of phenological plasticity to become maladaptive in novel environments (Valladares et al., 2014; Uelmen et al., 2016).

An added complexity is the potential for populations across a species' range to differ in the magnitude or even perhaps direction of phenological plasticity. Because edge populations often experience more extreme or variable environments than **central populations** (Chevin and Lande, 2011; Lázaro-Nogal et al., 2015; but see Volis et al., 1998; Mägi et al., 2011), they may have evolved greater phenological plasticity than central populations to better track the window of suitable conditions from year to year. As such, **leading edge populations** (i.e., poleward or higher latitude or elevation) may be poised to expand into novel environmental conditions beyond the contemporary range edge (Hargreaves and Eckert, 2019). **Trailing edge populations** (i.e., equatorial or lower latitude or elevation), meanwhile, could harbor phenological plasticity in response to temperature or adaptive genetic variation that could benefit migration of genotypes poleward within the historical range (Hampe and Petit, 2005). Furthermore, either leading or trailing edge populations could persist *in situ* via phenological plasticity to changing climate conditions. Alternatively, edge populations may actually exhibit more canalized phenology, limiting plastic responses to environmental change, due to local adaptation to harsh environmental conditions (e.g., cold temperatures or drought) or, in the case of leading edge populations, shorter growing seasons (Gugger et al., 2015). Despite these conflicting theories, we have little empirical evidence for how patterns of phenological plasticity vary across species ranges (Eckert et al., 2008) or about the consequences of phenological plasticity in range shifts.

Finally, phenological plasticity can have consequences for longer-term persistence beyond the range edge, but studies rarely consider the costs and benefits of plasticity in range expansion beyond initial establishment. For example, phenological plasticity may have reproductive or demographic costs (Colautti et al., 2010; Reed et al., 2010) or involve correlated shifts in other life history traits such as resource acquisition (Sheth and Angert, 2016) or other phenological stages like germination or fruiting (Haggerty and Galloway, 2011). In addition, phenological plasticity likely affects biotic interactions (Benning et al., 2019) and patterns of gene flow (Weis, 2015) in ways that could either impede or facilitate persistence and adaptation to novel conditions. Each of these consequences may cause any benefits of phenological plasticity during range shifts to be ephemeral, but they are rarely considered despite their potential importance in determining whether phenological plasticity could enable not only expansion but persistence beyond the range edge.

Given the growing recognition of the role that phenological plasticity plays in range limits (Griffith and Watson, 2005; Morin et al., 2008; Wadgymar et al., 2015; Chapman et al., 2017), more forecasts of species range shifts under climate change that incorporate phenology are likely to appear. Now is a timely moment to synthesize the evidence for variation in phenological plasticity across and beyond species' ranges, identify potential consequences of phenological plasticity in range shifts, and identify future directions for incorporating phenological plasticity into forecasts of species ranges under climate change.

GEOGRAPHIC VARIATION IN PHENOLOGICAL PLASTICITY ACROSS SPECIES' RANGES

We first review the evidence for geographic patterns in phenology across species' ranges to test specific hypotheses related to the role of phenology in climate-mediated range shifts. We focus on evaluating the evidence for how plasticity and local adaptation shape geographic clines in phenology (H1) as well as whether the magnitude of phenological plasticity varies across species' ranges (H2). We also address the evidence for two other interesting but less-studied hypotheses: the potential for phenological plasticity to either stabilize range edges or contribute to range shifts

(H3) and variation in adaptive potential in phenology across species' ranges (H4). *Literature review:* We searched ISI Web of Science on December 1, 2020, for studies that compared variation in phenology across a species' geographic range (see **Supplementary Appendices S1–S3** for methods and data). Specifically, we searched for empirical studies that explicitly compared at least one phenological variable between two or more populations that differed in range position, such as across latitudinal or elevation gradients. This requirement potentially excluded studies examining phenology at multiple sites that did not test for geographic differences in phenology and long-term studies from single localities (see Wolkovich et al., 2012; Thackeray et al., 2016; Tansey et al., 2017; Chmura et al., 2019; Piao et al., 2019 for syntheses of long-term studies). This yielded 107 studies, including data for a total of 300 phenological variables across 234 plants (45 unique forb and 44 unique tree species) 53 insects (43 species), 7 mammal (5 species), 5 bird (3 species), and 1 amphibian species. For each study, we evaluated results for each phenological variable (hereafter "phenophases") examined across two or more populations of a given species in a given dataset (hereafter "cases"). In 117 cases, phenology was examined observationally in natural populations, while in 183 cases phenology was examined under experimental settings (**Figure 1**). The studies reviewed had a mean population number of 20.73 (median = 8; range = 2–240; values exclude one study with thousands of sites (Roy et al., 2015; **Supplementary Appendix 4 Figure A1**). The majority of latitudinal studies were at a continental or country-wide scale (>1000 km), while elevational studies spanned hundreds of meters. We grouped phenophases into four categories: emergence (23 cases), growth and development (155 cases), reproduction (97 cases), and senescence/autumn phenology (25 cases) (see **Supplementary Appendix 1 Table A1** for phenophase definitions).

We used these studies to evaluate support for eight hypotheses related to the role of phenological plasticity in range shifts (**Figure 2**). In each subsequent section, we first describe the conceptual motivation for each hypothesis and then evaluate the fraction of relevant cases that support, do not support, or yield mixed evidence for that hypothesis. We note that this qualitative approach does not address the magnitude of particular patterns or statistically account for non-independence among cases due to publication or study system (Gurevitch et al., 2001), but is most flexible given the wide range of approaches and metrics reported in these papers which precludes quantitative comparison. The majority of studies identified temperature as the primary climatic factor varying across geographic gradients, but in the handful of cases that focused on precipitation (e.g., drought, snowmelt), we characterized patterns with respect to spatial precipitation gradients (e.g., Bender et al., 2002; Eckhart et al., 2004; Torres-Martínez et al., 2017). We therefore focus our hypotheses on geographic and associated temperature and precipitation gradients. We recognize that these hypotheses are necessarily simplistic and that many ecological and evolutionary factors (e.g., photoperiod, soil characteristics, microclimatic variation, species interactions, etc.) could influence phenological patterns across geographic gradients (see Section "Costs and Benefits of Phenological Plasticity Beyond the Range Edge"). However, these broad patterns should be most generalizable for making predictions about the role of phenology in geographic range shifts across a variety of species.

Evidence for Geographic Gradients in Phenological Plasticity (H1a-c)

We first addressed general geographic patterns in phenology across species' ranges and their contribution from plasticity and genetic adaptation. Later onset of spring and colder environments at high latitude and elevation should result in delayed emergence, slower growth and development, delayed reproduction, and earlier senescence in nature (**Figure 2**: H1a). However, these natural clines may be driven by some combination of phenological plasticity and/or genetic adaptation of local populations. For example, single populations may exhibit plasticity in phenological traits that mimic natural gradients; this would be consistent with adaptive plasticity in which individual populations respond to environmental variation by altering phenology to match that observed in local populations (**Figure 2**: H1b) (Soularue and Kremer, 2012; Ensing and Eckert, 2019). Similarly, populations across the range may have genetically based differences in phenology when grown in common environmental conditions. **Co-gradient genetic variation** occurs if genetic differences mimic the natural cline, whereas genetic differences that oppose the natural cline ("**counter-gradient genetic variation**," sensu Conover, 1990; Conover and Schultz, 1995) can evolve to either minimize changes in traits across the natural gradient or compensate for maladaptive plasticity (**Figure 2**: H1c). For example, populations in colder climates may evolve more rapid development to compensate for shorter growing seasons (Eckhart et al., 2004; Conover et al., 2009).

We first evaluated the hypothesis that populations across a geographic gradient should vary in phenology such that leading edge populations have delayed emergence, growth, and reproduction and earlier senescence relative to trailing edge populations (H1a). To test this hypothesis, we scored whether phenology demonstrated a **geographic cline** (used interchangeably with "natural cline") in naturally occurring populations and whether this cline was in the expected direction (e.g., a positive slope of spring reproductive phenology with elevation or latitude). Of the 294 cases for which we could evaluate phenological differences across a natural gradient, the vast majority reported significant clines in phenology (84%). We note that publication bias could play into this finding, as studies that do not detect a geographic cline might not be published. Of these, 23% were in an unexpected direction (e.g., earlier emergence in poleward or higher elevation populations; **Figure 3**: H1a). We also examined patterns in plant vs. animal taxa separately. Trends for variation in phenology across geographic gradients were similar (**Supplementary Appendix 4 Figures A2a, A3a**), with 60% of plant and 62% of animal studies detecting expected geographic clines in phenology. However, the number of plant cases (n = 228) far exceeded animal cases (n = 66), and few animal studies address the remaining hypotheses (**Supplementary Appendix 4 Figures A2, A3**). We additionally examined whether annual vs. perennial plants

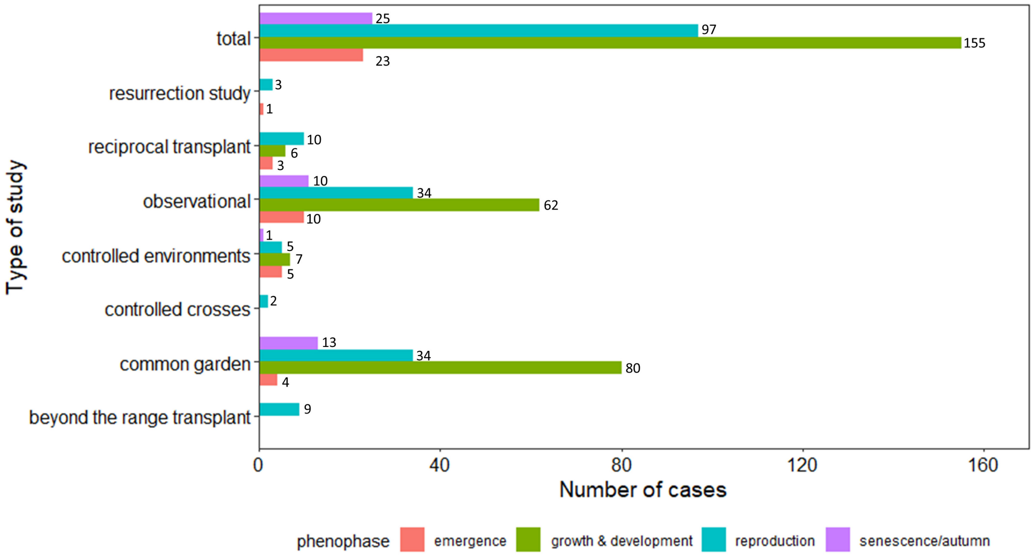

FIGURE 1 | Frequency of each type of study conducted across each phenophase, including emergence (red), growth and development (green), reproduction (blue), and senescence or autumn phenology (purple). Studies were considered observational or experimental, the latter including resurrection studies, reciprocal transplants, controlled environments (i.e., greenhouse or growth chambers), controlled crosses, common gardens, or beyond the range transplants. Note that values here represent cases, or separate datasets, such that a single publication could include multiple types of cases (e.g., data from natural populations, a reciprocal transplant experiment, and a controlled environment greenhouse experiment).

differed in their responses; patterns were qualitatively similar, although the vast majority of studies were conducted using perennials (n = 185 perennials vs. 35 annuals) (**Supplementary Appendix 4 Figure A4**).

We next examined whether plasticity in phenological traits was consistent with the direction of the natural cline in phenology (H1b). For example, if reproductive phenology is delayed in higher latitude populations experiencing colder climates, then we would expect single populations to also exhibit delayed reproduction when grown in higher latitudes or colder temperatures. Assuming that locally expressed phenology is adaptive in that environment, such patterns would indicate adaptive plasticity (Ensing and Eckert, 2019). We evaluated this hypothesis by comparing the slope of phenological plasticity across the natural cline to the slope across an environmental gradient. We most often used observational patterns of the natural cline because this data was more frequently available; however, when possible we assessed whether plasticity was adaptive by comparing patterns of population differentiation under common environments. We identified 107 cases that quantified phenological plasticity for one or more populations, either in transplant and/or climate manipulation experiments. Of these, the majority (78%) documented plasticity in the same direction as natural geographic clines (this pattern was again similar in plant and animal taxa; **Supplementary Appendix 2 Figures A2, A3**), suggesting that phenological plasticity may often be in a direction that facilitates the expression of local phenologies under novel environmental conditions (**Figure 3**: H1b). However, 16% of cases documented phenological plasticity in the opposite direction of geographic clines, consistent with maladaptive phenology that could contribute to range contractions, and an additional 6% found mixed patterns with some but not all populations exhibiting maladaptive plasticity.

Finally, we looked for evidence of co- vs. counter-gradient patterns of genetic variation in phenology in studies that compared two or more populations in a common environment (H1c; note that the studies used to test H1c are a subsample of those used to test H1b). If phenological plasticity is adaptive, we would predict either no genetic differentiation (i.e., perfect plasticity) or co-gradient genetic variation in which evolution has favored phenological traits in the same direction as environmental effects across species' ranges. Alternatively, counter-gradient genetic variation could evolve in response to growing season constraints (e.g., later spring, earlier fall, colder temperatures). In this case, leading edge populations, which we predicted would demonstrate delayed emergence, growth, and reproduction and earlier senescence in nature, would instead express more rapid emergence, growth, and reproduction and delayed senescence when grown under common environmental conditions. Of the 56 cases that tested for genetically based differences in phenology, the majority (66%) were consistent with co-gradient genetic variation, whereas 27% were consistent with counter-gradient genetic variation and 7% found mixed results with more variable patterns of genetic differentiation (**Figure 3**: H1c). Interestingly, most instances of co-gradient variation were detected for phenological traits related to reproduction (72%, or 13/18 cases) whereas counter-gradient variation was equally as likely as co-gradient variation for phenological traits related to growth and development (54%, or 14/26 cases). Although sample sizes for particular phenophases are limited, this is broadly consistent with prior evidence for counter-gradient

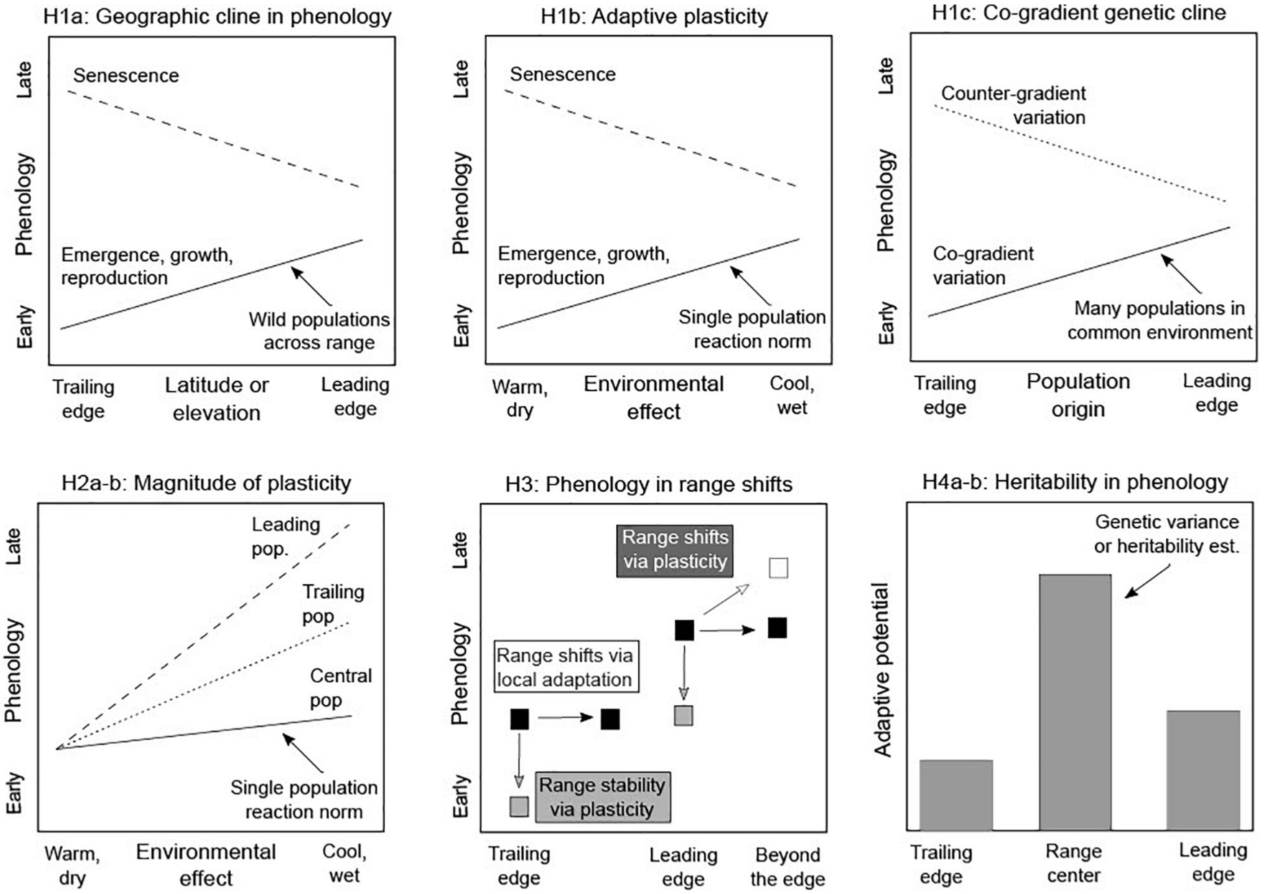

FIGURE 2 | Conceptual diagram illustrating hypotheses for the potential role of phenological plasticity in range shifts under climate change. (H1) Each line indicates the slope of phenological responses across a geographic gradient spanning (a,c) the trailing (equatorial/low elevation) to leading (poleward/high elevation) edge or (b) an associated environmental gradient wherein trailing edge populations experience warmer, drier conditions while leading edge populations experience colder, wetter conditions. (H1a) Phenology demonstrates a geographic cline in wild populations; later onset of spring and colder environments at high latitude and elevation should result in delayed emergence, slower growth and development, and delayed reproduction (solid line), and earlier senescence (dashed line) in leading relative to trailing edge populations. (H1b) Phenology demonstrates adaptive plasticity, such that individual populations grown in common conditions respond to environmental variation (i.e., reaction norm) by altering phenology in a way that is consistent with geographic clines in H1a (note that warmer populations are on the left side of the axis, consistent with the trailing edge). (H1c) Phenology demonstrates co-gradient genetic variation (solid line), such that populations grown in common environments demonstrate genetic differences mirroring geographic clines (vs. counter-gradient genetic variation; dotted line). (Expectations for spring phenology shown.) (H2) Each line represents the reaction norm for a single population (solid = central; trailing = dotted; dashed = leading) grown under contrasting environmental conditions (warm/dry vs. cool/wet) (e.g., in common gardens or climate manipulations). (H2a) The magnitude of phenological plasticity (i.e., responsiveness to environmental variation) is greater in populations from range edges vs. centers, and (H2b) from leading edges vs. trailing edges. (H3) Boxes show the range shift of a population in space. Phenological plasticity may allow populations to suitably shift their phenology to persist *in situ* (i.e., “range stability,” light gray boxes) or to expand beyond the range edge (white box). Alternatively, local adaptation in phenology can drive range shifts by causing populations to track suitable climate for a given phenology in space (black boxes). (H4a) Adaptive potential in phenology (i.e., genetic variance or heritability) is greater in populations from range centers vs. edges, and (H4b) from leading vs. trailing edges.

genetic variation in growth and development (Angilletta, 2009; Conover et al., 2009).

Evidence for Greater Phenological Plasticity in Leading Edge Populations (H2a-b)

Across geographic gradients, environmental conditions at range margins can prime edge populations to either persist in place or shift the species’ range poleward (Lenoir et al., 2008). Edge populations, particularly at the leading edge, are often assumed to experience harsher and more temporally heterogeneous environments, which could affect plastic responses and the selective pressures leading to local adaptation (Chevin and Lande, 2011) (although we note that edge populations do not necessarily occur in harsher or less stable habitats (Granado-Yela et al., 2013), and climate may impose novel stresses on rear edge habitats (Hampe and Petit, 2005). Additionally, rates of warming relative to historical climate have been more pronounced in high relative to low elevation/latitude environments over the past 50 years (Root et al., 2003; McGuire et al., 2012). For these reasons, we might expect that populations

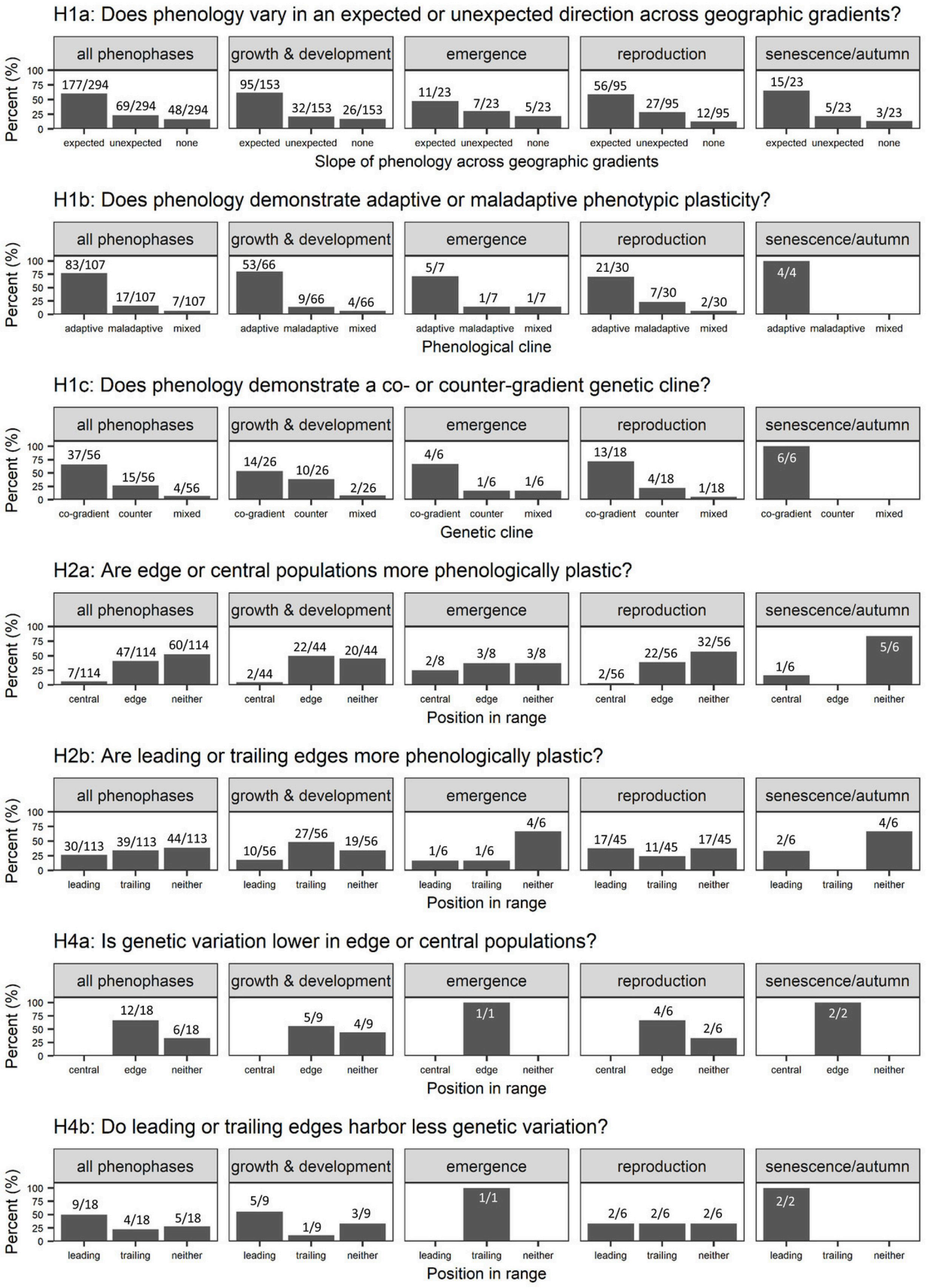

FIGURE 3 | Percent of cases supporting each of the hypotheses outlined for (left to right) all phenophases combined, growth and development, emergence, reproduction, and senescence/autumn phenology. Values represent the number of cases for or against each hypothesis out of the total number of cases that addressed that hypothesis. (H1a) We examine whether the leading edge (i.e., higher latitude or elevation) populations demonstrate delayed spring phenology (growth and development, emergence, and reproduction) and earlier autumn phenology relative to trailing edge (i.e., lower latitude or elevation) populations. "Expected" slopes indicate that phenology follows this pattern; "unexpected" indicates the reverse; "none" indicates no pattern across a geographic gradient. (H1b) We examine whether phenology demonstrates adaptive phenotypic plasticity (i.e., phenological plasticity is in the same direction as the geographic cline and so shifts phenotypes in the direction that would be adaptive in the novel environment), maladaptive plasticity (i.e., phenological plasticity is not consistent with the geographic cline), or mixed evidence. (H1c) We examine whether phenology demonstrates co-gradient genetic clines (i.e., many populations grown in a common environment demonstrate phenological plasticity consistent with the geographic and phenotypic cline), a counter-gradient genetic cline ("counter"), or mixed evidence. For (H2), we examine whether (H2a) edge versus central and (H2b) leading vs. trailing edge populations (or neither) demonstrate greater phenological plasticity, respectively. (H3) is not shown on this figure due to low sample size. For (H4), we examine whether (H4a) edge vs. central and (H4b) leading vs. trailing edge populations (or neither) demonstrate lower genetic variation in phenological traits, respectively.

along geographic gradients show differences in the magnitude of phenological plasticity that reflect variation in climatic conditions (Valladares et al., 2014). Specifically, we examined the hypotheses that edge populations would show greater phenological plasticity than central populations (**Figure 2**: H2a), and similarly that leading edge populations would be more plastic than trailing edge populations (**Figure 2**: H2b). Alternatively, leading edge populations could be less plastic than trailing edge or central populations if extreme environmental conditions impose stronger selection on phenological and other traits, potentially leading to genetic canalization (Angert et al., 2011; Sheth and Angert, 2014), or if edge habitat is more suitable.

We identified 114 cases that compared phenological plasticity in central vs. edge populations and 113 that compared leading vs. trailing edge populations. We used the authors' designations for central, leading, or trailing populations. Contrary to our hypotheses, most studies failed to find consistent and statistically significant differences in the magnitude of phenological plasticity across species ranges. Central and edge populations often did not differ in their phenological plasticity (53%, or 60/114 cases), and this pattern was consistent across different phenophases (**Figure 3**: H2a). (Although in animals, 73% of cases (11/15) detected greater plasticity in edge populations, while evidence among plants was more mixed; **Supplementary Appendix 4 Figures A2b, A3b**). However, when differences were detected, edge populations were more plastic than central populations in 41% of cases (47/114) whereas central populations were most plastic in only 6% of cases. Additionally, leading and trailing edges often did not differ in phenological plasticity (39%, or 44/113 cases). Leading edges were more plastic than trailing edges in only 27% of cases (20/113) and trailing edges were actually more plastic than leading edges in 35% of cases (39/113 cases) (**Figure 3**: H2b). Perennial plants in particular were more likely to demonstrate greater plasticity in their trailing edge populations, especially for growth and development (57% of cases, or 27/47; **Supplementary Appendix 4 Figure A4**). This pattern differed between plant and animal taxa: trailing edges were slightly more likely to demonstrate greater plasticity than leading edges in plants (38%, or 37/98 cases; although plants were just as likely to demonstrate no differences in plasticity between leading and trailing edges), while leading edges more often demonstrated higher plasticity than trailing edges in animals (60%, or 9/15 cases; **Supplementary Appendix 4 Figures A2c, A3c**).

Evidence for Adaptive Phenology Facilitating Range Shifts and Persistence Beyond the Range Edge (H3)

Phenological plasticity has most often been discussed in the context of tracking shifting climate conditions in time, as an alternative to range shifts which track shifting climate conditions in space. In this view, phenological plasticity should stabilize historical range boundaries, whereas local adaptation of phenology should facilitate poleward range shifts (Colautti and Barrett, 2013). In other words, maintaining a historically adaptive phenology may best facilitate expansion of leading edge genotypes beyond the historical range edge as long as conditions there track those in the historical range edge (**Figure 2**: H3) (Hargreaves and Eckert, 2019). However, the potential for phenological plasticity to facilitate range shifts has received less consideration, but may be important if migration rates do not perfectly track climate change or conditions beyond the range favor new phenology.

Testing whether expanding populations can persist beyond their current range edge, and the importance of phenological plasticity or local adaptation in this process, requires transplant experiments testing performance beyond the current range limit (Hargreaves et al., 2014). However, we found only four studies (spanning three species) that examined (only reproductive) phenology in transplants beyond the range edge (Eckhart et al., 2004; Wadgymar et al., 2015; Benning et al., 2019; Hargreaves and Eckert, 2019). Two of these showed that leading-edge genotypes expressed adaptive phenology, and had greater fitness, than central or trailing-edge genotypes when transplanted beyond the range (Wadgymar et al., 2015; Hargreaves and Eckert, 2019). However, only one study found that adaptive phenological plasticity benefitted fitness beyond the range edge (Wadgymar et al., 2015). In contrast, studies with *Clarkia xantiana* suggest that maladaptive phenology limits performance in beyond-the-range transplants (Eckhart et al., 2004; Benning et al., 2019). Interestingly, none of these studies detected greater phenological plasticity in edge populations relative to central populations.

Evidence for Lower Genetic Variation in Edge Populations (H4a-b)

In addition to plasticity in phenology, populations may also adapt to novel climatic conditions through evolutionary changes in phenology. The magnitude of genetic variation, the material for evolutionary change, in phenology will limit species' ability to adapt to novel environmental conditions either *in situ* or during range shifts. Populations may harbor different levels of genetic variation in phenological traits (Pironon et al., 2017), and theory predicts that edge populations might exhibit lower genetic variation than central populations for three reasons. First, edge populations are often more isolated than central populations (Hengeveld and Haeck, 1982; Brown, 1984; Leonardi et al., 2012). Second, edge populations are often less abundant, and smaller population sizes can result in decreases in vital rates toward the range edge (Sexton et al., 2009). Third, edge populations presumably persist in less optimal environmental conditions than central populations, assuming that a species' range represents its ecological niche. These three conditions - isolation, smaller populations sizes, and marginality - are predicted to decrease genetic diversity within a population (Lawton, 1993). We therefore predicted that edge populations harbor less genetic variation than central populations (H4a), potentially limiting range expansions under climate change (**Figure 2**: H4).

Seven studies in our dataset reported genetic variation in 18 total phenological traits for two or more populations spanning a geographic gradient (and almost all studies used perennial plants; **Supplementary Appendix 4 Figure A4**) (De Kort et al., 2016; Evans et al., 2016; Sheth and Angert, 2016; Firmat et al., 2017; Lustenhouwer et al., 2018; Bemmels and Anderson, 2019; Wenden et al., 2020). Of those, edge populations demonstrated lower genetic variation than central populations in 67% of cases (12/18), and the remaining cases failed to find consistent or statistically significant differences (**Figure 3**: H4a). Interestingly, no cases reported lower genetic variation in central populations.

Patterns of genetic variation could also differ between leading and trailing edge populations, with greater climate variability and/or gene flow from the center of the range perhaps maintaining greater genetic variation in phenology at leading range edges compared to trailing range edges (Davis and Shaw, 2001; H4b). Alternatively, trailing edge populations often have longer and more stable histories (i.e., persistence during interglacial periods) than leading edge populations and often respond to different environmental factors and so may exhibit unique genetic variation that could benefit species' persistence and range shifts under future climates (Hampe and Petit, 2005; Rehm et al., 2015). Of the 18 cases addressing genetic variation in leading vs. trailing edge populations, genetic variation in phenological traits was lowest in leading edge populations in 50% of cases (9/18) and in trailing edge populations in 22% of cases (4/18). Thus, we find some evidence for lower adaptive potential in phenology in edge populations, and particularly leading edge populations, which would further suggest the importance of plasticity in mediating phenological shifts. However, we caution that this is based on a small number of studies and in roughly one third of cases populations did not show clear patterns in adaptive potential across geographic gradients.

Implications for the Role of Phenological Plasticity in Range Shifts

Taken together, we found surprisingly mixed evidence for hypothesized patterns in phenological plasticity across species' ranges. Phenology often demonstrated a geographic cline in the studies reviewed here, though in a quarter of cases it was in an unexpected direction (**Figure 3**: H1a). In these cases, leading edge populations demonstrated earlier emergence, growth and development, reproduction, and/or later senescence than trailing edge populations. We might find these patterns in cases where other phenological cues (e.g., photoperiod; see below) are important or if species' ranges are fragmented (such that central populations are isolated). Most studies detected adaptive plasticity, indicating that phenological plasticity may often be in a direction that facilitates the expression of adaptive phenologies under novel environmental conditions. Given that the direction of phenological plasticity will determine the initial success of a population experiencing novel environmental conditions (Ghalambor et al., 2007), such adaptive plasticity will likely facilitate population persistence *in situ* as well as enable edge populations to expand into novel environmental conditions beyond the range edge. However, despite this general trend, we note that some cases found either direct evidence of maladaptive plasticity (16%) and/or counter-gradient genetic variation (37%), suggesting that environmental effects on phenology may actually decrease fitness and contribute to range contractions in a minority of species. Similarly, in a review of population vs. genetic differentiation, Stamp and Hadfield (2020) found that 20% of traits exhibit maladaptive plasticity. This pattern of mostly adaptive, but some maladaptive, plasticity in phenology under climate change is broadly consistent with observations that leading-edge range expansions are more common than trailing-edge range contractions in terrestrial species (Sunday et al., 2012).

Despite strong support for adaptive clines in phenology, we did not detect clear trends in either the magnitude of phenological plasticity or adaptive potential in phenology between edge vs. central populations. The only conclusion we are able to make based on our literature review is that central populations do not generally have greater phenological plasticity or lower adaptive potential than edge populations. Otherwise, we found very mixed support for either greater phenological plasticity and lower adaptive potential at range edges, or no consistent geographic trends in the magnitude of plasticity or adaptive potential. If plasticity and adaptive potential do not generally show predictable geographic clines, then that would suggest that the spatial pattern of persistence and range shifts may be more idiosyncratic, depending on the dynamics of local populations.

Additionally, we actually found more studies detecting greater phenological plasticity and adaptive potential in trailing edge populations than in leading edge populations (although this pattern was only true for plants). Although this is in contrast to our hypotheses, there are several possible reasons for these patterns. First, leading edge populations often experience a narrow set of harsh environmental conditions; cold, short growing seasons at high latitudes or elevations can select for canalized phenology under strict time constraints (Gugger et al., 2015). As poleward populations already have a compressed growing season, they may lack the plasticity to further advance their phenology (Clark et al., 2014). In this case, leading edge range limits might be set by an inability to complete reproduction (Morin et al., 2007; Chuine, 2010). Further, greater plasticity at trailing edges could allow populations to adjust their phenology and persist in place as local environments shift (e.g., glacial refugia during the Quaternary; Petit et al., 2003), potentially preventing range contractions at the trailing edge (**Figure 2**: H3). Finally, trailing edge populations may maintain greater genetic variation due to their more stable demographic histories, high levels of genetic differentiation, and local adaptation between populations (Petit et al., 2003; Hampe and Petit, 2005), which could potentially provide a source of species-level genetic diversity that would promote persistence under novel conditions. If trailing edge (or central) populations have more genetic variation than leading edge populations, as we found some support for in our review, then gene flow from these populations could provide crucial genetic material for range expansions (see Hampe and Petit, 2005 for a review of the importance of rear edge populations).

Ultimately, range shifts will also require population persistence beyond the range edge. As described, we only found four studies that assessed phenology in transplants beyond the range edge. Of these, two included a climate manipulation designed to test how range edge populations respond to climate change (Wadgymar et al., 2015; Hargreaves and Eckert, 2019). Overall, results for fitness beyond the range edge were mixed. Evidence in *Chamaecrista fasciculata* suggests that local adaptation to contemporary conditions in leading edge populations combined with gene flow from trailing edge populations of alleles that are adaptive under warming could facilitate range expansions (Wadgymar et al., 2015). However, although northern populations of *Rhinanthus minor* also performed best beyond the range edge, this was due to increased fecundity under warming rather than earlier flowering (Hargreaves and Eckert, 2019). In contrast to these two studies, two subspecies of *Clarkia xantiana* demonstrated later phenology at and beyond their range edges, resulting in low fitness beyond the range edge (Eckhart et al., 2004; Benning et al., 2019). However, *C. xantiana* did flower earlier in dry seasons, suggesting that phenological plasticity over time (rather than across space) in response to variable environmental conditions could enhance performance. Altogether, the limited number of studies and variability in these results highlights a need for reciprocal transplant experiments that test for local adaptation or plasticity in phenological traits and their effects on fitness and population persistence, which will ultimately determine successful colonization beyond the range edge.

COSTS AND BENEFITS OF PHENOLOGICAL PLASTICITY BEYOND THE RANGE EDGE

Climate-mediated range shifts will require not only initial establishment beyond the range edge, but consideration of other factors influencing long-term persistence in novel environments. Below, we outline several additional ways in which phenological plasticity may mediate ecological and evolutionary dynamics that govern population persistence beyond the range edge.

Mismatched Phenological Cues Within vs. Beyond the Range Edge

Variation in phenological responses to climate is in part due to variation in the environmental cues that regulate phenological plasticity. For example, plasticity may be driven by temperature, photoperiod, winter chilling, growing season length, or soil conditions, and the seasonal windows in which these cues influence phenology may also differ across species' ranges and with novel climate change (Frei et al., 2014; Körner et al., 2016; Cooper et al., 2019; Wenden et al., 2020). Here we outline potential constraints on the role of phenological plasticity in facilitating range shifts. Understanding how multiple environmental variables interact to drive phenological plasticity, instead of just temperature, across geographic gradients will be necessary to predict range shifts and develop effective adaptation strategies (e.g., assisted migration).

Phenology may be responsive to photoperiod rather than (or in addition to) temperature. As climate warming pushes phenology to new seasonal limits both at the early and late end of the growing season, photoperiod might constrain warming-induced phenological shifts (Richardson et al., 2018). For example, shorter photoperiods during early phenophases such as bud break can dampen phenological advances (Körner and Basler, 2010; Meng et al., 2021) and slow development (Fu et al., 2019). This could prevent plants from emerging too early and risking exposure to harsh conditions like frost (Flynn and Wolkovich, 2018). Additionally, *Picea* from high elevations exhibit greater sensitivity to photoperiod (Körner et al., 2016), suggesting potential variation in photoperiod responses across species' ranges. Since phenological responses to photoperiod and its interaction with temperature are not as well-studied as temperature alone (Meng et al., 2021), future studies may need to examine how photoperiod might limit phenological advances and potential shifts in species' distributions.

In addition to photoperiod, winter chilling and temperatures, growth season length, and exposure to harsh soil conditions can limit phenological responses. Similarly to photoperiod constraints, winter chilling requirements are also hypothesized to limit early development (Vitasse et al., 2014). As temperatures rise, chilling requirements can be either only partially met or met later in time (Fu et al., 2015). For these reasons, species that are not constrained by chilling requirements, such as pedunculate oak (*Quercus robur*), often demonstrate greater phenological sensitivity to temperature than species that are limited by chilling, such as European beech (*Fagus sylvatica*) (Wenden et al., 2020). Similarly, phenology can respond to winter warming as much as spring warming, but its effects are understudied. Species in the United States and United Kingdom, for instance, delay flowering in warmer winters but advance flowering in warmer springs (Cook et al., 2012), and early-flowering native prairie forbs advance flowering in response to warming winters as much as warming springs (Zettlemoyer et al., 2021). At leading range edges, growing season length constraints may also limit the degree to which phenology can shift (e.g., risk of frost at either end of the growing season; de Valpine and Harte, 2001; Inouye, 2008; Munguía-Rosas et al., 2011; Pardee et al., 2019). Finally, changes in soil moisture (and other soil factors like depth or fertility; Blume et al., 2016) can also affect phenology, though evidence for the direction of this effect is mixed as drought can either delay (Adams et al., 2015) or advance phenology (Giménez-Benavides et al., 2006; Gugger et al., 2015). Moreover, interactions between warming and drought are particularly likely to matter in water-limited regions, such as might occur at trailing range edges in low-elevation (Giménez-Benavides et al., 2006) or Mediterranean environments (Hänel and Tielbörger, 2015). Altogether, because abiotic factors other than spring temperature can influence phenology, range shifts are likely to be a balancing act between phenological plasticity in response to temperature and costs or limitations associated with responses to other facets of the environment.

Correlated Traits

The timing of development and reproduction is an important aspect of life history, and advancing phenology in response to climate change may lead to correlated shifts in other life history or resource-use traits that could constrain lifetime fitness or even limit evolutionary responses (Etterson and Shaw, 2001). For example, earlier reproduction is often correlated with smaller size at reproduction (Bale et al., 2002; Franks and Weis, 2008; Colautti et al., 2010) and a switch from more resource conservative to more resource acquisitive traits (e.g., greater specific leaf area, higher nitrogen content; Wright et al., 2004; Sheth and Angert, 2016). Indeed, there is increasing evidence that advancing phenology under climate change is leading to more compressed life-cycles and faster life-history strategies (Dingle et al., 1990; Berner and Blanckenhorn, 2006; Välimäki et al., 2013; Zettlemoyer et al., 2017; Peterson et al., 2020). However, the consequences of these multivariate trait shifts for absolute fitness appear to be mixed. Although earlier flowering is often correlated with higher reproductive success in plants (Munguía-Rosas et al., 2011; Lustenhouwer et al., 2018), other studies have found reduced reproductive success due to advancing or compressed life cycles under climate change (Burgess et al., 2007; Colautti et al., 2010; Haggerty and Galloway, 2011; Rafferty et al., 2016). Such changes in correlated traits could also have important implications for the longer-term persistence and evolutionary potential of populations (Cotto et al., 2019). On the one hand, faster life histories and reduced generation times should facilitate rapid adaptation to environmental change. On the other hand, correlated shifts across multiple traits may increase the potential for antagonistic genetic correlations to constrain evolutionary responses (Etterson and Shaw, 2001; Chevin, 2013).

Although here we have focused on the timing of reproduction, due to its emphasis in the literature, it is important to note that shifts in early phenological events such as emergence can also modify the timing of subsequent phenophases (Donohue, 2002). Different phenophases can vary in their plasticity or environmental cues (Mediavilla and Escudero, 2009; Buckley et al., 2015; Wadgymar et al., 2015), but phenological shifts are rarely studied in the context of the entire life cycle of an organism and early phenophases such as germination or emergence are particularly understudied (**Figure 1**). Future studies should focus on shifts in early phenophases as well as correlated phenological traits across ontogeny. Ultimately, understanding the traits that potentially trade-off with flowering time (both other phenophases and correlated traits) will be crucial to predicting population responses and range shifts under climate change.

Mismatched Species Interactions

Not only can climate limit species' distributions and range shifts, but biotic interactions are also likely to shape geographic range edges. In particular, competition, predation, and hybridization could constrain range expansions, while mutualisms could extend or limit range expansion (Louthan et al., 2015). Below we highlight a few examples of potential mismatched species interactions that could arise due to altered phenology across geographic gradients (see Louthan et al. (2015) for a review on the role of species interactions in determining species' geographic range limits and Visser and Gienapp. (2019) for a review of phenological mismatches).

First, altered phenology could affect species' likelihood of experiencing predation and herbivory beyond the range edge. For example, in *Clarkia xantiana* ssp. *xantiana*, delayed phenology beyond the range edge dramatically increases the probability of fatal herbivory, maintaining this range limit (Benning et al., 2019). This interaction is further complicated by climate, as phenology is further delayed in wet years, resulting in 25% higher herbivory beyond the range edge in wet relative to drier years (Benning et al., 2019). In contrast, phenological escape from herbivores and granivores has been shown to facilitate range shifts in several plant taxa, particularly for non-native species invading new ranges (Mlynarek et al., 2017). For insect populations expanding poleward, such escape of potential food sources would likely lead to extirpation (Cahill et al., 2013).

Perhaps more widely considered, climate-driven phenological mismatches between host plants and pollinators are likely to affect persistence beyond range edges. While demographic costs of such mismatches have been considered (Visser and Gienapp., 2019), few studies examine spatial variation in synchrony between species in the context of climate change and range shifts. However, phenological synchrony between species can vary across geographic gradients. For instance, in southern areas, the butterfly *Anthocharis cardamines* is well-synchronized with its local hosts because they demonstrate similar advancements in spring phenology in response to warming. In the north, on the other hand, relative phenology between the butterfly and host plants is shifting with warming, mostly due to more limited phenological plasticity in *A. cardamines* (aligning with the prediction that climate change will lead to weaker phenological advancements in consumers relative to resources; Renner and Zohner, 2018). This scenario again points to the potential importance of trailing edge populations as a source of potentially adaptive phenology during poleward expansion (Posledovich et al., 2018). Not only can climate change affect the synchrony of pollinators, but pollination efficacy can also vary with warming (Rafferty and Ives, 2012). Analyses of pollination synchrony and success over geographic gradients will be necessary to determine whether populations that shift poleward as a result of phenological plasticity can persist in the context of novel environments and commensurate shifts in species interactions.

Phenological mismatches constraining range shifts could also occur within a given trophic level. Phenological shifts will vary from year-to-year and across space depending on local environmental conditions, and the relative importance of the different variables that might affect phenology (e.g., temperature, photoperiod, precipitation) varies among species. For instance, flowering phenology shifts at different rates across elevations in the southwestern United States, advancing at lower elevations but not necessarily at higher elevations (Rafferty et al., 2020). These divergent responses can disrupt species interactions across trophic levels, as described above, but can also reshuffle communities (CaraDonna et al., 2014) and disrupt important interactions within a species such as gene flow between subpopulations or access to mates (see below). More specifically, synchronous flowering with other community members can increase pollinator visitation (Burkle et al., 2013). However, we have a limited understanding of the biological consequences of interspecific phenological synchrony (Zohner et al., 2018), and no studies to our knowledge have investigated interspecific phenological synchrony across species' ranges or beyond the edge.

Effects on Gene Flow

Although many traits may be important in mediating species' climate tolerances, shifts in reproductive phenology are unique in their potential to directly disrupt patterns of gene flow across a species' range (Levin, 2009; Franks, 2015). Differences in flowering time have been shown to generate assortative mating within populations (Weis and Kossler, 2004) as well as mediate gene flow between populations (Antonovics, 2006). Thus, climate-mediated shifts in phenology could have profound impacts on patterns of genetic variation within and among populations, ultimately affecting the adaptive potential of populations in response to climate change.

Within populations, several studies have found more variable and less synchronized reproductive phenology in response to climate change, perhaps reflecting differences among individuals in phenological plasticity (CaraDonna et al., 2014; Hall et al., 2018; Zohner et al., 2018). Such reductions in reproductive synchrony within populations are likely to decrease opportunities for outcrossing, limit within-population genetic variation, and decrease reproductive success (Augspurger, 1981; Giménez-Benavides et al., 2006). For example, Hall et al. (2018) found that the fitness benefits of earlier flowering under advancing snowmelt were at least partially counteracted by costs associated with decreased reproductive synchrony. However, most studies of phenological shifts have emphasized population-level averages and simple metrics (i.e., day of first flower) rather than detailed individual-level data on phenological distributions needed to quantify shifts in synchrony under climate change.

Among populations, phenology can be a critical driver of patterns of gene flow. For example, gradients in the timing of snowmelt, and thus flowering phenology, have been shown to be significant predictors of genetic isolation in several alpine plants (Hirao and Kudo, 2004; Yamagishi et al., 2005). In the context of climate change, phenological plasticity may disrupt these patterns of historical gene flow. For example, advancing flowering phenology actually led to greater separation of peak flowering, and reduced potential for gene flow among populations along elevational gradients in *Trillium erectum* (Rivest et al., 2021). Alternatively, adaptive phenological plasticity could facilitate the spread of warm-adapted alleles by enabling trailing-edge genotypes to successfully migrate and interbreed with populations throughout the species' range, contributing to greater genetic variation and adaptive potential (Ensing and Eckert, 2019). On the other hand, expanding leading-edge populations could potentially be limited by "swamping" gene flow from central populations (Kirkpatrick and Barton, 1997) or reduced genetic diversity following colonization (e.g., founder events; Sjölund et al., 2019) that constrain the ability of range-edge populations to adapt to novel environmental conditions. For example, there is some evidence that adaptive genetic differentiation is weaker along steeper environmental elevational gradients vs. more gradual latitudinal gradients due to gene flow (Bachmann et al., 2020). The extent to which phenological plasticity will shape gene flow, and thus adaptation and range shifts under climate change, is still very much an open question.

IMPROVING FORECASTS OF RANGE SHIFTS BY EXAMINING PHENOLOGICAL PLASTICITY ACROSS AND BEYOND GEOGRAPHIC RANGES

We have reviewed and outlined different routes by which phenological plasticity could facilitate or hinder range shifts. However, no studies have demonstrated that phenological plasticity facilitates range shifts and persistence beyond contemporary range edges, despite the common assumption that phenological plasticity facilitates population growth and spread (McLean et al., 2016). Recognizing how phenological plasticity could facilitate range shifts, and particularly expansions at the leading edge, is an important first step to designing empirical studies to test these processes. We envision several approaches for testing the role of phenological plasticity in range shifts: (1) filling in gaps in our knowledge; (2) incorporation and evaluation of phenology in improving models of species distributions, (3) examining phenological responses to experimental manipulations of climate change across geographic gradients including (i) genetic variation in phenological traits and (ii) phenological synchrony across and within trophic levels; (4) beyond the edge transplants in nature; and (5) greater consideration of the role of trailing populations in range shifts. We address each of these points below.

We identified several gaps in our current knowledge. First, relatively few studies address the role of phenophases beyond growth/development and reproduction. Emergence and senescence could also influence range shifts, but combined they only accounted for 14% of the studies reviewed here. Given that each of these phenophases bracket species' life cycles and/or growing seasons, and therefore may impose the outer limits on how much phenology can shift, understanding their role will be critical to predicting overall phenological plasticity and fitness during range shifts. Emergence and senescence, as well as measurements of the start, peak, and end of the growing season, could benefit from increased use of remote sensing data across species' geographic ranges (see Piao et al., 2019 for a review on the use of remote sensing data for phenological observations). Second, while Europe and North America accounted for 282 cases, only five studies came from Asia [three from Japan (Ishizuka et al., 2015; Sakurai and Takahasi, 2016; Jeong et al., 2020), one from China (Tang et al., 2017), one from India (Datta et al., 2017)], one from Mali (LaBarbera and Lacey, 2018), and one from Chile (Bull-Hereñu and Arroyo, 2009). Although this is likely partially because many studies address poleward shifts toward colder climates, biasing results toward the northern hemisphere, tropical alpine species face similar climate threats but their responses to climate change are relatively understudied (Telwala et al., 2013).

Models offer a potentially powerful approach to test the role of phenology in driving or constraining species' range shifts.

Several studies have used species' phenological traits to develop models of their geographic distribution, suggesting an important role for phenology in determining range limits (e.g., Chuine and Beaubien, 2001; Morin et al., 2008; Chapman et al., 2014; Duputié et al., 2015), and some of these have included variation in phenology across populations or geographic gradients (Chapman et al., 2017; Gauzere et al., 2020). Such models provide a fruitful avenue to explore the potential consequences of variation in phenological plasticity and/or genetic variation in phenology across geographic gradients. In particular, studies that compare the predictive accuracy of models based on alternative assumptions about the role of plasticity would be insightful. However, ultimately we need empirical data to parameterize and test these models, and we envision three empirical approaches for testing the potential role of phenological plasticity in range shifts.

To test whether leading or trailing edges have greater phenological plasticity and whether that plasticity can facilitate both expansion and persistence beyond the range edge, we need (1) experiments combining phenological measurements across geographic gradients with manipulations of climate change as well as (2) transplants beyond contemporary range edges. Across a geographic gradient, phenological plasticity can enable persistence *in situ*, expansion to similar climatic conditions within the historical range, or expansion to newly suitable locations beyond the historical range. For these scenarios, we need to understand how trailing, central, and leading edge populations vary in phenological plasticity in response to environmental conditions that vary with geography. Additionally, genetic variation among populations from across these gradients will influence how well populations can adapt or respond plastically to different environments, but very few studies examine adaptive potential in phenology across geographic gradients. Similarly, few studies examine phenological synchrony across geographic gradients, but interactions across trophic levels (e.g., with pollinators and food sources), within trophic levels (e.g., competition or facilitation among co-flowering species), or within the same species (e.g., access to mates) will affect the fitness consequences of phenological shifts and thus whether populations can persist.

Climate warming will generally result in a shift of the favorable conditions for growth and reproduction poleward and upward in elevation. Studies that transplant individuals into new parts of the historical range that also impose a climate manipulation mimicking future environmental conditions offer critical insights into how populations throughout the range may respond and migrate during forecasted climate change. Taking this a step farther, transplants beyond current range edges represent the most powerful experimental approach for examining whether populations can actually persist in a new location. Beyond-the-edge transplants, which only represented four studies reviewed here, allow us to examine whether edge populations are primed for expansion or if the negative effects of small population size, genetic drift, or inbreeding might thwart colonization beyond the edge. They could also differentiate between two potential mechanisms of range expansion: phenological plasticity vs. local adaptation in phenology (**Figure 2**: H3). Yet even beyond-the-range transplants have often omitted several crucial parts to understanding range shifts: early life-history stages, multiple generations and multiple populations from various locations from within the species' contemporary range (Hargreaves and Eckert, 2019). The latter in particular may become increasingly important if trailing edge populations are better-suited to the warmer temperatures expected under future conditions (Grady et al., 2011), indicating their potential in range shifts and species conservation.

Indeed, our review points to the possibility for trailing edge populations to demonstrate greater phenological plasticity and genetic variation in phenological traits than leading edge populations. If this pattern is generally true and individuals from trailing edge populations demonstrate sufficient phenological plasticity or adaptive potential, they could play an important role in stabilizing species' trailing edges and/or dispersing potentially adaptive alleles poleward that could enable adaptation to novel habitats and climates (Gibson and Reed, 2008; Wadgymar et al., 2015). However, we know relatively little about how trailing edge populations might contribute to range shifts, suggesting that individuals from trailing edges should be included in studies examining species' responses to climate change such as transplants along geographic and environmental gradients where we can estimate genetic variation under simulated future climates. For example, genetic variation in both germination and flowering phenology was highest in populations of *Boechera stricta* transplanted upslope and decreased in populations transplanted downslope, suggesting that range shifts may be facilitated by increased genetic variation (Bemmels and Anderson, 2019). Similarly, in *Chamaecrista fasciculata*, colonists from the trailing edge benefitted leading edge populations by introducing adaptive alleles (Wadgymar et al., 2015). These scenarios point to the possibility that trailing edge genotypes could be used to help mitigate extinction risk through assisted range expansion (Loss et al., 2011), although the benefits and goals of this approach are debated (Vitt et al., 2010; Hällfors et al., 2017). Overall, trailing edge populations may have enough genetic variation and/or plasticity to increase the chance that individuals can expand and persist beyond their current range limits, but trailing edge populations remain understudied and the performance and demography of trailing edge populations under novel environmental conditions remains an open area for research.

SUMMARY

As climate change progresses, phenological plasticity is likely to play an important role in mediating population persistence and species' range shifts. Our review of the literature suggests that phenotypic plasticity will often be in an adaptive direction that allows populations to match local phenotypes, and that trailing and central populations may be critical sources for phenological plasticity and genetic variation in phenology relative to leading edge populations. However, it remains difficult to make generalizations about the role of phenological plasticity in range shifts due to lack of empirical data. Importantly, we identify several gaps in our current understanding including relatively few studies that investigate phenophases related to emergence or senescence, and few studies that compare either patterns of adaptive potential in phenology across geographic gradients or the role of phenology in mediating range shifts. In particular, we highlight beyond-the-range transplant experiments that quantify phenological plasticity for multiple populations as being particularly fruitful. Shifting phenology may also influence longer-term ecological and evolutionary dynamics of populations during range shifts, such as correlated life history shifts, mismatched species interactions, and patterns of gene flow, that remain relatively understudied. Given that shifts in phenology have been one of the most consistent and dramatic biological responses to climate change, we urge future research to carefully dissect its causes and consequences for species range shifts.

AUTHOR CONTRIBUTIONS

MZ and MP conceived the manuscript and conducted the literature review. MZ wrote the first draft of the manuscript and both authors contributed to revisions. Both authors contributed to the article and approved the submitted version.

SUPPLEMENTARY MATERIAL

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GLOSSARY

Adaptive plasticity: Environmental responses that shift a phenotype in the same direction that would be favored (i.e., have higher fitness) in that environment; or, in the absence of fitness data, inferred as the direction that would match the locally observed phenotype in that environment.

Central population: Populations located within the core of a species' current geographic distribution.

Co-gradient genetic variation: Genetically based differences in the phenotype expressed by populations in a common environment that mimic the natural (geographic) cline.

Counter-gradient genetic variation: Genetically based differences in the phenotype expressed by populations in a common environment that oppose the natural (geographic) cline.

Geographic cline: Variation in a phenotype expressed in wild populations across a geographic (e.g., latitude or elevation) gradient.

Leading edge population: Populations residing at the current leading range edge; here, more poleward or higher elevation populations.

Leading range edge: The margin of a species' distribution that is predicted to become more climatically suitable under climate change, potentially facilitating expansion beyond the historical range edge.

Maladaptive plasticity: Environmental responses that shift a phenotype away from the optimal phenotype in that environment; or, in the absence of fitness data, inferred as the direction away from the locally observed phenotype in that environment.

Phenological plasticity: A non-genetic shift in the timing of life-history events (here, "phenophases") in response to change(s) in the (a)biotic environment.

Trailing edge population: Populations residing at the current trailing range edge; here, more equatorial or lower elevation populations.

Trailing range edge: The margin of a species' distribution that is predicted to become less climatically suitable under climate change, potentially leading to local extirpation and contraction of the historical range edge.

Range shift: Change in the geographic distribution of a species due to range contractions and/or expansions beyond historical range edges.

Reaction norm: The relationship between an environmental variable and the phenotype expressed by a given genotype or population; the pattern of phenotypic plasticity.

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Evidence of Range Shifts in Riparian Plant Assemblages in Response to Multidecadal Streamflow Declines

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Riparian corridors are thought to form hydrological refugia that may buffer species and communities against regional climate changes. In regions facing a warming and drying climate, however, the hydrological regime driving riparian communities is also under threat. We examined recruitment in response to streamflow declines for species inhabiting the riparian zone in southwest Western Australia, testing the extent to which the riparian system has buffered riparian communities from the drying climate. We stratified 49 vegetation transects across the >600 mm per annum regional rainfall gradient encompassed by the Warren River Catchment. Local hydrological conditions were estimated over two 10-year periods; 1980–1989, and 2001–2010, to quantify changes in the flood regime. Mixed effects models tested the relationship between rainfall and flooding on the relative frequency of immature to mature individuals of 17 species of trees and shrubs common to the riparian zones. At the low-rainfall extent of their geographic range, the relative frequency of immature riparian species decreased with declining flow, whereas at the high-rainfall extent of their geographic range the relative frequency of immature individuals increased with declining flow. These results suggest that the geographic ranges of riparian species may be contracting at the low-rainfall margin of their range, while at the high-rainfall margin of their geographic range, reduced flooding regimes appear to be opening up new habitat suitable for recruitment and narrowing the river corridor. No such patterns were observed in upland species, suggesting the river may be buffering upland species. We discuss these findings and their implications for ongoing management and species conservation in a region projected to face further, significant rainfall declines.

Keywords: climate change, environmental flows, LiDAR, Mediterranean climate, range contraction, recruitment, riparian vegetation, stream flow decline

INTRODUCTION

For many species, survival over the coming decades will depend on their ability to adapt to the new climatic conditions *in situ*, or shift geographic range to maintain their climatic optimum (Parmesan, 2006; Aitken et al., 2008). In stark contrast to mobile organisms where analyses of distributional shifts have been shown to match climatic shifts (Chen et al., 2011; Lenoir et al., 2020), sessile organisms, particularly those with longer generation times, can be much more constrained in their responses to climate change (Lenoir and Svenning, 2015; but see Ström et al., 2011).

In a strict sense, determination of range shifts in response to climate change requires temporally replicated data (Bertrand et al., 2011; Feeley et al., 2011; Telwala et al., 2013). In lieu of such datasets, range shifts in plant species have been inferred by examining the skew in abundance distributions (Breshears et al., 2008; Murphy et al., 2010), or by exploiting the long generation times and comparing the distribution of seedlings relative to the adult population (Lenoir et al., 2009; Zhu et al., 2012, 2014; Fei et al., 2017). The assumption is made that the range inhabited by new recruits is representative of the optimal climatic envelope within current climate space, while the distribution of adults represents a climate envelope characteristic of former conditions (Lenoir et al., 2009).

Species range expansion is typically observed as the establishment of seedlings beyond the former adult range (Galiano et al., 2010; Vitasse et al., 2012). While range contraction can manifest as recruitment failure at range margins (Zhu et al., 2012; Bell et al., 2014), adult mortality events are typically taken as more 'conclusive' evidence. These mortality events can be evident for long-lived species following catastrophic disturbance events (Allen et al., 2010; Brouwers et al., 2013; Matusick et al., 2013; Harris et al., 2018), or as more gradual declines in growth and crown dieback (Stella et al., 2013). Juvenile recruitment within an existing range, however, can be much more sensitive to incremental changes in environmental conditions and provide an early indication of a site becoming unsuitable (Lloret et al., 2009; Bell et al., 2014; Garssen et al., 2014).

There is a growing body of evidence that topographic and hydrological features in the landscape may reduce exposure to regional climate changes and buffer organisms from broader environmental changes (Dobrowski, 2011; Lenoir et al., 2017; McLaughlin et al., 2017). Riparian zones are predicted to buffer the suboptimal climatic conditions in regions experiencing a warming and drying climate, affording species more time to adapt to the new environmental conditions. The buffering effect of riparian systems in the face of climate warming hinges on the resilience of the hydrological processes under changed climatic conditions (Davis et al., 2019). In regions with warming and drying climates, the hydrological regime driving water availability in riparian systems is also under threat (Barron et al., 2012), placing specialist riparian species under stress from both hydrological conditions and increasing competition from upland species (Garssen et al., 2014).

Here, we test the ecological impacts of multidecadal streamflow declines on the riparian plant communities of south-west Western Australia (SWWA). We examine the relative frequency of immature versus mature individuals of riparian and upland species inhabiting the riparian zones in response to recent changes in local hydrological conditions. We hypothesize, first, that riparian species that are restricted to near-channel habitats, due to their higher sensitivity to surface water availability, will show a contracted geographic range of immature individuals relative to the observed geographic range of the adult population. Second, we hypothesize that less moisture-demanding upland species will be buffered from regional declines if they inhabit the riparian zone, and therefore the distribution of immature individuals is likely to match the distribution of mature individuals for upland species.

MATERIALS AND METHODS

Study System

The Warren River, and its major tributaries the Tone River and Murrin Brook of the SWWA are cumulatively about 275 km in length (**Figure 1A**) and transect a shallow topographical gradient to a maximum elevation of 385 m asl (Geoscience Australia, 2016). Native vegetation, in either reserves or indigenous forestry, is the dominant land cover across approximately two-thirds of the catchment (**Figure 1A**) (DPIRD, 2020). A few sub-catchments in the lower Warren are important agricultural regions and withhold water in dammed gullies for irrigation. In these sub-catchments, water abstraction limits are set to ensure a sustainable ecological flow (Department of Water, 2012).

Mean annual temperatures vary little across the catchment (between 14.3 and 15.7°C). By contrast, mean annual rainfall ranges from over 1200 mm per annum (mm pa) at the mouth of the river, to less than 550 mm pa in the headwaters (between 1901 and 1960, Bureau of Meteorology, 2010). A significant decline in the frequency and magnitude of wet weather systems has been observed in SWWA since the 1970's (Hope et al., 2006), resulting in a 16% decline in rainfall, and culminating in reductions of over 50% in surface runoff in some rivers and water storage dams (Petrone et al., 2010). This trend in declining rainfall is predicted to continue under modeled future climate scenarios (Barron et al., 2012; Silberstein et al., 2012; Hope et al., 2015). As the major climatic driver of vegetation types across the region, rainfall declines are predicted to shift optimal climatic envelopes for vegetation communities (Hamer et al., 2015; Ramalho et al., 2017).

Topography

Accurate spatial quantification of topography and vegetation structure running the length of the Warren River was obtained using an aerial LiDAR (light detecting and ranging) survey. A 500 m wide band, spanning the length of the Warren and its tributaries was carried out from the 13th to the 16th of January 2015 by AAM Geospatial Pty Ltd from a fixed wing aircraft using a Q780 laser system with a pulse rate frequency of 180 kHz. The laser returns had a horizontal accuracy of 0.55 m and vertical accuracy of 0.30 m, and were supplied as point clouds, comprised of x: longitude, y: latitude, and z: elevation meters above sea level. The point clouds were classified algorithmically by AAM into ground, infrastructure and vegetation points, and a 1×1 m resolution digital ground model (DGM) was interpolated from the ground points. The LiDAR survey was conducted during summer when the river had ceased to flow and much of the upper half of the catchment was dry. This enabled us to capture elevation across the dry river bed or water level of permanent water bodies.

Sampling Design

Vegetation sampling sites were stratified by rainfall isohyet, defining five strata, $\leq$600, 600–800, 800–1000, 1000–1200 and $>$1200 mm (**Figure 1A**). Within each stratum, 20 potential survey locations, spaced at least 1 km apart and randomly assigned to the true left or true right bank, were randomly generated

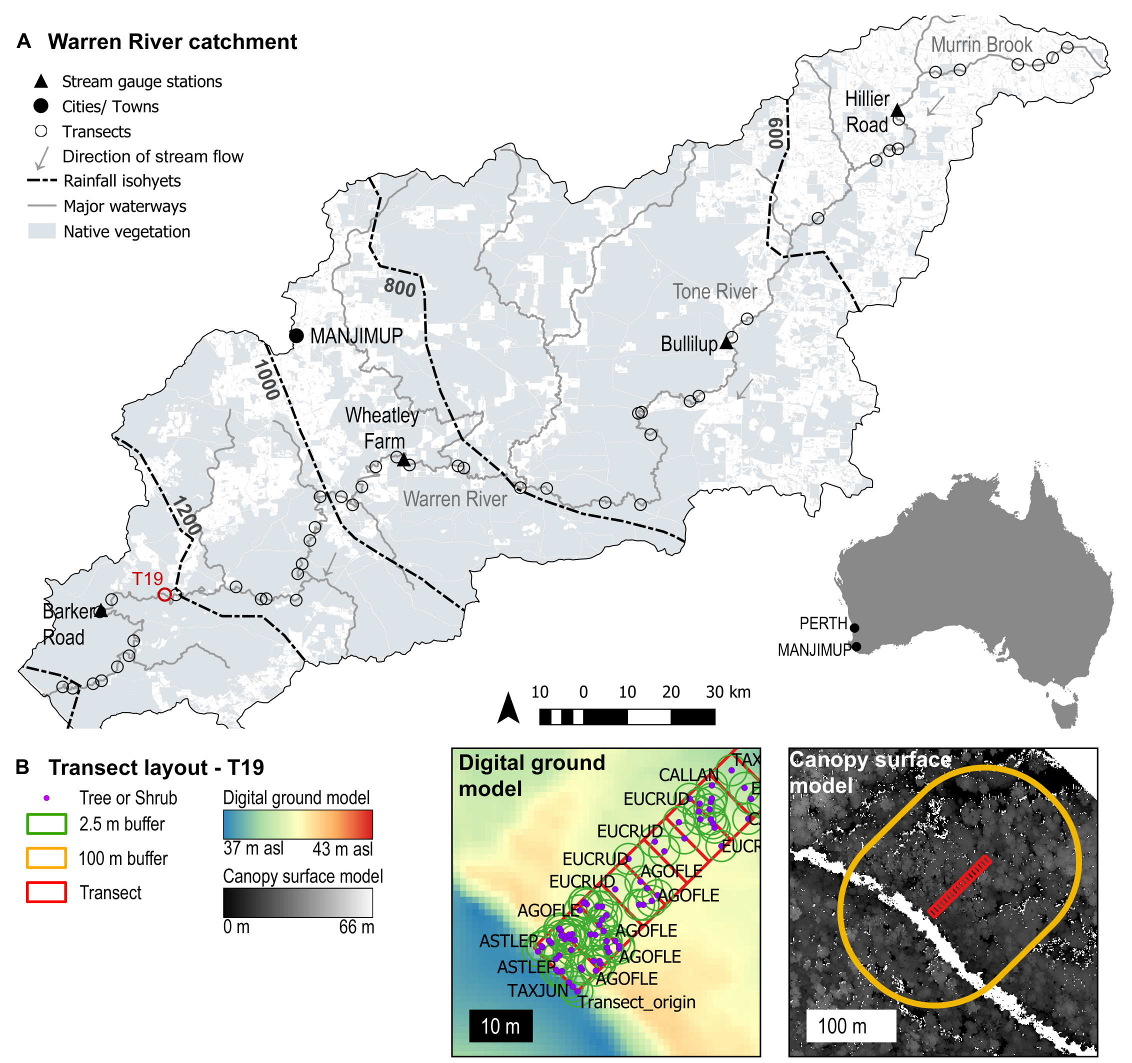

FIGURE 1 | The Warren River Catchment and vegetation survey design. **(A)** The Warren River Catchment in the south-west of Western Australia marking the locations of vegetation transects, the Department of Water Gauge stations (Department of Water and Environmental Regulation, 2016), and the coverage of native vegetation (DPIRD, 2020), on basemaps sourced from Geoscience Australia (2016). **(B)** The layout of vegetation transects, demonstrated with T19, where transects were rectified using aerial imagery, field photographs and digital elevation models. The elevation of each tree was calculated relative to transect origin. Forest structure was quantified within buffer zones of 2.5 m for individual plants, and 100 m for transects. Note that the river in the canopy surface model is white, where no vegetation points were recorded.

in ArcGIS 10.3.1 (ESRI Inc.). The feasibility of sampling at each of these locations was assessed during site visits, aiming to survey 10 sites per zone. Sites were rejected if: (1) the area was disturbed by human infrastructure such as roads or bridges or the site was visibly impacted by (2) herbicide use; or (3) recent fire. Vegetation survey sites were classified into flood plains or steep banks. Once five sites of either landform had been selected within a zone, all further sites of that landform were rejected to ensure surveys covered a representative range of geomorphic habitats. Difficult access (e.g., steep granite cliffs) within the 1000–1200 mm pa zone meant that only eight sites were sampled in this zone. An additional site was sampled in the <600 mm pa zone to increase the total area sampled across the narrow riparian zones of the upper catchment. A total of n = 49 sites (≤ 600 mm, n = 11; 600–800 mm, n = 10; 800–1000 mm, n = 10; 1000–1200 mm, n = 8; > 1200 mm, n = 10) were surveyed once each, during one of two consecutive summers, December 2013 to April 2014, and November 2014 to May 2015.

Vegetation Sampling

A 10 m wide transect was run at each site from the water's edge (the edge of the dry river bed in the upper catchment) to the end of the riparian zone. Transect length was determined by site geomorphology, and a change in the dominant vegetation type, varying in length from 5 to 90 m (**Figure 1B**). The coordinates at the ends of each transect were marked using a GPS unit (GPSMAP® 62s, Garmin) and the location of each plant rooted within the transect recorded. The position of each plant relative to the transect line was recorded to the nearest 0.5 m. All trees and shrubs were identified to species level following the nomenclature of the Western Australian Herbarium (Western Australian Herbarium FloraBase, 1998).

As the majority of the trees and woody shrubs in the region (predominantly Fabaceae, Myrtaceae, and Proteaceae; **Table 1**) retain a woody capsule/fruit after seed set, each plant was searched for the presence of fruit or flowers to assess whether an individual was reproductively immature or mature, as a binary response. *Agonis flexuosa* was the only species observed to sucker and reproduce vegetatively, but without a means to identify an immature individual decisively as the product of sexual or vegetative reproduction both were included and the results treated with added caution. *Astartea leptophylla* and, less often, *Eucalyptus rudis* were observed to layer where a branch had been damaged, or coppice from the base of mature individuals, and these were considered part of the parent plant. In these low-power systems (Pettit and Froend, 2001b), layering and coppicing seemed to serve as an adaptation to extend the life of a single diseased or damaged individual, rather than as a means to replicate (H. White personal observation). A binary response of reproductive status was used as opposed to size-class structure based on heights or stem diameters for two reasons: first, to estimate broad 'recruitment' trends and reduce the temporal bias of the single time point sample; and second, a size-based age classification could not be consistently applied across the length of the catchment due to the variation in growth rates imposed by the rainfall gradient.

The transect coordinates were spatially rectified to the DGM, LiDAR vegetation point clouds and field photographs in ArcGIS 10.3.1 to account for field GPS error. The position of each plant within a transect was spatially adjusted to the rectified transect position to obtain corrected geographic coordinates. The absolute elevation (m asl) and elevation relative to the transect origin (i.e., above base flow) for each plant was extracted from the DGM and used to calculate hydrological parameters.

Streamflow

To investigate species distribution patterns in relation to surface water and flood regime, parameters describing ecologically important aspects of flow were estimated using the DGM and maximum daily stage height data obtained from the West Australian Department of Water and Environmental Regulation (DWER) for four gauging stations situated in the main channel along the Warren and Tone Rivers (**Figure 1A**, Hiller Road, Bullilup, Wheatley Farm and Barker Road Crossing, Department of Water and Environmental Regulation, 2016). Past and recent flow conditions were estimated by selecting two 10-year periods. 1980 to 1989 represents a past condition and was selected as the first decade where three of the gauges on the main channel were in place (Barker Road was established April 1966, Wheatley Farm in 1970 and Bullilup in 1978). The second period, 2001 to 2010, was selected to represent recent conditions based on the availability of data from the Hiller Road gauge station, which was established in June 2000, but was then offline from 2013 to 2015 (**Figure 2**). Unfortunately, continuous flow records are not available for periods predating the 1970s 'step decline' in precipitation, so the selected periods are likely to underestimate overall flow reduction. However, there is likely to have been a lag period between rainfall change and subsequent ecological impacts of flow reduction, therefore we assume that the 1980s period reflects 'low' impacts of flow reduction, while the 2000s period reflects 'high' impacts of flow reduction. Importantly, further significant shifts have been observed in streamflow since the 1980s (**Figure 2**; Petrone et al., 2010).

To measure the change in the flooding regime between these two periods, linear models were constructed modeling the maximum daily stage height above baseflow at the four gauge stations, as a function of elevation (m asl) for each day of the two 10-year periods (see **Supplementary Material 1** for detailed methods). Then, taking the lowest absolute elevation of each vegetation sampling transect (i.e., the dry river channel or summer water level as baseflow) the estimated maximum stage height was interpolated (or extrapolated) at each transect elevation to generate a time-series for each transect site (**Supplementary Figure S1.2**).

These time-series were used to estimate the frequency and duration of inundation events experienced by each plant based on its elevation to the nearest 0.1 m from 0.5 m above baseflow. Frequency (F) describes the estimated frequency of inundation presented as a value between 0 and 1: where 0 indicates that the individual plant was not inundated during the 10 years period; and 1 indicates that the water level equaled or exceeded the elevation at least once a year for each year of the 10 years period. Duration (D) indicates the mean number of days a plant is estimated to have been inundated per year over the 10-year period, calculated as the mean number of days per calendar year that the water level was estimated to equal or exceed the elevation of an individual plant. The differences in frequency and duration between the historical and recent rainfall periods were calculated, and the resultant differences, ΔF (change in frequency) and ΔD (change in duration), were retained alongside recent frequency and recent duration, respectively, as predictors in statistical models.

Forest Structure

To control for variation in surrounding land use and microclimate on seedling establishment (Davis et al., 2019), we used the LiDAR vegetation point clouds to quantify habitat structure using LAStools (Isenburg, 2017) and ArcGIS 10.3.1. The forest structure was described at two scales, the landscape scale was described by an area encompassing a transect and a 100 m buffer, and the microclimate of individual plants was approximated using a 2.5 m buffer around the point location of each tree or shrub (**Figure 1B**). Metrics describing forest structure were calculated from ground normalized point clouds and a 1 × 1 m resolution canopy surface model (CSM) describing the maximum canopy height in each pixel (see **Supplementary Material 1** for detailed methods). At the transect scale, we obtained the following metrics for each transect and its surrounding 100 m buffer: the maximum point height, and the laser penetration rates through six vertical height strata: the penetration rate to 24 m; penetration through 24 to 16 m; 16 to 8 m; 8 to 3 m;

TABLE 1 | Habitat and reproductive traits of the woody trees and shrubs common to the riparian zone of the Warren River Catchment.

Species	Family	Upland/ Riparian	Rainfall range*	Form	Seed storage	Seed dispersal mode	Vegetative growth and/or resprouting	References
Astartea leptophylla	Myrtaceae	Riparian	696–1208 mm	Spreading tree or shrub (to 5 m)	?In soil	Wind and water dispersal	Non-lignotuberous; reproduces by layering	Rye, 2013; Hopley and Byrne, 2018
Eucalyptus rudis	Myrtaceae	Riparian	399–896 mm	Tree (5–20 m)	Canopy stored	Seed falls with receding water, found in flood debris	Seedlings and juvenile plants develop lignotubers, some layering observed[†]	Pettit and Froend, 2001a,b
Melaleuca cuticularis	Myrtaceae	Riparian	374–1045 mm	Tree or shrub (1–7 m)	Canopy stored	Dispersed by gravity	Non-lignotuberous	Barlow and Cowley, 1988; Brophy et al., 2013
Melaleuca rhaphiophylla	Myrtaceae	Riparian	382–1031 mm	Tree or shrub (2–10 m)	Canopy stored	Seed falls year round, found in flood debris	Non-lignotuberous	Pettit and Froend, 2001a,b; Brophy et al., 2013
Melaleuca viminea	Myrtaceae	Riparian	356–1044 mm	Shrub or tree (6–5 m)	Canopy stored	Dispersed by gravity, then water	Non-lignotuberous	Brophy et al., 2013
Taxandria juniperina	Myrtaceae	Riparian	659–1166 mm	Erect tree or shrub (to 27 m)	Canopy stored	Dispersed by gravity	Non-lignotuberous	Wheeler and Marchant, 2007
Agonis flexuosa	Myrtaceae	Facultative	694–1176 mm	Tree or shrub (to 10 m)	Canopy stored	Dispersed by gravity	Lignotuber, layering and suckering[†]	Wheeler and Marchant, 2007
Banksia seminuda	Proteaceae	Facultative	727–1250 mm	Shrub or tree (1–25 m)	Canopy stored	Winged seed, cones found in flood debris	Non-lignotuberous	Hancock et al., 1996; Pettit and Froend, 2001a
Callistachys lanceolata	Fabaceae	Facultative	570–1168 mm	Erect shrub or tree (1.5–7 m)	In soil	Dispersed by gravity	Non-lignotuberous	Hopley and Byrne, 2018
Hakea oleifolia	Proteaceae	Facultative	630–1214 mm	Erect shrub or tree (2–10 m)	Canopy stored	Winged seed	Non-lignotuberous	Groom and Lamont, 1996
Acacia pulchella	Fabaceae	Upland	413–1070 mm	Shrub (0.3–3 m)	In soil	Fire stimulates germination	Non-lignotuberous	Monk et al., 1981
Hibbertia cuneiformis	Dilleniaceae	Upland	627–1210 mm	Erect or sprawling shrub (1–3 m)	In soil or possibly ant nests	Fleshy yellow to orange aril. ?ant dispersal	Lignotuber	Wheeler, 2003
Hovea elliptica	Fabaceae	Upland	673–1148 mm	Slender shrub (0.6–3 m)	In soil or possibly ant nests	Seed with fleshy aril. ?ant dispersal	Non-lignotuberous	Ross, 1989
Leucopogon obovatus subsp. *revolutus*	Ericaceae	Upland	485–1210 mm	Erect, robust shrub (to 2.5 m)	?Fruits (fleshy drupe) falls to ground when green	?Further dispersal by birds and maybe reptiles	Multi-stemmed at the base (Lignotuber)	Hislop and Chapman, 2007; Hislop, 2011
Leucopogon propinquus	Ericaceae	Upland	558–1152 mm	Erect shrub or tree (0.3–2 m)	Fruits (fleshy drupe) falls to ground when green	Further dispersal by birds and maybe reptiles	Propagates vegetatively from underground storage rhizomes	Keighery, 1996; Norman and Koch, 2008
Melaleuca incana	Myrtaceae	Upland	545–1130 mm	Shrub or tree (4–5 m)	Canopy stored. Seed capsules remain on the shrub some years	?Dispersed by gravity	?Non-lignotuberous	Brophy et al., 2013
Trymalium odoratissimum subsp. *trifidum*	Rhamnaceae	Upland	653–1169 mm	Large shrub or small tree (1–9 m)	In soil	Dispersed by gravity, a small aril points to ant dispersal	Non-lignotuberous	Hancock et al., 1996; Kellermann et al., 2008; Etchells et al., 2020

Information primarily sourced from Florabase (Western Australian Herbarium FloraBase, 1998), The Flora of Australia (Flora of Australia, 2021), and Flora of the South West (Wheeler et al., 2002).

**Rainfall range estimated from species records obtained from the Atlas of Living Australia (2021). Rainfall range presents the 5th and 95th percentiles of mean annual precipitation (Precipitation – Annual bio12).*

[†] Traits observed by the authors in the field. [?] Trait uncertain.

3 to 0.5 m and penetration to ground level ($\leq$0.5 m) from the point clouds. A further four metrics were obtained from the CSM: the range, mean, coefficient of variation (CV) and variance (var) in maximum canopy height across each transect and buffer zone. At the scale of each individual, we obtained the laser penetration rates through the six vertical height

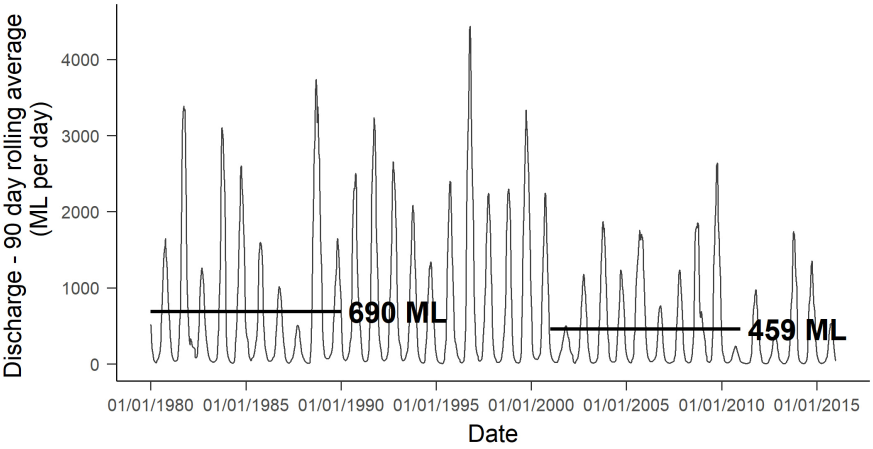

FIGURE 2 | Ninety day rolling mean daily discharge at Barker Road Gauge Station from 1980 to 2016. Black lines indicate mean daily discharge for the two, 10-year periods, 1980 to 1989 and 2001 to 2010 (Department of Water and Environmental Regulation, 2016).

strata, and the mean and the maximum height from the CSM around each tree.

To manage collinearities and reduce the number of predictors, a principal component analyses (PCA) was run for each of the transect and individual variable sets in the 'vegan' package (Version 2.4-2; Oksanen et al., 2017). The resultant PC1 and PC2 axes, T_PC1 and T_PC2 (accounting for 73 and 16% of the variation, respectively) at the transect level, and I_PC1 and I_PC2 (accounting for 52 and 18% of the variation, respectively) at the individual tree level, were incorporated as covariates in the following analyses (see **Supplementary Material 1** for detailed methods).

Statistical Analysis

We selected 17 species of trees and woody shrubs that were sufficiently abundant (>50 individuals) to investigate the effects of rainfall and shifts in hydrological regime on recruitment. Of the 17 species, six were classed as obligate riparian species, four as facultative riparian species and seven were classed as upland species (**Table 1** and **Figure 3**). As information on the flood ecology of many of these species is limited to just the original taxonomic descriptions in several cases, classification of life history classes was necessarily based on limited published information supplemented by field observations of the authors, adapting definitions by Rood et al. (2010).

A generalized linear mixed model (GLMM) was fitted for each species using a binomial distribution and a logit link (Bolker et al., 2009) in the 'lme4' package (Version, 1.1-23; Bates et al., 2015) in R version 4.0.2 (R Core Team, 2020). The response variable indicates the probability (the 'log odds') that a given plant is immature (coded as '1') rather than mature (coded as '0'), as predicted by the set of modeled environmental covariates described below. For clarity of graphical display, model predictions calculated using the predict.lme function in lme4 were back-transformed on to a 'proportion' scale, rather than log-odds ratios. Values approaching 1 indicate a largely immature population, with few adult individuals and many recruits. Conversely, values approaching 0 indicate a largely mature population, with few recruits, and a low probability of encountering an immature individual (**Figure 4A**).

The variables describing transect level (T_PC1 and T_PC2) and individual level (I_PC1 and I_PC2) variation in forest structure were included as fixed covariates to control for variation in land use, and microclimatic conditions independent of the hydrological parameters. To account for non-independence of individuals sampled within a transect, a random intercept was included for transect identity.

Hydrological conditions were defined using combinations of five fixed predictors F, ΔF, D, ΔD, and historic rainfall, and their interactions (**Supplementary Material 2**). Rainfall was included as historic rainfall only, rather than a measure of change in rainfall, because the two variables were highly correlated, and historic rainfall is more easily interpreted (**Supplementary Material 1**). Moreover, F and D were also highly correlated (Pearson's $r = 0.78$, $p < 0.05$), indicating individuals that were regularly inundated were also inundated for longer durations annually. Rather than discarding one set of the collinear parameters, a two-phase model selection approach was used to identify the parameter set which best fitted each species.

Initially, global models were constructed to test the effects of estimated flood duration (D, ΔD, rainfall inclusive of all two- and three-way interactions) and estimated flood frequency (F, ΔF, rainfall inclusive of all two- and three-way interactions) separately. The global models were simplified using model selection procedures comparing Akaike Information Criterion for small sample sizes (AICc) in the 'MuMIn' package (Version 1.15.6; Barton, 2016). For each parameter set, the most parsimonious model within 2 AIC units of the top model was selected as the 'best fit' model (Arnold, 2010). Subsequently, the AIC of the best flood frequency model was compared to the best model fitted for flood duration, and the final model was taken as the model with the lowest AIC out of either model set. A complete list of candidate models and resultant AIC values are presented in **Supplementary Material 2**.

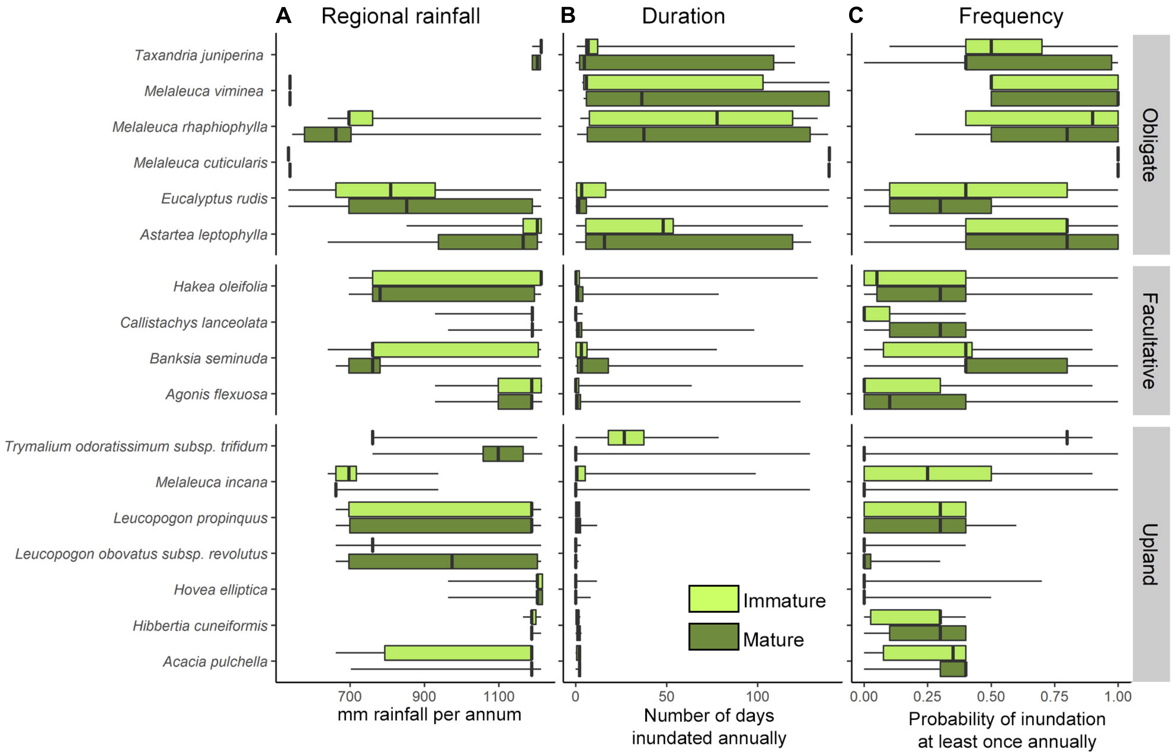

FIGURE 3 | Range of hydrological conditions estimated for mature and immature individuals inhabiting the riparian zone of the Warren River Catchment. Estimated hydrological parameters are **(A)** mean annual rainfall (mm), and river flow metrics flood **(B)** duration, and **(C)** frequency estimated as the recent conditions (from 2001 to 2010). The limits of boxes mark the lower and upper quartiles (25%, 75%) centered around the median (bold center line) of the species distribution. Whiskers indicate the min and max (range).

Prior to analysis, all of the continuous predictors and covariates were centered and scaled by 2 standard deviations (Gelman, 2008). Models were assessed for over-dispersion, however no adjustment was necessary. Model fit was assessed using the Nakagawa and Schielzeth (2013) R^2 approach.

RESULTS

Riparian Species

Reliable models were obtained for three of the six obligate riparian species examined, *Astartea leptophylla*, *Eucalyptus rudis,* and *Melaleuca rhaphiophylla* (**Table 2A**). Of these, the relative frequency of immature to mature individuals only differed significantly along the examined hydrological gradients in *A. leptophylla* (**Table 2A** and **Figure 4B**). The relative frequency of immature *A. leptophylla* was greater within regions experiencing a greater decline in annual flood frequency (ΔF, **Table 2A** and **Figure 4B**), particularly in regions with medium to high rainfall. Populations at the low rainfall extent were less likely to be immature individuals (**Figure 4B**); no immature *A. leptophylla* were surveyed in regions drier than 850 mm pa, despite mature individuals ranging out to 640 mm pa (**Figure 3**). The relative frequency of immature *M. rhaphiophylla* differed with estimated duration of flooding, change in duration (ΔD) and their interaction, but with a total of 13 immature individuals of the 144 plants surveyed, the model was not statistically significant (**Table 2A**). The modeled co-variates did not explain variation in the relative frequency of immature to mature individuals in the common and wide-ranging *E. rudis*. Models failed to converge for the remaining three obligate riparian species, *Melaleuca cuticularis*, *Melaleuca viminea,* and *Taxandria juniperina* due to the narrow range of observed variation in responses to predictors (**Supplementary Material 2**).

The four facultative riparian species, *Banksia seminuda*, *Agonis flexuosa*, *Hakea oleifolia* and to a lesser extent *Callistachys lanceolata*, revealed relationships with differing aspects of the estimated flow regime and the rainfall gradient (**Table 2A**). The relative frequency of immature *B. seminuda* was higher under high rainfall conditions, and immature individuals were more likely to be found in sites with low flood frequency across its entire range (**Table 2A** and **Figure 4F**). While the relative frequency of immature *Agonis flexuosa*, including both new recruits and immature individuals suckering off nearby plants, was higher under high regional rainfall, there were also significant interaction effects between rainfall, recent flood frequency and its change, indicating that high rainfall alone is insufficient to predict the occurrence of immature individuals (**Table 2A** and **Figures 4C,D**). As observed for *A. leptophylla*,

TABLE 2 | Generalized linear mixed effects models testing the relative frequency of immature to mature individuals of **(A)** riparian and **(B)** upland species along the riparian zones of the Warren River as a function of mean annual rainfall (Rn), and either inundation duration (D) and change in duration (ΔD) or flood frequency (F) and change in flood frequency (ΔF). Variation in forest structure is described at transect and individual level as the covariates, T_PC1 and T_PC2, and I_PC1 and I_PC2, respectively. The proportional change in variance (PCV) for the random effect (transect identity) is calculated between the null and final models. The Akaike Information Criterion (AICc) is a relative measure of goodness of fit scaled to the number of parameters in the model. $R^2_{GLMM(m)}$ is the marginal variance explained by all fixed factors and $R^2_{GLMM(c)}$ is the conditional variance explained by both fixed and random factors (Nakagawa and Schielzeth, 2013). NA indicates a term was not tested due to collinearities within the fixed predictor set. In species where the model fit was not better than the null model, results are shown for the null model only. Model coefficients highlighted in bold indicate significant predictors. Note, some models failed to converge due to insufficient variation within the tested environmental variables or age classes, and are therefore not presented for *Melaleuca cuticularis*, *M. viminea*, and *Taxandria juniperina*. †denotes an obligate riparian species. A complete list of tested models is provided in **Supplementary Material 2**.

(A)

Riparian species	***Melaleuca rhaphiophylla*†**	***Astartea leptophylla*†**	***Eucalyptus rudis*†**	***Agonis flexuosa***	***Banksia seminuda***	***Hakea oleifolia***	***Callistachys lanceolata***
Fixed effects	*n* = 144 (13)	*n* = 261 (91)	*n* = 206 (127)	*n* = 737 (537)	*n* = 94 (44)	*n* = 153 (86)	*n* = 64 (9)
Intercept$_{(null)}$	**–3.29 [–5.39, –1.18]**	**–1.73 [–3.25, –0.21]**	0.45 [–0.14, 1.03]	**0.64 [0.06, 1.22]**	–0.95 [–2.53, 0.63]	–0.84 [–1.91, 0.25]	**–1.9 [–3.14, –0.72]**
Intercept$_{(full)}$	–9.90 [–20.08, 0.29]	**–1.01 [–1.99, –0.03]**		0.57 [–0.17, 1.31]	–0.18 [–1.02, 0.66]	–0.93 [–2.17, 0.31]	**–4.08 [–8.06, –0.09]**
I_PC1	3.54 [–0.40, 7.47]	**–1.41 [–2.37, –0.45]**				**–1.55 [–2.77, –0.32]**	
I_PC2							
T_PC1	NA			NA	–3.21 [–5.17, –1.25]		NA
T_PC2	NA	NA		NA		NA	NA
D	–4.47 [–10.46, 1.52]						
ΔD	–1.34 [–11.72, 9.04]					**1.29 [0.36, 2.22]**	
D: ΔD	–23.78 [–57.32, 9.77]						
F				0.58 [–0.06, 1.21]	**–1.74 [–2.99, –0.50]**		–4.24 [–9.51, 1.04]
ΔF		**–1.28 [–2.17, –0.39]**		0.41 [–0.15, 0.96]			–3.43 [–7.92, 1.07]
Rn		**2.16 [0.21, 4.10]**		0.26 [–1.15, 1.67]	**4.29 [1.95, 6.64]**	NA	–3.03 [–7.16, 1.11]
F: ΔF				**–1.84 [–2.79, –0.89]**			
F: Rn				**2.70 [1.28, 4.12]**			
Rn: ΔF				**–1.47 [–2.85, –0.08]**			
VC for random effects$_{(Transect)}$	106.6	2.872	1.464	2.248	0.2831	2.88	2.016
VC for Fixed effects	63.22	2.40		1.05	3.30	0.90	7.79
PVC$_{(Transect)}$	–2185.1%	60.9%		–66.3%	93.4%	–29.8%	–1682.5%
$R^2_{GLMM(m)}$	0.0%	28.0%		16.0%	48.0%	12.8%	59.5%
$R^2_{GLMM(c)}$	0.1%	61.6%		50.1%	52.1%	53.5%	74.9%
AICc$_{(Null)}$	86.7	247.3	257.7	773.2	109.5	184.3	55.9
AICc$_{(Full)}$	83.7	233.7		739.6	98.2	175.1	50.2

(B)

Upland species	***Acacia pulchella***	***Hibbertia cuneiformis***	***Hovea elliptica***	***Leucopogon obovatus* subsp. *revolutus***	***Leucopogon propinquus***	***Trymalium odoratissimum* subsp. *trifidum***	***Melaleuca incana***
Fixed effects	*n* = 51 (30)	*n* = 64 (42)	*n* = 90 (51)	*n* = 57 (45)	*n* = 99 (36)	*n* = 237 (87)	*n* = 780 (92)
Intercept$_{(null)}$	–0.54 [–4.87, 3.79]	0.87 [–0.04, 1.78]	**0.52 [0.75, 1.79]**	**1.11 [–0.18, 2.39]**	**–0.69 [–1.34, –0.05]**	**–3.77 [–6.33, –1.20]**	**–1.14 [–2.24, –0.04]**
Intercept$_{(full)}$		**1.77 [0.17, 3.36]**				**–2.05 [–2.89, –1.14]**	**–2.16 [–3.67, –0.66]**
I_PC1						–1.63 [–3.26, –0.001]	**0.88 [0.24, 1.51]**
I_PC2		**1.77 [0.28, 3.25]**					
T_PC1		NA					NA

(Continued)

TABLE 2 | Continued

(B) Upland species	***Acacia pulchella***	***Hibbertia cuneiformis***	***Hovea elliptica***	***Leucopogon obovatus* subsp. *revolutus***	***Leucopogon propinquus***	***Trymalium odoratissimum* subsp. *trifidum***	***Melaleuca incana***
T_PC2		NA					NA
D	NA						
ΔD	NA						
D: ΔD							
F	NA						**1.10 [0.10, 2.10]**
ΔF	NA					–0.36 [–1.45, 0.72]	
Rn						**–5.55 [–7.10, –4.00]**	NA
F: ΔF							
F: Rn							
Rn: ΔF						**–2.98 [–5.25, –0.71]**	
VC for random effects$_{(\text{Transect})}$	12.13	1.567	0.6446	1.865	0.3155	0.0	4.421
VC for Fixed effects		0.78				10.91	0.76
PVC$_{(\text{Transect})}$		–823.9%				100.0%	–49.5%
$R^2_{\text{GLMM(m)}}$		13.9%				76.8%	9.0%
$R^2_{\text{GLMM(c)}}$		41.7%				76.8%	61.2%
AICc$_{(\text{Null})}$	68.9	86.0	127.1	55.4	132.7	144.8	446.8
AICc$_{(\text{Full})}$		83.4				134.9	437.8

the relative frequency of immature *A. flexuosa* individuals under high rainfall increased in floodplain zones that were undergoing declines in flood frequency, but only where sites still experienced a high probability of flooding (**Table 2A** and **Figure 4C**). By contrast, sites experiencing declining flood frequency at the low rainfall extent of the geographic range, particularly where flood frequency had declined to less than 0.1 (i.e., flooded once in the 10 years period), had low relative frequency of immature *A. flexuosa* (**Table 2A** and **Figures 4C,D**).

For *Hakea oleifolia*, the riparian zones that underwent the greatest declines in flood duration had the lowest relative frequency of immature *H. oleifolia*, regardless of rainfall zone or recent duration (**Table 2A** and **Figure 4E**). For *Callistachys lanceolata*, although the best fit models detected differences in the relative frequency of immature individuals with rainfall, flood frequency and change in flood frequency, there were very low frequencies of immature individuals (just 9 of 64 individuals) recorded in total (**Table 2A**), which severely limited the power of the analysis.

Upland Species

Recruitment varied significantly in relation to the examined hydrological or rainfall gradients in just two of the seven upland species, *Trymalium odoratissimum* subsp. *trifidum* and *Melaleuca incana* (**Table 2B**, **Figure 5**, and **Supplementary Material 2**). The relative frequency of immature individuals was higher in frequently flooded regions for both species (**Figures 3**, **5**). In *T. odoratissimum* subsp. *trifidum*, this result was largely driven by the presence of 82 (of a total of 87) immature individuals recorded within a single, low rainfall transect, all of which were present at sites more frequently inundated than observed in the adult population (**Figure 5A**).

DISCUSSION

Recruitment failure at a species range margin can be indicative of a disconnect between the geographic and climatic ranges of a species and an advanced warning of an impending range shift. Utilizing one of the world's most striking, geographically stratified rainfall gradients, that has undergone one of the greatest observed declines in rainfall, we tested the effect of streamflow decline on the riparian plant species in SWWA. We show that the relative frequencies of immature versus mature individuals of a number of riparian species differed significantly with the magnitude of divergence from the historical hydrological regime. At the drier, low rainfall, margins of species geographic ranges, declines in streamflow were a key driver of reduction in the frequency of immature individuals, indicative of recruitment failure and impending range contraction at the geographic range margins. At the higher rainfall margins of species geographic ranges, however, immature abundance increased in response to streamflow declines suggesting that riparian communities are expanding into habitats where historically they may have been excluded by high inundation regimes. In contrast to riparian species, the majority of the upland species examined showed little recruitment response to changing hydrological gradients or regional rainfall gradients. This consistency in recruitment could indicate that the river may be stabilizing recruitment processes across the current distributions of upland species despite regional rainfall declines. Here, we discuss these findings and their implications for ongoing management

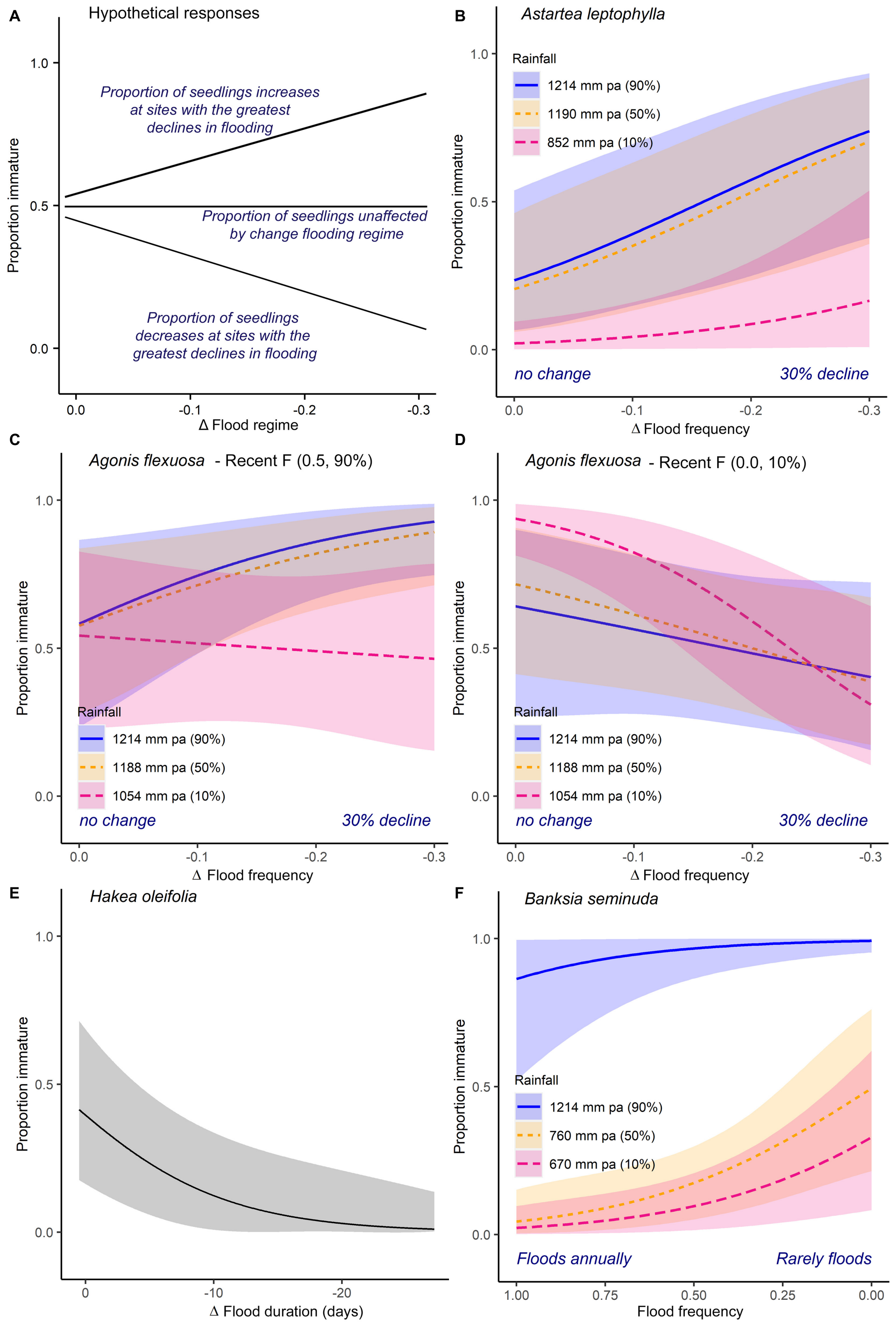

FIGURE 4 | Variation in the relative frequency of immature to mature individuals of riparian tree and shrub species modeled as a function of their hydrological conditions. A positive slope indicates an increasing likelihood of immature individuals being found at sites experiencing a greater decline in flooding; conversely, a negative slope indicates a decreasing likelihood of immature individuals being found at sites experiencing a greater decline in flooding. Hydrological parameters examined include mean annual rainfall (mm pa, percentiles), recent flood frequency (for the period 2001 to 2010), and the change in flood frequency (between two the ten-year periods 1980 to 1989 and 2001 to 2010). Flood frequency is presented as the probability that individuals are likely to be inundated at least once in any one calendar year, where 1 indicates annual flooding and 0 indicates individuals were never flooded. The fitted lines (±95% confidence intervals) represent the 10th, 50th, and the 90th percentiles of model predictions from binomial generalized linear mixed effects models (see methods for details). Note that percentiles for each predictor vary between species because each species is distributed over a distinct rainfall or hydrological range. **(A)** Presents hypothetical responses of a plant species to declining flooding regimes. Models are presented for **(B)** the riparian shrub *Astartea leptophylla*; the canopy tree *Agonis flexuosa* under **(C)** the 90th percentile and **(D)** the 10th percentile of the recent flood frequency; **(E)** the facultative riparian trees, *Hakea oleifolia* and **(F)** *Banksia seminuda*.

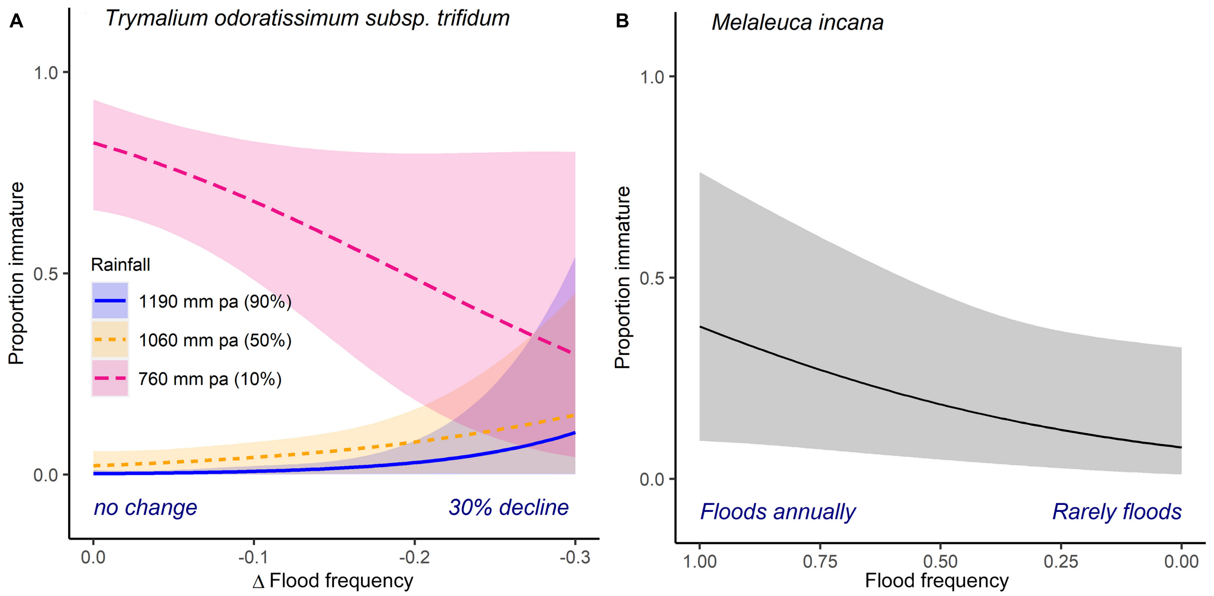

FIGURE 5 | Variation in the relative frequency of immature to mature individuals of upland tree **(A)** *Trymalium odoratissimum* subsp. *trifidum* and shrub **(B)** *Melaleuca incana* modeled as a function their hydrological conditions. Flood frequency and rainfall are as described in **Figure 3**. The fitted line (±95% confidence intervals) represents model predictions from binomial generalized linear mixed effects models.

in a region projected to face further, significant rainfall declines.

Geographic Shifts in Average Environmental Conditions for Riparian Species

The declines in streamflow observed over the past 30 years have resulted in a marked change in recruitment for a number of riparian species in response to declining frequency and duration of inundation. Declines in flood frequency interacted with rainfall for many species. The probability of immature occurrence was lower at the low rainfall extent of a species geographic range in the riparian species *Agonis flexuosa*, *Astartea leptophylla*, and *B. seminuda*. Although statistically insignificant, it is worth noting that in the sampled populations of a further species, riparian obligate *M. rhaphiophylla* and facultative riparian species, *C. lanceolata*, immature plants were observed at estimated relative frequencies of just 9 and 14% respectively. Cumulatively, the results presented here demonstrate lower occurrences of immature individuals at the drier extent of these species geographic ranges, which could precede a contraction in range or selection for a shift in their climatic optima.

The major assumption in examining distributions at a single time point to deduce range mismatch between immature and mature populations, is that differences are indicative of a shift in environmental conditions away from climatic optima rather than the natural divergence between the recruitment niche and the mature niche (Grubb, 1977; Máliš et al., 2016). This phenomena is particularly apparent in riparian systems, where early establishment is highly dependent on surface and shallow soil water until root systems gain access to permanent groundwater sources (Mahoney and Rood, 1998; Stella et al., 2010; Capon et al., 2016). Moreover, mature vegetation has the potential to significantly alter its own flow regime over its lifetime by redirecting currents and altering depositional processes (Corenblit et al., 2007; Osterkamp and Hupp, 2010). Here, by including estimates of recent frequency and duration of inundation as independent parameters from the observed changes over time, our results strongly suggest that it is the change in streamflow rather than (or in addition to) the absolute streamflow driving the range mismatch.

The relationship between occurrence of immatures and streamflow decline suggests species are failing to recruit under current conditions, be it through sexual reproduction or through vegetative reproduction as in the case of *Agonis flexuosa*. While in many riparian systems, a high variability in disturbance and flood regime are known to drive recruitment events, the high predictability and low interannual variance in the flood regime in these river systems has been suggested to drive a stable and continuous recruitment regime (Pettit and Froend, 2001b; Pettit et al., 2001). An examination of the reproductive phenology of the two obligate canopy trees, *M. rhaphiophylla* and *E. rudis*, indicates that phenological coupling has evolved to time seed fall with drying weather and the retreat of the river channel each summer (Pettit and Froend, 2001b). For most of the riparian species in this region, seed is stored in the canopy (**Table 1**) and release is triggered by environmental cues, namely, the desiccation of the seed capsule. In *M. rhaphiophylla*, this results in a continuous low level of seed fall throughout the year, which is similar in *E. rudis* except that *E. rudis* has a peak during the early summer coinciding with the summer decline in stream flow, exposing suitable germination sites (Pettit and Froend, 2001b). *Astartea leptophylla* is the only obligate riparian species which is not reported to store seed for any length of time, it flowers over summer and produces seed quickly (Rye, 2013). The reduction in winter rainfall, and subsequent stream flow in the SWWA has not been even; instead, the greatest change observed has been a reduction in rainfall in autumn and early winter which acts to extend the length of the summer period by delaying the onset of wet winter conditions (Silberstein et al., 2012; Hope et al., 2015). The observed decline in recruitment in the drier extent of species ranges could be due to drying conditions restricting seedling establishment, attributable to the lower rainfall itself, or to the greater intermittency of surface waters at the lower rainfall sites (Stromberg et al., 2005; Stella and Battles, 2010; Stella et al., 2010). In this case, the changing hydrological conditions could be acting differently for different species. For spring seeding species, a longer summer season could reduce survival in the first few summers before the roots have access to the water table, whereas for summer and autumn seeding species there may be a lack of suitable recruitment sites with an extension to the summer dry season. As coarse estimates of hydrology are used here, further investigation is required to fully understand the demography and recruitment requirements of these species, particularly for *A. leptophylla* where seed fall occurs during summer and autumn and does not seem to be triggered by environmental cues. The assumption here is that the change in environment is acting on seedling establishment, but equally a reduction in seed production or viability could also be driving the decline. Longer periods without surface waters could reduce seed production from stressed mature plants (Jensen et al., 2008), or lower reproductive success could also be attributed to poor pollination success from fragmentation, particularly in the upper catchment (Hopley and Byrne, 2018), changes to biotic interactions, or a number of these factors acting synergistically.

Evidence for Narrowing of the Riparian Corridor

In contrast to the reductions observed in immature abundance under lower rainfall conditions, declining flood frequencies under higher rainfall conditions increased the relative frequency of immature to mature individuals in the examined riparian species. Previous examination of size-class distributions on the neighboring Blackwood River found no differences in the distributions of *E. rudis* or *M. rhaphiophylla* seedlings and mature trees in relation to elevation across the floodplain, and determined that these low-power river systems do not experience the destructive forces which can restrict succession on more powerful rivers (Pettit and Froend, 2001b) and can lead to a naturally high abundance of new recruits and saplings on the high flood frequency sites. Increases in riparian seedling abundances, as well as vegetation density and cover, are known to result from flow reduction due to damming or water extraction (Shafroth et al., 2002; Gordon and Meentemeyer, 2006; Kingsford, 2016), particularly within facultative riparian species (Rood et al., 2010). The initial increase in vegetation cover post-damming, is principally attributed to increases in germination sites with declining flood waters, i.e., moist, damp sediments, as well as a reduction in the erosive flows seasonally clearing establishing seedlings (Mahoney and Rood, 1998; Taylor et al., 1999; Johnson, 2000; Polzin and Rood, 2006). The increases in the frequency of immature individuals observed in the areas of greatest deficit, is a strong indicator that the riparian corridor may be beginning to narrow; a repeat survey of selected sites in the future would confirm this.

Stability in the Upland Populations

In five of the seven upland species examined, the distribution of immature and mature individuals did not differ with regard to metrics describing aspects of streamflow or regional rainfall. Notwithstanding the hydrological parameters, rainfall is considered one of, if not the most important, abiotic determinants of species distribution in the region (Hopper and Gioia, 2004). Consistency in the relative frequency of immature to mature individuals across the rainfall gradient indicates stable range margins within the riparian zones. In species where the surveyed area included the eastern-most limits of their distribution, such as the upland shrubs *L. propinquus*, *L. obovatus* subsp. *revolutus,* and *H. elliptica* (Western Australian Herbarium), these results may be indicative of the river buffering species from regional rainfall declines observed to date (Reside et al., 2014; McLaughlin et al., 2017). The ability of the riparian corridors to extend the range of a species outside normal climatic conditions has been demonstrated in SWWA. *Trymalium odoratissimum* subsp. *trifidum* (formerly known as *T. floribundum*; Hancock et al., 1996) is considered an upland species in the Warren Region, in lower rainfall forests to the north of the study region, however the northern subspecies *T. odoratissimum* subsp. *odoratissimum* is restricted to gullies (Hancock et al., 1996). Further examination of the relative frequencies of immature to mature across the non-riparian extent of their ranges is critical to understanding range change in the upland species.

Implications for Climate Change

Over the past 30 years, the riparian vegetation of the Warren Catchment has been subjected to reductions in mean estimated duration of inundation of up to 27 days per year and sites are becoming inundated over fewer winters. The results presented here demonstrate that these declines are affecting recruitment in the common riparian species. At the drier extent of species ranges, declines have resulted in a lower relative frequency of immature to mature individuals, potentially presenting early warnings of a longitudinal range contraction. Meanwhile at the higher rainfall extent of the catchment, increasing frequencies of immature plants on riparian floodplains experiencing declines in inundation frequency indicate the expansion of the riparian vegetation into areas that were previously uninhabitable, and potentially narrowing of the river channel. Downscaled climate models for the SWWA project declines of between 5 and 75 fewer flow-days per year by 2030, on top of the deficits already observed (Barron et al., 2012). Given the apparent shifts in climatic optima already observed here, further flow reductions are likely to significantly impact the riparian vegetation. How these impacts will manifest remains to be seen, but the results presented indicate that a geographical contraction of range of the riparian species is likely. The majority of the riparian species (both facultative and obligate) did not show an upper rainfall limit to their distribution, i.e., all species were observed within the lower reaches of the river, so there is almost no potential for compensatory range expansion.

Despite these observations, we do not anticipate a complete collapse of the riparian flora. First, the projections for summer rainfall are highly uncertain (Hope et al., 2015), but have the potential to drive selection away from the stable continuous recruitment pattern that currently exists to one which may be more episodic and dependent on environmental extremes. Sporadic summer storms could ease drought conditions for the first, critical summer of seeding establishment. As a number of these species exhibit a serotiny with varying degrees of environmental plasticity in seed release, a boom-bust style recruitment pattern could become more important in the future. For example, wide spread flooding resulting from a cyclonic depression in 1978 has been attributed with a mass recruitment event of *E. rudis* and *M. rhaphiophylla* (Pettit et al., 2001; Bureau of Meteorology, 2021). Second, even with significant reductions in river flows, the river is unlikely to cease to flow completely (Barron et al., 2012) thus habitat will continue to be available for riparian species, where soils are too saturated for upland species to survive, albeit over a smaller geographic range. Instead, we might expect to see a compositional shift to a greater proportion of mesic, facultative and upland species as further reductions in the inhibitory high flow events are observed (Froend and Sommer, 2010; Garssen et al., 2014). The results presented here suggest that in this river system, and likely others where rainfall is low in the upper catchment, riparian zones may have a limited capacity to buffer species from climate change induced range shifts. Rather, those species already dependent on the riparian zones as refugia in arid landscapes are actually at greater risk. A complementary study in a system with a contrasting rainfall gradient in which the majority of rain falls in the headwaters would provide a valuable insight into the ability of riparian zones to buffer species range movements under differing precipitation regimes. Understanding which features of the landscape have the potential to provide refugia in a changing climate is critical to advance our ability to predict range shifts and identify important sites for protection.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

HW, JS, and RD conceived and designed the study, contributed to the preparation of the manuscript. HW collected the data. HW and RD analyzed the data. All the authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.605951/full#supplementary-material

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A Test of Species Distribution Model Transferability Across Environmental and Geographic Space for 108 Western North American Tree Species

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Predictions from species distribution models (SDMs) are commonly used in support of environmental decision-making to explore potential impacts of climate change on biodiversity. However, because future climates are likely to differ from current climates, there has been ongoing interest in understanding the ability of SDMs to predict species responses under novel conditions (i.e., model transferability). Here, we explore the spatial and environmental limits to extrapolation in SDMs using forest inventory data from 11 model algorithms for 108 tree species across the western United States. Algorithms performed well in predicting occurrence for plots that occurred in the same geographic region in which they were fitted. However, a substantial portion of models performed worse than random when predicting for geographic regions in which algorithms were not fitted. Our results suggest that for transfers in geographic space, no specific algorithm was better than another as there were no significant differences in predictive performance across algorithms. There were significant differences in predictive performance for algorithms transferred in environmental space with GAM performing best. However, the predictive performance of GAM declined steeply with increasing extrapolation in environmental space relative to other algorithms. The results of this study suggest that SDMs may be limited in their ability to predict species ranges beyond the environmental data used for model fitting. When predicting climate-driven range shifts, extrapolation may also not reflect important biotic and abiotic drivers of species ranges, and thus further misrepresent the realized shift in range. Future studies investigating transferability of process based SDMs or relationships between geodiversity and biodiversity may hold promise.

Keywords: species distribution model, forest inventory, prediction error, species range, extrapolation, transferability

INTRODUCTION

Unprecedented environmental change caused by human activity threatens biodiversity and its associated ecosystem functions and services that humanity relies upon (Chapin et al., 2000; Scheffers et al., 2016). In this era of rapid global change, forecasts of biodiversity changes have the potential to inform conservation decisions to minimize extinctions (Botkin et al., 2007). Species distribution models (SDMs) are one of the most accessible tools for spatial predictions of biodiversity at biogeographic extents and various open-source software packages are available for SDM implementation (Brown, 2014; Thuiller, 2014; Kass et al., 2018). Part of the popularity of correlative SDMs lies in the increasing availability of data needed to fit them (i.e., species occurrence records and satellite remotely sensed environmental data; Turner, 2014; Record and Charney, 2016). In addition, process-based data on species' demography, dispersal, biotic interactions, and other data needed for fitting mechanistic SDMs is often lacking, especially across the entirety of a species range (e.g., for process-based demographic distribution models (Evans et al., 2016; Kindsvater et al., 2018) or range wide models incorporating biotic interactions (Zarnetske et al., 2012; Belmaker et al., 2015). Despite the limitations of SDMs (Pearson and Dawson, 2003; Belmaker et al., 2015), they remain a common and useful tool for predicting potential changes in species distributions and suitable habitat (Record et al., 2018). Understanding the limitations of SDMs is thus necessary to inform their appropriate use.

Studies typically assume that correlative SDMs capture some aspect of a species' niche which can be generalized to other times or locations (Anderson, 2013). This assumption is known as model transferability — the ability of a model to generate precise and accurate predictions for a new set of observations (i.e., in space or time) that were not used in fitting the model (Yates et al., 2018). Transferability of SDMs is typically assessed with three types of 'validation' data (reviewed by Bahn and McGill, 2013; Werkowska et al., 2017; Sequeira et al., 2018; Yates et al., 2018): (1) independently collected data (e.g., Elith et al., 2006), (2) temporally independent data (e.g., Record et al., 2013), and (3) spatially independent data (e.g., Randin et al., 2006).

Studies assessing SDM transferability across taxa and geographic locations have shown inconsistent results — some SDMs transfer well, and others do not (reviewed by Sequeira et al., 2018; Yates et al., 2018). For instance, Duncan et al. (2009) investigated five South African dung beetle species to see if their native ranges could predict their invasive ranges in Australia and found that this approach worked well for two of the species, but not for the other three. Using a similar approach that leveraged native and invasive distribution data, Ibáñez et al. (2009) found that spatially explicit hierarchical Bayesian SDMs parameterized with data from both the native and invasive geographic ranges of three woody plants generated better predictions of the presence/absence of them in their invasive range than models fitted with data only from their native geographic range. This result suggested that the niches of these species may be better captured by incorporating information from the native and invasive geographic ranges of these invasive species. Whereas Duncan et al. (2009) and Ibáñez et al. (2009) illustrate some instances where SDMs transfer in geographic space, other studies illustrate poor transferability of SDMs. For instance, a study of the presence and absence of 54 alpine and subalpine plants on the ability of SDMs to transfer in geographic space between Switzerland and Australia found that overall transferability was poor (Randin et al., 2006). A cross-time study from tropical montane cloud forests showed that extrapolation in environmental space in the present led to poor transferability when predicting the past (Guevara et al., 2018). A study of mammals from North America and Australia found that Maxent models did not transfer well when training and testing data from different geographic regions were dissimilar in their environmental conditions, resulting in collinearity shifts between training and testing environmental predictor variables (Feng et al., 2019). These inconsistent results suggest that there are theoretical and technical knowledge gaps inhibiting effective SDM transferability.

To improve SDM transferability a recent review by 50 experts identified fundamental and technical knowledge gaps that need to be addressed (Yates et al., 2018). One of the fundamental knowledge gaps was determining the limits to extrapolation (spatial and/or temporal) in model transfers. A focus on spatial limits to extrapolation is especially promising because spatially independent data provide the best test of SDM transferability (Bahn and McGill, 2013). Further, independently collected data may introduce noise due to differences in methodology and still does not affirm that the data are spatially independent (Elith et al., 2006). In addition, temporally independent data sets do not guarantee that there is no temporal autocorrelation between data used for model fitting and data used for model validation (Bahn and McGill, 2013).

Assessments of transferability in space often take three approaches:

(i) *Holdout geographic transferability* involves testing models fit in different locations but within the same portion of environmental space (e.g., as measured by a convex hull in environmental space). For instance, one might test transferability within the same geographic region, in which case training and testing plots may be relatively near one another. In such cases, similar mechanisms underlying spatial autocorrelation may persist in both testing and training data, and hence one has more confidence that the same ecological processes are relevant in both the training and testing data (Record et al., 2013; Sillero and Barbosa, 2020).

(ii) *Novel geographic transferability* involves testing transferability to a different geographic region, in which case training and testing plots are considerably more spatially distant. Such tests are useful to remove patterns of spatial autocorrelation between training and testing data, however rather different processes may constrain occurrence patterns in different regions (e.g., different types of disturbance; (Dirnböck et al., 2003; McAlpine et al., 2008) and the potential for extrapolation to different processes is greater.

(iii) *Environmental transferability* requires extrapolation in environmental space, which may be in the same or a different geographic region from the training data. Tests of environmental transferability are useful in evaluating the generality of the fitted response curves (i.e., occurrence-environment relationships) to characterize a species niche but the niche may be considerably truncated in the fitting region (Thuiller et al., 2004). A truncated niche may lead to response curves that are inappropriate for extrapolation (e.g., one side of a unimodal response, when truncated, appears to be monotonic, which will extrapolate poorly; Hannemann et al., 2016).

In addition to determining limits to spatial extrapolation, Yates et al. (2018) also identified a knowledge gap in determining how model complexity influences transferability as an impediment to confidence in transferring SDMs. Model complexity may refer to the number of explanatory variables (i.e., dimensionality; Peterson, 2011), transformations of those explanatory variables (i.e., 'features' with regards to machine learning) and/or the intricacies of the algorithm that characterizes the shape of the occurrence-environment relationships and is tightly linked to the number of parameters in the model (Werkowska et al., 2017; Brun et al., 2020). As with any modeling, in the spirit of generality, simpler SDMs are preferred over complex models (i.e., Occam's Razor; Young et al., 2010).

Merow et al. (2014) reviewed algorithm complexity in SDMs to ask how much intricacy is needed for optimal extrapolation. They found that simpler parametric models (e.g., generalized linear models) may miss thresholds that distinguish presence from absence locations in relation to the environment, whereas more complex non-parametric models (e.g., generalized additive models) may extrapolate poorly when the response curve forms odd shapes at the edge of the observed data range if there are few points there. In a similar vein, they also found that machine learning models that use a flat response beyond the observed data range (i.e., clamping) tend to overestimate an organism's environmental tolerance. How model complexity influences the ability of SDMs to transfer and extrapolate in space remains a fundamental knowledge gap that limits our confidence in SDMs for conservation applications (Yates et al., 2018).

To improve understanding of spatial limits to SDM extrapolation and to quantify how model complexity influences transferability, we assessed three types of transferability—holdout geographic transferability, novel geographic transferability, and environmental transferability—for 11 model algorithms of varying complexity. We used presence/absence data for 108 tree species from the United States Forest Service's Forest Inventory and Analysis (FIA). These data serve as an optimal study system for tests of transferability due to the abundant presence and absence sampling across geographic and environmental space, which allows for explicit testing of factors affecting transferability and therefore results can be more aptly applied to other systems (Sequeira et al., 2018).

We addressed the following questions:

1. How does transferability in geographic space (i.e., holdout geographic transferability vs. novel geographic transferability) depend upon SDM algorithms?
2. What is the relationship between predictive performance of SDMs and amount of extrapolation in novel geographic space?
3. What is the relationship between predictive performance of SDMs and amount of extrapolation in environmental space in a novel geographic region?
4. Does the relationship between predictive performance of SDMs and amount of extrapolation in geographic and environmental space vary with SDM algorithms?

With regards to questions three and four, the intent of this study is to explore how models transfer in space when there are likely differences between the environmental conditions in training and testing regions as parts of our study region are likely to experience no-analog conditions (Williams and Jackson, 2007), thus we provide a stringent test of spatial transferability (Muscarella et al., 2014). We conclude with a discussion of alternative approaches to SDMs for situations when predictive performance declines at the spatial limits to SDM extrapolation, such as process-based models and approaches that focus on understanding distributions of geologically diverse areas rather than distributions of species.

MATERIALS AND METHODS

Occurrence Data

The United States Forest Service's (USFS) FIA National Program provides data on species presence/absence, abundance, and basal area in established plots for all individuals >12.7 cm diameter at breast height. Given that the goal of this study was to use the dense FIA data to understand how common uses of SDMs under the data limitations faced by most studies for which these types of climate envelope models are run (i.e., presence/absence or presence-only), we chose to model presence/absence rather than abundance or basal area. We downloaded all available FIA data within our study region with inventory years from 1950 to 2000 in the western United States (N 25.893–49.000°, W 124.799–97.175°; **Figure 1**), which included 286,551 census plot locations encompassing 254 species. Species were deemed present in a plot if they were observed anytime between 1950 and 2000 and were considered absent if otherwise. We recognize that generally it is not recommended to mix FIA plots for calculations of abundance (e.g., basal area) from different inventories prior to 2001 given that plot sizes varied from region to region depending on forest stand conditions before the United States Forest Service adopted a uniform nationwide sampling strategy (Gillespie, 1999; Bechtold and Peterson, 2005). However, we felt that using the 1950–2000 data was appropriate given that the data used for this study were presence/absence rather than abundance and the goal of this study was to explore SDM transferability for which studies from the literature are often comprised of presence-only observations (e.g., museum specimens) that lack any information

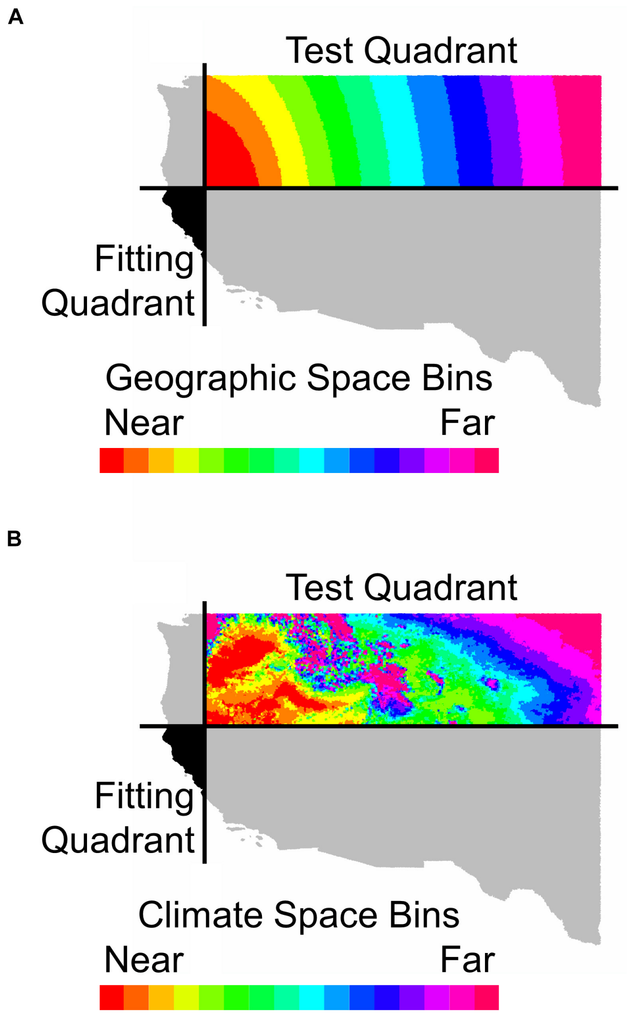

FIGURE 1 | An illustration of how holdout sites were binned by distance **(A)** in geographic space or **(B)** in environmental space from the fitting region for *Calocedrus decurrens.* This map depicts the geographic extent of all FIA data used in the study. The horizontal and vertical black lines in **(A,B)** represent median latitude and longitude, respectively. The black area shows the quadrant used for model fitting and gray shaded quadrants were neither used for model fitting or testing. The colored areas indicate bins in either geographic or environmental space used for model testing with near and far referring to distance in geographic or climatic space.

on the amount of area searched for a given species. Furthermore, using the pre-2001 data in this study enabled us to increase the number of plots in the study region by an order of magnitude (i.e., from tens of thousands to hundreds of thousands of plots) to provide more information on species distributions throughout the western United States.

Exact plot locations of FIA data are not publicly available due to legal concerns regarding privacy of landowners. The USFS 'fuzzed' and 'swapped' the exact plot locations of the data used in this study by masking the locations within a 500-acre area and exchanging plot coordinates for <10% of ecologically similar plots within the same county, respectively. In our analyses, we included only the 108 species with >120 presences (**Supplementary Data Sheet 1**).

Environmental Data

For fitting and predicting the models, we downloaded monthly climate data (i.e., precipitation and temperature) with a resolution of 30 arc seconds from the NASA Earth Exchange Downscaled Climate Predictions (NEX-DCP30[1]) spanning the period from 1950 to 2000, which combines PRISM data from 1981 to 2000 and CMIP5 retrospective model runs to provide a long-term climatic average (Daly et al., 1994; Thrasher et al., 2013). We used the longer-term NEX-DCP30 historic climatic data for fitting models, as opposed to Worldclim historic climate from 1970 to 2000, because longer-term climatic averages provide better predictive power for long-lived species, such as trees (Lembrechts et al., 2019). For each year, we used the monthly data to generate 19 annual bioclimatic variables with the 'biovars' function from the dismo package in R (Hijmans et al., 2020). We averaged across all years from 1950 to 2000 to generate a single set of bioclimatic layers for model fitting and prediction. We did not include non-climatic predictor variables (e.g., elevation, soil, other physiographic variables) because many attempts to predict range size neglect non-climate factors, and this analysis was meant to compare only uses of that simplified approach.

Since some, but not all, of the models we used required uncorrelated predictor variables to meet model assumptions (e.g., GLM), we ran all models once with correlated variables and once excluding the minimum number of bioclimatic predictor variables with correlations $\geq |0.7|$ (Dormann et al., 2013; Feng et al., 2019; Sillero and Barbosa, 2020; **Supplementary Figure 1**). This left nine bioclimatic variables for modeling: mean diurnal range (bio2), isothermality (bio3), maximum temperature of the warmest month (bio5), temperature annual range (bio7), mean temperature of the wettest quarter (bio8), mean temperature of the driest quarter (bio9), precipitation of the driest quarter (bio17), precipitation of the warmest quarter (bio18), and precipitation of the coldest quarter (bio19). Because we subdivided our data into quadrants for each species (**Figures 1, 2**), standardizing predictor variables across all four quadrants would have left each quadrant unstandardized independently, whereas standardizing the quadrants separately would have introduced differences between training and testing data. Therefore, to preserve our capacity to test transferability, we did not standardize predictor variables prior to fitting.

Species Distribution Models

The term SDM covers a variety of types of models with different types of responses (e.g., presence-absence, presence-only, abundance) and predictor variables (e.g., climate, elevation, soil, location, other physiographic information). In this paper we consider SDMs that are often referred to as climate envelope or climatic niche models, wherein we only consider climatic predictor variables and a presence/absence response. We compared the predictive ability of 11 model algorithms contained within the Biomod2 version 3.1 package in R: Generalized

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[1] https://cds.nccs.nasa.gov/nex/

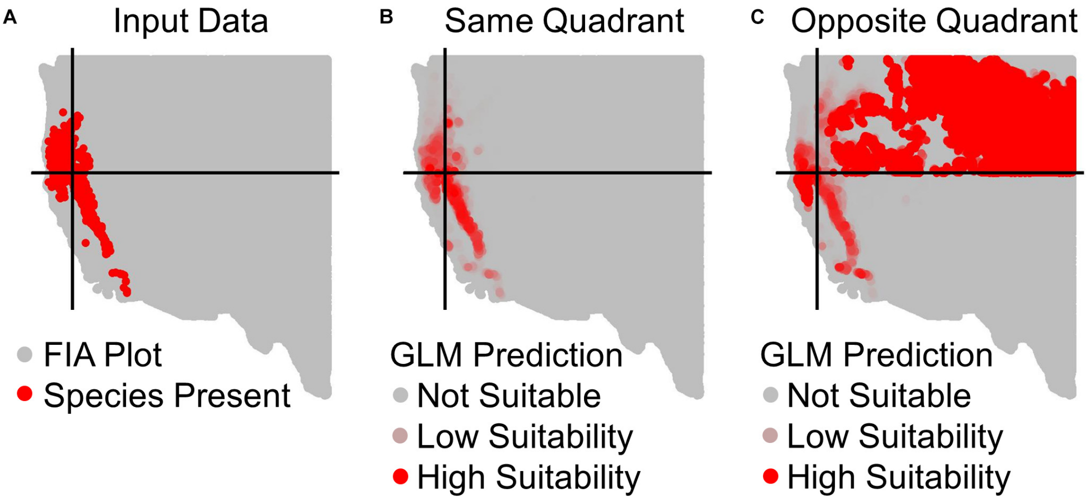

FIGURE 2 | Example prediction maps for *Calocedrus decurrens* using GLM. **(A)** The input FIA plots, where red are presences and gray are absences. Black lines designate the median latitude and longitude of presence plots, dividing the geographic space into our four quadrants specific to this species. **(B)** GLM predictions within the same quadrant as training data, where the intensity of red denotes the continuous output of habitat suitability. **(C)** GLM prediction to the opposite quadrant from the training data. The extreme over-prediction seen here in the northeast quadrant of the novel region predictions was a recurrent pattern typical across all quadrants and algorithms, except for SRE.

Linear Model (GLM), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Classification Tree Analysis (CTA), Artificial Neural Network (ANN), Surface Range Envelop (SRE), Flexible Discriminant Analysis (FDA), Multiple Adaptive Regression Splines (MARS), Random Forest (RF), Maximum Entropy (Maxent), and an ensemble prediction based on these 11 algorithms (Thuiller et al., 2009, 2016). We considered this wide spectrum of algorithms to capture the range of feasible ways in which one might capture occurrence-environment relationships. A review of >200 published papers using biomod2 prior to 2016 showed that common practice by users of this software is to use the default tuning for algorithms (Hao et al., 2019). To maintain consistency with this general practice and given the computational infeasibility of tuning individual settings for the nearly 5000 individual SDMs that we fit in this study, we used biomod2 default tuning choices[2]. Merow et al. (2014) have demonstrated that many of the 11 algorithms we considered can be made to produce very similar response curves to each other by choosing different combinations of settings. Our use of the default settings means that performance comparisons among algorithms in this study can best be interpreted as a comparison of response curves with differing complexity (cf. Merow et al., 2014) rather than an examination of which algorithm is best – since one algorithm may perform as well as another if different settings were chosen.

Evaluation of Model Transferability

Effect of SDM Algorithm Complexity on Geographic Transferability

To address Question 1, we tested each of the 11 model algorithm's ability to predict species' occurrence at points within the same geographic extent as points used for model training (holdout geographic transferability) and to points outside of the geographic extent used for model training (novel geographic transferability) by splitting our entire geographic region into four quadrants based on the median latitude and longitude of presence data for a given species (**Figure 1A**). For each of the four quadrants (northwest, northeast, southeast, southwest), we fit each algorithm using all FIA plots within that quadrant. We then used the algorithm to predict to the FIA plot locations in the opposite quadrant. This quadrant approach is a common method for partitioning data to test SDM transferability across space (Feng et al., 2019), especially to explore the possibility of encountering no-analog environmental conditions (Muscarella et al., 2014). For example, the fit to the northeast was used to predict to the southwest. To assess predictive performance, we measured the area under the receiver operating curve (AUC), sensitivity (1 – false negative rate), specificity (1 – false positive rate), and accuracy (ACC; the fraction of correct prediction i.e., the sum of true positives and true negatives divided by the total number of validation points; Fielding and Bell, 1997). To assess sensitivity and specificity, we first converted continuous model outputs to binary values using a threshold that optimized the sum of sensitivity and specificity (Liu et al., 2005; Lobo et al., 2008). We also used AUC to examine predictions to FIA plots in the same quadrant as the training data, once with the full set of FIA points used for both training and predicting, and once with 70% of the points used for training and 30% for testing.

We used ANOVA to test for significant differences in performance between the 11 algorithms we fitted that represented differing levels of SDM algorithm complexity (Question 1). Three separate ANOVAs with Type II sums of squares were fit to compare between SDM algorithm performance based

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[2] https://doi.org/10.6084/m9.figshare.c.5360402

on AUC, (1) across all plots used to train the models, (2) at testing plots not used to train the models, but within the same geographic extent as the training data, and (3) in a novel geographic extent. Three separate ANOVAs were also fit to assess SDM algorithm differences in ACC, true positive rates, and true negative rates in novel geographic extents. Fitting separate ANOVAs for these measures of predictive performance facilitated the interpretation of Tukey's honestly significant differences (HSD) *post hoc* test. Because of occasional failures of algorithms to converge within biomod2, we ensured a balanced design by only including quadrant × species combinations in which the performance statistics yielded usable values for all models run. Failures to converge represented 1.6% of predictions to novel geographic regions and 9.0% of predictions to the training geographic region.

Limits to Extrapolation in Geographic and Environmental Space

To address Questions 2–4, we also examined the relationship between predictive performance and extrapolation distance outside the 19-dimensional climatic (i.e., environmental) space and outside the 2-dimensional geographic space of the training data. We measured the distance between every test FIA plot in the validation data and the centroid of the training data in the opposite quadrant (**Figure 1**). Distance was measured by first normalizing the distance along each variable axis, then calculating Euclidean distance, and finally dividing by the square root of the number of dimensions (i.e., two for geographic or number of climatic variables for environmental) to obtain a normalized distance in standard-deviation units. Within the testing quadrant, we binned the validation points, so that each bin would have enough points to confidently calculate goodness-of-fit metrics (e.g., AUC, ACC). To explore limits to extrapolation in geographic space, we binned points based on geographic proximity to the training region centroid, with 10,000 points per bin (**Figure 1A**). To explore limits to extrapolation in environmental space, we binned points based on proximity in environmental space to the fitting region centroid with 10,000 points per bin (**Figure 1B**).

We assessed goodness-of-fit of the models with two metrics: AUC and ACC. We note that AUC can be problematic as a predictive metric because it weights omission and commission errors equally (Lobo et al., 2008). AUC is more problematic when generating pseudoabsences with presence-only data, but less so when using presence/absence data as we use in this study. As such, we report both AUC and ACC (Lobo et al., 2008). To assess differences in limits to extrapolation of the SDMs in geographic space by algorithms, we fit two GLMs where the response was either AUC or ACC and algorithm (e.g., GLM, GAM, etc.) entered the GLMs as a fixed factor with geographic distance entered as a covariate. We also included an interaction between geographic distance and model algorithm to determine if algorithms varied at different rates in their ability to extrapolate in geographic distance. To assess limits to extrapolation of the SDMs in environmental space, we fit similar mixed effect models where the covariate was distance in environmental, rather than geographic, space. These GLMs were fit with Type III sums of squares given the inclusion of the interaction term. The data were analyzed with separate GLMs for AUC and ACC for geographic and climatic distance to facilitate the interpretation of Tukey's HSD test. All R code and data used in the analyses along with the ODMAP (Overview, Data, Model, Assessment, and Prediction) protocol documenting the SDMs (Zurrell et al., 2020) are available on Figshare[3].

RESULTS

Question 1 – Overall Transferability Differences Among Algorithms

All results in figures presented in the main text are from the algorithm runs with the full suite of bioclimatic explanatory variables (see **Supplementary Figures 2–8** for results from algorithms run with the subset of nine uncorrelated variables). Performance of all algorithms was qualitatively similar whether all bioclimatic predictors were used to fit the algorithms versus the subset of nine uncorrelated variables, except for GLM which had worse predictions when using only uncorrelated variables. Generally, all algorithms performed best when testing plots were located within the training region (**Figure 2B**) where average AUC values for all algorithms were >0.7 (**Figure 3B**). A substantial portion of predictions into novel regions for all algorithms performed worse than would be expected by random chance (**Figures 2C**, **3C** and **Table 1**). When testing plots within the training region, the ranked AUC for random forest was much better than when predicting to a novel region, suggesting that the algorithms were overfit (**Figure 3**). When testing plots in novel geographic regions, the models with the highest mean AUC and the highest summed sensitivity and specificity were Maxent, GLM, and GAM (**Figure 3**). However, GLM had lower AUC, lower ACC, and higher true negative rates when run with uncorrelated variables (**Supplementary Figures 2, 3**). A common pattern across most algorithms was the tendency for extreme over-prediction in the novel regions, wherein species with narrow true ranges were predicted to occur at most plots (**Figure 2C**). The one exception to this pattern was SRE, which tended to make more conservative occurrence predictions for the novel region compared to the training region (**Figure 4A**). In both the training regions and the novel regions, all algorithms but SRE had false negative rates lower than expected by chance but false positive rates higher than expected (**Figures 4B,C**).

Question 2 – Extrapolation Versus Distance in Geographic Space

Differences in the ability of SDMs to extrapolate in geographic space (i.e., where plots were binned based on geographic proximity to the training region centroid, with 10,000 plots per bin) depended on the metric of predictive performance used. The ability of SDMs to extrapolate in geographic space

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[3] https://doi.org/10.6084/m9.figshare.c.5360402

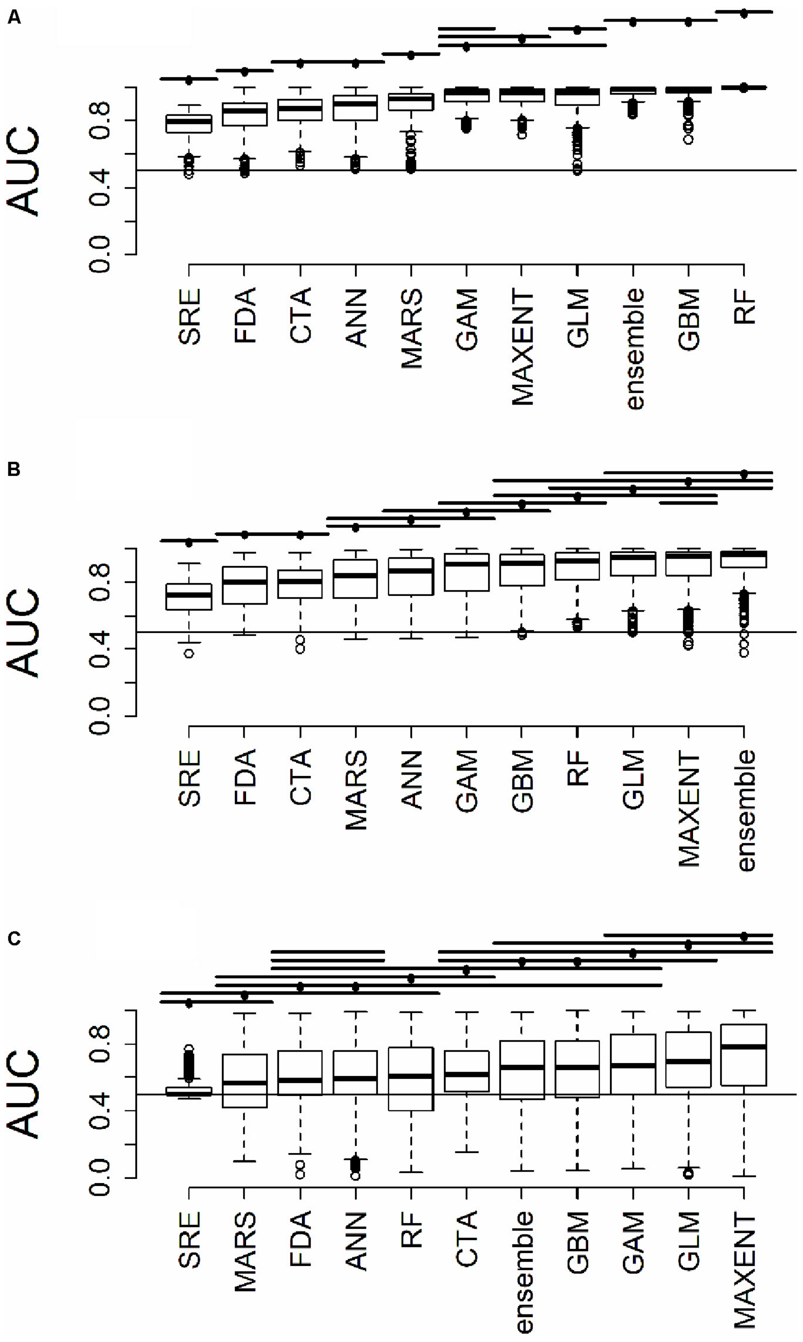

FIGURE 3 | Distribution of AUC for model predictions **(A)** across all plots used to train the algorithms **(B)** at testing plots not used to train the algorithms, but within the same geographic extent as the training data, and **(C)** in a novel geographic extent. Horizontal bars above the boxplots represent significant Tukey *post hoc* groups. Black dots within the Tukey group bars represent the reference algorithm – all algorithms beneath a given bar are not significantly different from the reference algorithm for that bar. Multiple black dots on a given bar indicate that the Tukey groups are identical for multiple algorithms.

declined significantly with increasing distance from the fitting region when predictive performance was assessed with AUC (**Figure 5A**; $F_{1,10847} = 9.25$, $p < 0.005$). However, the rate at which predictive performance declined with geographic distance was not significant when assessed with ACC (**Figure 5C**; $F_{1,10847} = 2.11$, $p > 0.1$).

Question 3 – Extrapolation Versus Distance in Environmental Space

Differences in the ability of SDMs to extrapolate in environmental space were more consistent and significant across metrics of predictive performance used. The ability of SDMs to extrapolate in environmental space declined significantly with increasing

TABLE 1 | Fraction of predictions to novel regions in which species distribution models performed better than random (AUC greater than 0.5).

Algorithm	Fraction
GLM	0.79
CTA	0.72
GBM	0.71
Ensemble	0.69
GAM	0.69
FDA	0.69
Maxent	0.68
RF	0.65
ANN	0.64
MARS	0.59
SRE	0.46

Fractions were calculated from up to 432 possible predictions for each algorithm (4 quadrants × 108 species), however not all species were included for all algorithms due to convergence failures during fitting.

distance from the fitting region when model performance was assessed with both AUC (**Figure 5B**; $F_{1,15563} = 18.84$, $P < 1.4 \times 10^{-5}$) and ACC (**Figure 5D**; $F_{1,15563} = 6.70$, $P < 0.01$).

Question 4 – Differences Among Algorithms in Extrapolation Versus Distance

When SDMs were extrapolated in geographic space, there were no significant differences in predictive performance as measured by AUC between algorithms ($F_{10,10847} = 10.6$, $p = 0.4$) nor was there an interaction between algorithms and distance of extrapolation in geographic space ($F_{10,10847} = 2.63$, $p = 0.99$; **Figure 6**). Similarly, there were no significant differences in predictive performance as measured by ACC between algorithms ($F_{10,10847} = 16.8$, $p = 0.08$) nor was there an interaction between algorithms and distance of extrapolation in geographic space ($F_{10,10847} = 5.45$, $p = 0.86$; **Supplementary Figure 9**).

When SDMs were extrapolated in environmental space, there were significant differences in predictive performance as measured by AUC between algorithms ($F_{10,15563} = 21.2$, $p = 0.02$), but *post hoc* comparisons revealed that these were mainly driven by differences in predictive ability between Maxent and artificial neural network algorithms. There was a significant interaction between algorithms and distance of extrapolation in environmental space ($F_{10,15563} = 27.1$, $p = 2.5 \times 10^{-3}$; **Figure 7**). In particular, the following algorithms' predictive capacities declined steeply with increasing extrapolation in environmental space relative to other algorithms: FDA, GAM, Maxent, and SRE. When ACC was used as the measure of predictive performance for extrapolation in environmental space, there was a significant interaction between algorithm and distance of extrapolation in environmental space ($F_{10,15563} = 22.1$, $p = 0.01$; **Supplementary Figure 10**), but differences between algorithms alone were not significant ($F_{10,15563} = 17.8$, $p = 0.06$). Averaged across all measures of predictive performance (i.e., AUC, ACC, true positive rates, and true negative rates) and across all species for transfers in environmental space, GAM had the best performance whether or not the full set of predictor variables or a reduced set of non-collinear predictor variables were used to fit the models.

DISCUSSION

Species distribution models can be an important tool for conservation by predicting range shifts as a consequence of global change (Elith and Leathwick, 2009; Franklin, 2010). Maps of potential range shifts can be essential for prioritizing reserves across landscapes, however, in some cases, the pressing need for conservation action can outweigh the caution necessary to properly interpret these predictions (Fitzpatrick and Hargrove, 2009; Jimenez-Valverde et al., 2011; Sequeira et al., 2018). As the appearance of no-analog climates is predicted to rise over the next century (Williams and Jackson, 2007), more research is necessary to understand the limitations of SDM transferability in geographic and environmental space. Thus far, transferability of SDMs to new time periods, geographic regions, and determining cross-taxa caveats, have shown inconsistent patterns that could be due to myriad factors (e.g., model algorithms, input data, parameterization). This lack of progress has prompted the call for more rigorous testing to learn about the limitations of extrapolation in geographic and environmental space, and to help establish general guidelines for model transfer (Yates et al., 2018). In this study, we explicitly tested the ability of SDMs of varying complexity to transfer in both geographic and environmental space for data rich tree species in the western United States. Our approach of fitting models in one quadrant of geographic space and predicting them in another quadrant of geographic space is a stringent test that may be akin to projecting occupancy under no-analog conditions that may arise in the western United States with climatic change (Williams and Jackson, 2007). We found that SDMs for this system and geographic region tend not to be transferable in geographic or environmental space. Furthermore, distance in environmental space determined predictive performance of the SDMs more than distance in geographic space or the type of algorithm used.

When interpreting the results of this study, it is important to note that the predictive performance metrics we used are not perfect. We note that, although commonly used for model performance evaluations, AUC, sensitivity, specificity, and ACC can be misleading (Lobo et al., 2008; Pontius and Parmentier, 2014). For instance, AUC is impacted by the "extent to which models are carried out," describes predictive performance across portions of the Receiver Operating Curve (ROC) space which may be biologically infeasible, weights commission and omission errors the same, fails to consider predicted probability outputs and model goodness-of-fit, and ignores the spatial distribution of model errors (Lobo et al., 2008). Future studies might consider other model predictive performance measures, such as graphical assessment of curves representing the Total Operating Characteristic (Pontius and Si, 2014), which provide a richer assessment of the information contained in the ROC. This approach was not taken in this study because it would have necessitated a visual interpretation

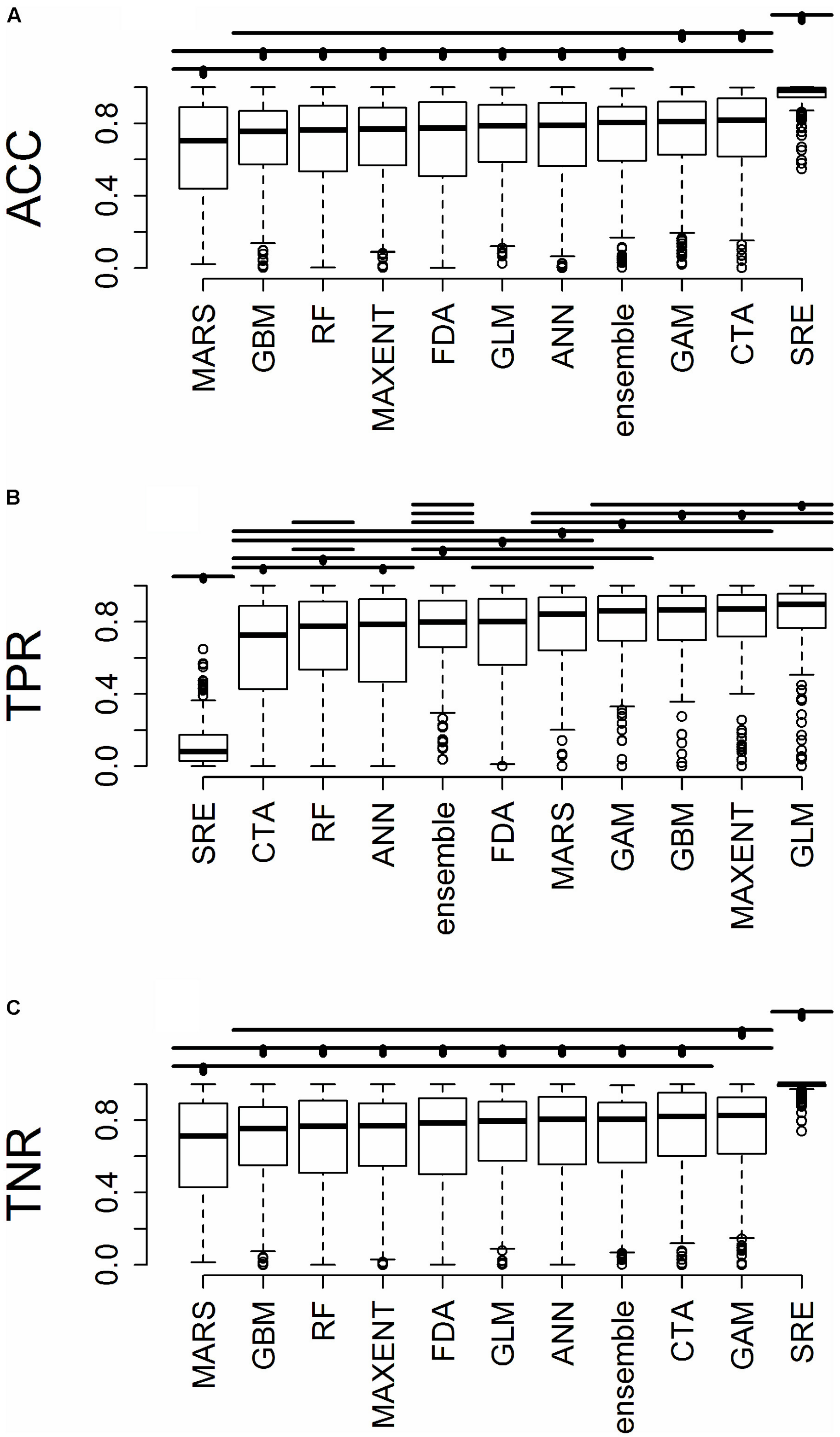

FIGURE 4 | For predictions into novel geographic regions, the distribution of **(A)** accuracy (ACC), **(B)** true positive rate (TPR), and **(C)** true negative rate (TNR). Horizontal bars above the boxplots represent significant Tukey *post hoc* groups. Black dots within the Tukey group bars represent the reference algorithm – all algorithms beneath a given bar are not significantly different from the reference algorithm for that bar. Multiple black dots on a given bar indicate that the Tukey groups are identical for multiple algorithms.

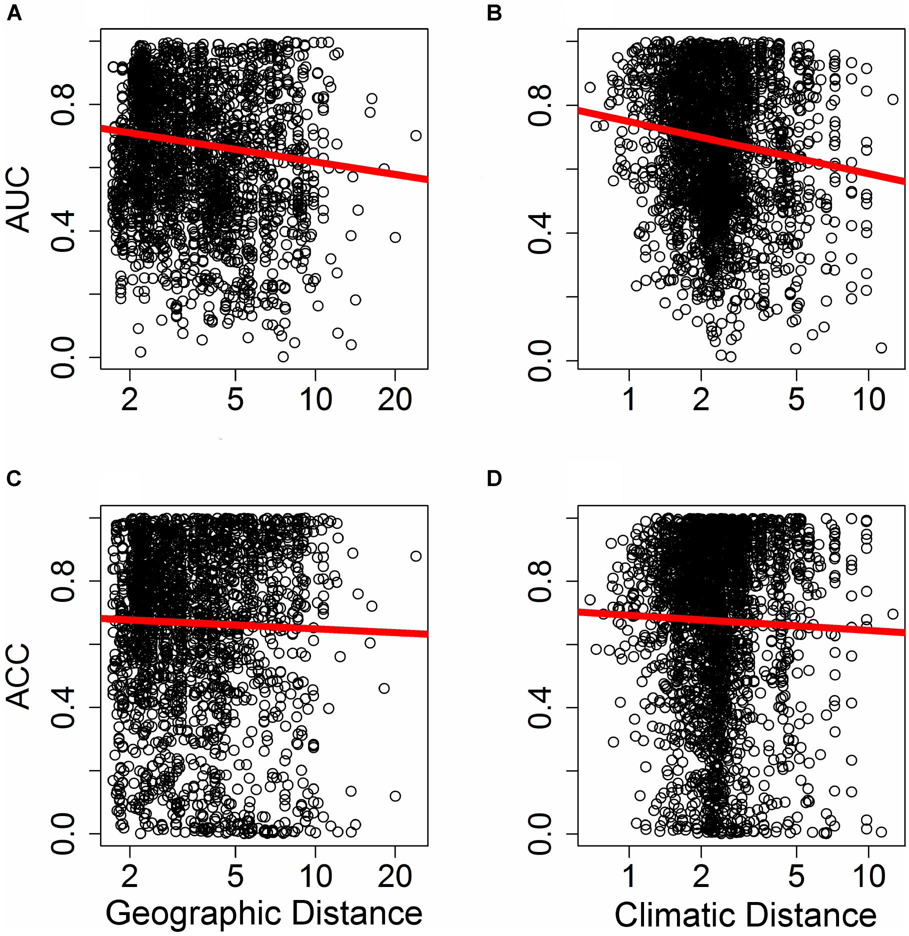

FIGURE 5 | Effect of distance in environmental space on predictive ability of species distribution models (SDM), measured as AUC **(A,B)** or ACC **(C,D)**. Each point represents AUC or ACC calculated within a single bin of up to 10,000 holdout points in a novel geographic region binned by distance through either geographic space **(A,C)** or environmental space **(B,D)** from the fitting region for one quadrant of a given species and a given SDM algorithm. Distance was measured by first normalizing the distance along each variable axis, then calculating Euclidean distance, and finally dividing by the square root of the number of dimensions (i.e., two for geographic space and 19 for climatic space) to obtain a normalized distance in standard-deviation units. The regression line represents a GAM fit to the data.

of thousands of curves (1 model algorithms × 108 species × 2 tests × 4 quadrants = 9504 curves). Future work that automates graphical interpretation or provides summary metrics describing the shape of the TOC curve, without loss of information, would make the use of these more sophisticated metrics possible for studies assessing many species across various model algorithms and tests of transferability.

Furthermore, the interpretation of the results of this study may be strongly dependent upon the field of study and understood purpose of SDMs. Averaged across many species, most algorithms with default tuning settings had median AUC values near 0.7 when applied to novel geographic regions in our study (**Figure 3C**). From a statistical perspective, this indicates that, on average, SDMs are informative. As a tool for developing and testing fundamental theories in ecology and evolution, this may be sufficient. Users at that level are often tuning algorithms beyond the default settings and/or including additional predictor variables (e.g., remotely sensed elevation, soils, other physiographic variables) and may thus achieve much better predictive performance (Guisan et al., 2007; Austin and Van Niel, 2011). However, the ultimate purpose for many SDMs is applied conservation – where many end-users of SDMs may not be aware of available non-climatic spatial data layers (Zarnetske et al., 2019) nor have the training or capacity to tune algorithms beyond the available default settings or to fully appreciate their statistical limitations. When predicting beyond the geographic area used for training, the algorithms in our study performed worse than random about 30% of the time for many of the commonly employed algorithms (**Table 1**). This may be an unacceptably high rate of failure for SDMs to serve as a useful tool for guiding individual species conservation. Determining policy and management decisions based on such unreliable predictions could be dangerously counterproductive. Imagine, for instance, designing reserve boundaries for high-profile endangered species using such models in unsampled regions. For one out of three species, the SDMs are likely to suggest reserve boundaries

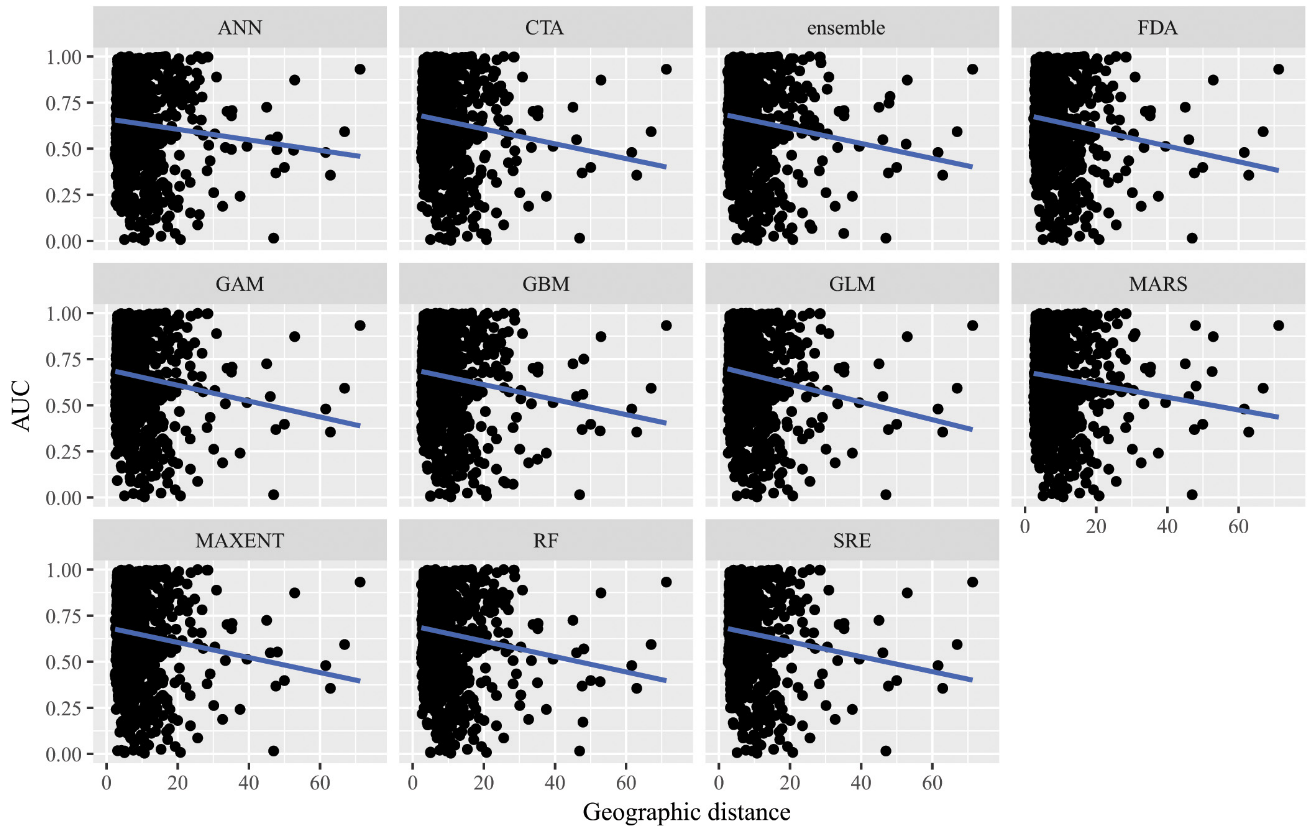

FIGURE 6 | Predictive performance of species distribution models with different algorithms as measured with AUC versus distance of extrapolation in geographic space in a novel geographic region. Distance was measured by first normalizing the distance along each variable axis, then calculating Euclidean distance, and finally dividing by the square root of the number of dimensions (i.e., 2) to obtain a normalized distance in standard-deviation units.

that capture fewer presences than if we were to blindly select arbitrary polygons from across the entire available map. With such odds, a manager may be better served by circling areas on a paper topographic map based on their own natural history understanding of the system.

Question 1 – Overall Transferability Differences Among Algorithms

When predicting species occurrence in novel regions, some algorithms performed better in terms of mean AUC and the highest summed sensitivity (e.g., Maxent, GLM, GAM; **Figure 3**; see also Heikkinen et al., 2012; Wenger and Olden, 2012). Maxent may have performed well in most cases because the default settings of biomod2 use threshold and hinge settings. These settings make a continuous environmental predictor binary by forcing responses to zero below a certain value and to one above that value (Merow et al., 2014). GLM had lower AUC, lower ACC, and higher true negative rates when run with uncorrelated variables (**Supplementary Figures 2, 3**) compared to the full suite of 19 correlated bioclimatic variables (**Figures 3**, **4**). The default settings for biomod2 allow for Akaike Information Criterion (AIC) variable selection within GLM. It is possible that the reduced set of nine bioclimatic variables contained explanatory variables with relatively weak relationships to species occurrence compared to some of the explanatory variables maintained in the full set of 19 bioclimatic variables. Thus, when AIC model selection occurred for the uncorrelated set of variables, there was selection bias where the parameters were poorly estimated for those explanatory variables with weak relationships to the occurrence response, resulting in poor predictive ability (Lukacs et al., 2010).

Questions 2 and 3 – Extrapolation Versus Distance in Geographic and Environmental Space

Decay in model performance with increasing geographic distance from training data depended on predictive performance metric (AUC and ACC in **Figure 5**). In contrast, as climatic distances became more dissimilar to training data, model performance declined significantly regardless of predictive performance metrics (AUC and ACC values in **Figure 5**). These results indicate a decay in predictive ability of algorithms in increasingly environmentally dissimilar regions. Further, the number of false negatives were consistently lower than the number of false positives expected by chance (i.e., higher true negative rate and lower true positive rate; **Figure 4**), showing a trend toward

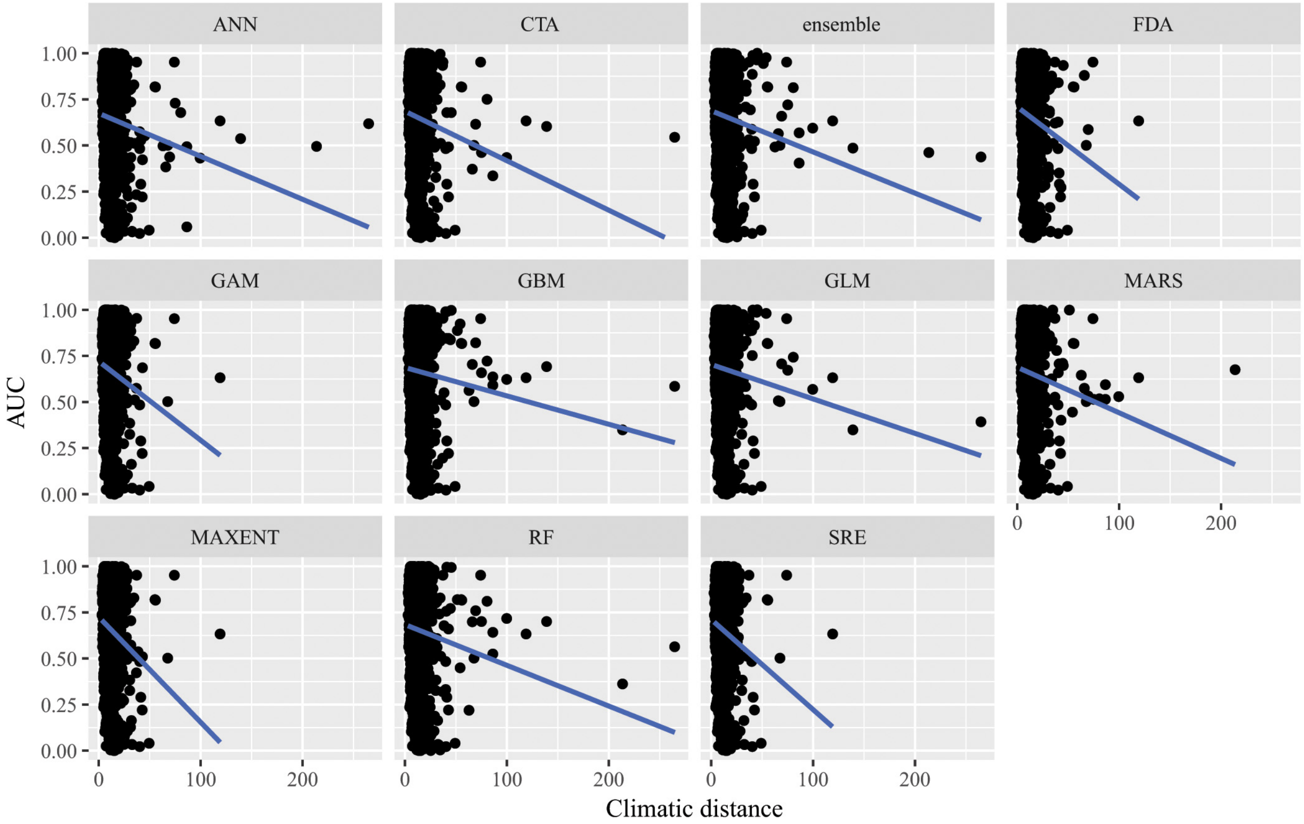

FIGURE 7 | Predictive performance of species distribution models with different algorithms as measured with AUC versus distance of extrapolation in environmental space in a novel geographic region. Distance was measured by first normalizing the distance along each variable axis, then calculating Euclidean distance, and finally dividing by the square root of the number of dimensions (i.e., 19) to obtain a normalized distance in standard-deviation units.

strong overprediction in novel regions, even for narrow ranged species (**Figure 2C**). These findings suggest that algorithms for this system and geographic region tend not to be transferable, particularly in environmental space. However, we also note that the opposite quadrant data partitioning approach used here to test SDM transferability is stringent. Different partitions of the training and testing data (e.g., if the training and testing quadrants had similar longitudinal bounds or using three of the four quadrants for training and one for testing) may have had better predictive performance in tests of transferability, and would be very informative as follow up-studies.

Question 4 – Differences Among Algorithms in Extrapolation Versus Distance

Our results suggest that for transfers in geographic space, no specific algorithm was better than another as there were no significant differences in predictive performance as measured by AUC or ACC across algorithms. However, there were significant differences in predictive performance for algorithms transferred in environmental space. Of the algorithms assessed, GAM performed best in transferring in environmental space, but it is important to note that GAMs' performance declined steeply with increasing extrapolation in environmental space relative to other algorithms.

Beyond model complexity, other potential reasons may explain the poor transferability of the models. For example, species-specific tuning can improve transferability in novel regions and climates (Guevara et al., 2018). Tuning has been shown to generate more realistic SDMs as opposed to using default settings (as used here). However, species-specific tuning of SDMs in training does not necessarily equate to better transferability to novel environments because the observed correlative species occurrence and environment relationship provides no insight into how the species will respond to no-analog conditions (Fitzpatrick and Hargrove, 2009; Heikkinen et al., 2012; Sequeira et al., 2018). In the future, the western United States is likely to experience no-analog climates, especially in regions of California (Williams and Jackson, 2007). Thus, tuning to specific species' current climate envelopes and predicting to future climates would not necessarily help in our study region, as any prediction would lead to strong extrapolation beyond current and paleo climatic conditions and therefore increase uncertainty in model predictions. Another potential explanation for poor transferability is the geographic partitioning of species occurrence records by the median latitude and longitude of points to determine the four testing quadrants. A common method of cross validation, dividing species occurrence records and training algorithms in quadrants results in likely truncation of the species full climate envelope (Muscarella et al., 2014). This can result in incomplete response curves in model training, leading to poor transferability (Thuiller et al., 2004; Owens et al., 2013; Guevara et al., 2018). Different partitions of the training and testing data (e.g., if the training and testing quadrants had similar longitudinal bounds or using three of the four quadrants for training and one for testing) may have led to better predictive performance in tests of transferability. Comparison of paleoclimatic and current climatic records compared to predicted future climatic conditions in our study extent suggest that no-analog climatic conditions are highly probable for this region of North America (Williams and Jackson, 2007), thus, our approach to testing transferability simulates the real-world challenge of predicting to a future using data that may not encompass the full breadth of species' niches.

CONCLUSION AND FUTURE DIRECTIONS

Understanding the limits to extrapolation for SDMs is important for biodiversity assessments (e.g., International Union for Conservation of Nature criteria) since future predictions of species distributions are often considered. The ability of decision makers to spatially plan conservation actions based on SDM predictions across time and space (environmental or geographic) relies on the transparency and documentation of the modeling approaches, including the degree of extrapolation and uncertainty (Sequeira et al., 2018). Assessing and communicating the uncertainty of these predictions to potential stakeholders avoids the misallocation of resources for conservation in regions where predictions are questionable (e.g., areas of strong overprediction; **Figure 2C**). For instance, Houlahan et al. (2017) suggested that when transferring models, there must be a minimum degree of similarity between the environmental conditions of the training and testing region for that prediction to be interpreted with a modicum of confidence. A possible solution to the lack of certainty of these predictions transferred to different times or regions is for modelers to delineate a "forecast horizon," or a threshold which demarcates a point at which predictions are too uncertain and likely no longer useful (Petchey et al., 2015). Though we did not explicitly do this here, this can easily be achieved in future studies by using a measure of performance and defining what is an acceptable level of algorithm performance quality (e.g., AUC, degree of environmental overlap between training and testing regions).

Given the results of this study, there is a strong need for more tests of algorithm transferability across taxa in different regions of the world. By increasing our understanding of limits to transferability within different regions and study systems, guidelines can be established on the appropriate use and interpretation of algorithm transfer. There would also be value to comparing the transferability of SDMs where the response variable is presence/absence or presence only to models where the response variable is non-binary (e.g., abundance, basal area for trees). Simplifying habitat suitability to a binary response may not be biologically realistic when there may be various reasons why a location is predicted to be suitable but the species is absent or why a species is detected but at that location it generally has trouble regenerating.

Though here we mainly discuss correlative SDMs in terms of transferability, mechanistic models, or models that incorporate biological processes that limit and shape species distributions (e.g., dispersal, biotic interactions, population dynamics; Belmaker et al., 2015; Buckley and Catford, 2016; Record and Charney, 2016) hold much promise and can potentially achieve higher transferability (Evans et al., 2016). However, these process-based models require abundant experimental data, are computationally intensive, and the influence of mechanisms added into such models may only operate at particular spatial scales, which has caused progress in this field to be slow thus far (Record et al., 2018; Sequeira et al., 2018) and therefore they too require further study within the context of transferability. There also may be great value to combining occurrence based correlative SDMs with process-based SDMs.

We also note that it is relevant to consider model transferability, even if the goal of conservation is not focused on an individual, often rare, species. In the last decade, some conservation efforts have begun to focus less on where individual species may shift their geographic ranges and more on specific attributes of Earth's surface that promote diversity of a large number of species (Lawler et al., 2015). This latter approach is often referred to as 'conserving nature's stage' wherein the organisms are the actors, and the stage is Earth's environment. The goal is to identify areas with higher habitat diversity that may harbor higher levels of biodiversity. This habitat diversity is termed geodiversity—variation in Earth's abiotic processes and features; (Zarnetske et al., 2019; Record et al., 2020). Schrodt et al. (2019) recently called for the international groups (e.g., the Group on Earth Observations Biodiversity Observation Network [GEOBON]) to consider a framework for identifying essential geodiversity variables (EGV) to complement the essential biodiversity variables (EBV) framework that places a strong emphasis on understanding potential changes in species distributions (Pereira et al., 2013). Ultimately, a focus on geodiversity still requires an understanding of the relationships between biodiversity and geodiversity across space and time (Read et al., 2020), which will also need to consider transferability of models linking geodiversity to biodiversity.

Moving forward, the decision to focus more on process based SDMs or geodiversity of parcels will depend on the regulatory bounds of any conservation organization. For instance, an emphasis on species distributions makes sense for legislation protecting species (e.g., the United States Endangered Species Act), whereas individual organizations purchasing land holdings may want to take the geodiversity and 'conserving nature's stage' approach. Regardless, process-based SDMs and models of geodiversity-biodiversity relationships necessitate the same understanding of how the models will transfer in space and time to conserve nature now and into the future.

DATA AVAILABILITY STATEMENT

looseness1 Publicly available datasets were analyzed in this study (Record et al., 2021). The following .csv and .Rdata files contain Forest Inventory and Analysis and climate data required to reproduce the analysis: REF_SPECIES.csv, all_FIA_locations.csv, all_FIA_presences.csv, and all_locations_data_2.R. The following .R files are R scripts, tested under R/3.1, that contain code to reproduce the analyses in the manuscript: climate_data_code.R, SDM_analyses.R. The Biomod default settings.Rmd file contains information on the default settings of biomod2 used in the analyses.

AUTHOR CONTRIBUTIONS

NDC, SR, and CM conceived the study. NDC and SR performed analyses. SR and BG led the writing. All authors interpreted results and edited drafts.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.689295/full#supplementary-material

Supplementary Figure 1 | Correlations between bioclimatic variables.

Supplementary Figures 2–8 | Results of analyses run with reduced set of nine uncorrelated bioclimatic explanatory variables.

Supplementary Figures 9–10 | ACC versus geographic or climatic distance for analyses run with unreduced set of correlated bioclimatic explanatory variables.

Supplementary Data Sheet 1 | List of 108 tree species fitted with species distribution models. Abbreviations are as follows: count (number of presences within study extent), species symbol (species code comprises the first two letters of generic and specific epithets), genus, species, variety, and subspecies.

Supplementary Data Sheet 2 | Performance of species distribution models in predicting presence or absence of tree species at Forest Inventory and Analysis (FIA) plots. Ten different algorithms ("Algorithm" column) including the ensemble forecast were applied to 108 species ("Species" column). For each species, the landscape was divided into four regions based on the cardinal quadrants (NE, SE, SW, NW in "Quadrant" column) for fitting each algorithm. Model performance was evaluated in either the fitting quadrant ("self" in "TestQuadrant" column) or on the diagonally opposite quadrant ("opp"). Performance metric evaluated here is the area under the receiver operating curve ("AUC" column).

Supplementary Data Sheet 3 | Supplementary Figures.

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Tree Mortality Risks Under Climate Change in Europe: Assessment of Silviculture Practices and Genetic Conservation Networks

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General Context: Climate change can positively or negatively affect abiotic and biotic drivers of tree mortality. Process-based models integrating these climatic effects are only seldom used at species distribution scale.

Objective: The main objective of this study was to investigate the multi-causal mortality risk of five major European forest tree species across their distribution range from an ecophysiological perspective, to quantify the impact of forest management practices on this risk and to identify threats on the genetic conservation network.

Methods: We used the process-based ecophysiological model CASTANEA to simulate the mortality risk of *Fagus sylvatica*, *Quercus petraea*, *Pinus sylvestris*, *Pinus pinaster*, and *Picea abies* under current and future climate conditions, while considering local silviculture practices. The mortality risk was assessed by a composite risk index *(CRIM)* integrating the risks of carbon starvation, hydraulic failure and frost damage. We took into account extreme climatic events with the $CRIM_{max}$, computed as the maximum annual value of the *CRIM*.

Results: The physiological processes' contributions to *CRIM* differed among species: it was mainly driven by hydraulic failure for *P. sylvestris* and *Q. petraea*, by frost damage for *P. abies*, by carbon starvation for *P. pinaster*, and by a combination of hydraulic failure and frost damage for *F. sylvatica*. Under future climate, projections showed an increase of *CRIM* for *P. pinaster* but a decrease for *P. abies*, *Q. petraea*, and *F. sylvatica*, and little variation for *P. sylvestris*. Under the harshest future climatic scenario, forest management decreased the mean *CRIM* of *P. sylvestris*, increased it for *P. abies* and *P. pinaster* and had no major impact for the two broadleaved species. By the year 2100, 38–90% of the European network of gene conservation units are at extinction risk ($CRIM_{max}$=1), depending on the species.

Conclusions: Using a process-based ecophysiological model allowed us to disentangle the multiple drivers of tree mortality under current and future climates. Taking into account the positive effect of increased CO_2 on fertilization and water use efficiency, average mortality risk may increase or decrease in the future depending on

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species and sites. However, under extreme climatic events, our process-based projections are as pessimistic as those obtained using bioclimatic niche models.

Keywords: climate change stresses, tree mortality, ecophysiology, genetic resources, conservation strategy, management practices, process-based model

1. INTRODUCTION

Sustainable forest management ultimately aims to attain a balance between society's increasing demands for forest products and services, and the long-term preservation of forest health and biodiversity. However, ongoing climate and global changes pose major challenges to this balance by affecting forest ecosystem functioning (Hanewinkel et al., 2012; Verkerk et al., 2020), the composition of communities and populations, and consequently the geographic distribution of species (Lindner et al., 2014). Therefore, there is an urgent need to understand the future ecological dynamics of forest ecosystems to guide sustainable management and conservation efforts.

Climate change interacts with other global change factors such as nitrogen deposition, atmospheric CO_2 concentration increase, 0_3 pollution, land use, and forest management. These factors may have antagonistic or partially offsetting effects on the physiological functioning of trees and the ecological dynamics of forests (Walther et al., 2002; Begon et al., 2006; Thuiller et al., 2006; Morin et al., 2008; Lindner et al., 2014; Pretzsch et al., 2014; Anderegg et al., 2015). For example, increasing atmospheric CO_2 concentration can increase water use efficiency on the one hand and photosynthesis on the other hand (see Walker et al., 2021 for a synthesis). Rising temperatures can also increase the length of the growing season (i.e., the period between leaf budburst and leaf fall; Davi et al., 2006b; Keenan et al., 2014) and consequently increase tree growth and forest productivity. However, the combination of rising temperatures and decreasing summer precipitation in some regions has been associated with increasing frequency and duration of droughts. This results in a decreasing tree growth and forest productivity (Zhao and Running, 2010; Reyer et al., 2014; Reyer, 2015), increasing risks of tree mortality (Allen et al., 2010) and increasing risk of disturbances (wildfire, pests; Seidl et al., 2014, 2017). In addition, a single climatic driver can have both positive and negative effects on tree performance; this is exemplified by the role of increasing temperature on the advance of leaf phenology (Bigler and Bugmann, 2018), which is expected to increase vegetation length, but also to expose plants to higher risk of late frosts (Vitasse et al., 2014).

Correlative bioclimatic niche models (BNMs) are popular modeling tools used to predict the future risk of mortality and species distribution ranges (Urban, 2015). A major strength of BNMs is that the data needed to calibrate them (e.g., species-specific presence/absence) are available in large numbers and with increasing resolution in open-access databases (Duputié et al., 2014). However, most BNMs are not mechanistic and are usually not able to take into account the physiological response of trees to new environments (e.g., the combination of increasing CO_2 concentration and increasing temperatures). Furthermore, the spatial variation in soil properties could have complex effects on species favorability, depending on the interaction between the soil-related water capacity, the climate-related water availability, and the species-specific physiological vulnerability to water stress (E Silva et al., 2012). These well-known limitations of correlative BNMs may explain the contradictory projections sometimes generated with different BNMs, as for *Abies alba* along the southern edge of its distribution (Mairota et al., 2013; Tinner et al., 2013).

Ecophysiological process-based models (PBMs) offer the advantage to simulate vegetation functioning in response to explicit climate and soil variability, through their impacts on plant physiology (e.g., Cramer et al., 2001; Dufrêne et al., 2005). Regarding the prediction of future tree species distribution range, comparisons of PBMs vs. BNMs showed that PBMs were generally less pessimistic (Morin and Thuiller, 2009; Cheaib et al., 2012). Ecophysiological PBMs were initially developed to simulate carbon and water fluxes in forest ecosystems, but can also be used to investigate the environmental drivers and physiological processes triggering tree mortality under climate change. For instance, they are particularly suitable to disentangle the physiological processes contributing to mortality in face of drought (McDowell et al., 2008), and the intricate roles of hydraulic failure (the loss of hydraulic conductivity resulting from xylem embolism) and carbon starvation (the depletion of carbon reserve resulting from stomata closure to avoid hydraulic failure). These same models are also able to model the phenology of plants and the dynamics of cold resistance of the organs (Leinonen, 1996).

Forest dynamics models also have a long tradition of being used to support forest management. Recently, both ecophysiological PBMs or forest dynamics models incorporating ecophysiological processes have been applied to evaluate how management and climate change may interact to influence forest dynamics (Oddou-Muratorio et al., 2020). For instance, simulations studies supported that decreasing stand density through thinning can improve the resistance of forests to climate change by decreasing the competition for water amongst the remaining stems, and can be used to inform thinning intensity and frequencies (Guillemot et al., 2014; Cabon et al., 2018). However, the consequences of management practices on forest ecophysiological functioning remain largely unknown. Hence, it is important to investigate if and how current locally prescribed management systems may mitigate the impacts of climate change on the risk of mortality.

Assessing the future physiological functioning and ecological dynamics of forest stands requires not only accounting for the multiple effects of climate change, and for their variation across tree species distribution ranges, but also for the adaptive response of tree populations and the possible effects of forest management on this response. The adaptive potential of tree populations in face of a changing environment is usually assumed to be non negligible: besides tracking their ecological niche spatially through migration, tree populations can adapt in the short-run through individual physiological tolerance, and/or in the long-run through evolutionary response to environment-induced natural selection (Benito Garzón et al., 2011; Oddou-Muratorio and Davi, 2014). Genetic diversity also represents a key resource that can be harnessed by managers for resilience (Fady et al., 2016). Existing networks of dynamic Genetic Conservation Units (GCUs) for forest trees represent a central reservoir of possible future options for adaptation of forests to climate change (**Supplementary Figure 1** for the GCUs distribution by species). In Europe, this network was set up to dynamically conserve forest genetic resources by preserving the ecological and evolutionary processes contributing to the adaptive potential of tree populations to environmental variations (Koskela et al., 2012). The European transnational network of forest tree GCUs contains 3,593 GCUs, representing 4,316 tree populations (http://portal.eufgis.org/). BNM projections indicate that many GCUs may have a high risk of extirpation under climate change, thus weakening the conservation network as a whole (Schueler et al., 2014). These projections indicate that 33–65% of conservation units, mostly located in southern Europe, will be at the limit or outside the current bioclimatic niche of their constituting species by 2,100. The highest average increase in the risk of extirpation throughout the network can be expected for coniferous trees.

The assessment of tree mortality risk under different climate change scenarios at continental scale is needed to support sustainable forest management in Europe in three ways : (i) to identify at continental scales areas of higher risk of mortality and better understand the main drivers of mortality risk in these areas; (ii) to assess the impact of locally prescribed silviculture on tree mortality risk; (iii) and to characterize the level of threat across the *in-situ* gene conservation networks. Here, we focused on the risk of mortality associated with droughts and frosts, two major risks likely to increase in the future (Augspurger, 2013; IPCC, 2014; Charrier et al., 2018). We used the ecophysiological and biophysical PBM CASTANEA (Dufrêne et al., 2005), to simulate the risk of hydraulic failure, carbon starvation, and frost damages of five tree species representative of the main European forest biomes: *Fagus sylvatica* and *Quercus petraea* for temperate deciduous broadleaved forests; *Picea abies* and *Pinus sylvestris* for high-latitude and high-altitude evergreen conifer forests; and *Pinus pinaster*, for low-latitude, evergreen conifer temperate forests (**Supplementary Figure 1**). Using a composite risk index of mortality (*CRIM*), we addressed the following issues: (1) How does the risk of mortality in face of drought and frost vary among species and across species' distribution ranges? We expected *CRIM* differences between species to emerge from their different sensitivity to the target climatic stress, which is modeled in CASTANEA through species-specific parameters. (2) What is the impact of forest management practices on this risk? We expected the potential mitigation effect of thinning on *CRIM* to vary among species and among climatic scenarios. (3) Will GCUs' risk of extinction increase under future climates, and are the projections of our PBM consistent with those based on BNMs? We expected a less pessimistic prediction of mortality risks and a lower number of GCUs with a high risk of extinction.

2. MATERIALS AND METHODS

2.1. CASTANEA Model

CASTANEA is an ecophysiological PBM used to simulate carbon and water fluxes in forest ecosystems (Dufrêne et al., 2005). Briefly, this model simulates the development of an average tree modeled by six functional compartments: canopy, branches, stem, coarse roots, fine roots, and reserves (an unlocated compartment corresponding to the Non-Structural Carbohydrates, NSC). The canopy is divided into five layers of leaves. Photosynthesis is hourly computed for each canopy layer using the model of Farquhar et al. (1980), analytically coupled to the stomatal conductance model proposed by Ball et al. (1987). The effect of temperature on photosynthesis is modeled using a response function of Rubisco-limited photosynthesis (Bernacchi et al., 2001). Maintenance respiration is modeled as proportional to the nitrogen content of the considered organs (Ryan, 1991). Growth respiration is computed from growth increment combined with a construction cost specific to the type of tissue (De Vries et al., 1974). Transpiration is also calculated hourly using the equations of Monteith (1965). The dynamics of Soil Water Content (SWC) is calculated daily using a three-layer bucket model. Soil drought drives stomata closure with a linear decrease when relative SWC is under 40% of field capacity (Sala and Tenhunen, 1996; Granier et al., 2000). In the carbon allocation sub-model (Davi et al., 2005; Cailleret et al., 2017), the allocation coefficients of biomass between the six compartments are daily calculated, depending on the sink force and on the phenology constraints. CASTANEA was originally developed and validated at stand scale for *F. sylvatica*, and then for *Pinus* sp. and *Q. petreae* (Davi et al., 2005, 2006a). The whole parameterization for the five species is detailed in **Supplementary Appendix 1**.

In this study, we focused on five output variables simulated by CASTANEA: (1) the Net Primary Production (NPP) and ring widths to assess the ability of the model to reproduce the bioclimatic niche, (2) the percent loss of conductivity (PLC) as an indicator of risk of hydraulic failure, (3) the NSC content as an indicator of risk of carbon starvation, and (4) the frost damage index (FD).

The CASTANEA version we used allows PLC to be computed based on daily midday water potential and species vulnerability curve to embolism (Petit-Cailleux et al., 2021; **Supplementary Appendix 2**). To simulate budburst, we used the UniChill model (Chuine et al., 1999) in its version described in Gauzere et al. (2017). The UniChill model is a sequential two-phases model describing the cumulative effect of chilling temperatures on bud development during the endodormancy phase (first phase) and the cumulative effect of forcing temperatures during the ecodormancy phase (second phase). We simulated damages due to frosts based on the Leinonen (1996) model. Briefly, this model evaluate the daily frost damage as:

$$FD_{daily} = \frac{1}{1+\exp\left(FS(FH-T_{min}\right)} \tag{1}$$

where FH is the frost hardiness (see **Supplementary Material 2**) and FS the frost sensitivity (fixed here to −2).

Then FD_{daily} is summed over the year.

$$FD_{yearly} = \begin{cases} \sum(FD_{daily}) & if\ \sum(FD_{daily}) < 1 \\ 1 & if\ \sum(FD_{daily}) > 1 \end{cases} \quad (2)$$

It is therefore sufficient for FD_{daily} to reach 1 on a single day to cause maximum annual damage. Note that we considered that trees were able to reflush after late frosts

We simulated stand mortality due to competition by using the relative density index (RDI), derived from the self-thinning rule (Reineke, 1933), as a threshold to limit stand density. RDI is classically defined as the ratio of actual stand density (N) to the maximum stand density attainable in a stand with the same average tree volume (Nmax): RDI = N/Nmax, where Nmax is defined as:

$$Nmax = e^{a+bDg} \quad (3)$$

with Dg the mean quadratic diameter, a the slope and b the intercept of the self thinning equation (Charru, 2012), these specific parameters are given in the **Supplementary Appendix 1**.

When N>Nmax, self-thinning occurs and stand density decreases to Nmax, which directly affects the Leaf Area Index (LAI) of the canopy. Indeed, the stand leaf area index (LAI_{stand}) is simply modeled from stand density (N), the average Leaf Mass per Area (LMA_{mean}), and the allometric relationship between tree size (dbh) and biomass of leaves (B_{leaves}).

$$\begin{cases} ln(B_{Leaves}) = \alpha_1 + \beta_1 * ln(dbh) \\ LA_{tree} = \frac{B_{Leaves}}{LMA_{mean}} \\ LAI_{stand} = \sum_{i=1}^{N} LA_{tree} \end{cases} \quad (4)$$

where the biomass of leaves depends on tree diameter.

Moreover, the reduction of stand density also decreases the biomass of the trunk, branches, reserves, and large roots of the average tree. All these effects (decreasing N, LAI, and biomass) were also applied where stand density is reduced by thinning (see section Management Practices below).

2.2. Climate Data and Scenarios

We considered the European area included within longitudes ranging from −11°W to 40°E and within latitudes ranging from 36°N to 66°N (continental Europe, excluding the arctic circle). CASTANEA requires the following daily climatic input variables: the minimum, mean and maximum temperatures (in °C), precipitation (mm), the wind speed ($m.s^{-1}$), the mean relative humidity (%) and the global radiation ($MJ.m^{-2}$). These data were derived for seven climatic scenarios (three current and four future scenarios) as detailed below (**Supplementary Table 1**, **Supplementary Figure 2**).

2.2.1. Current Climate

We used the Water and Global Change (WATCH)-Forcing-Data-ERA-Interim data set (WATCH in the following) to obtain current climate data at European scale (Weedon et al., 2014). This daily meteorological forcing dataset is available for the period 1979–2008 worldwide, with a spatial resolution of 0.5° per 0.5°. This resolution (the coarsest among the climate and soil data set) was used to divide Europe into 3,411 raster cells.

2.2.2. Future Climates

To take into account the uncertainties on future climatic scenarios (McSweeney et al., 2015), we used a combination of two daily regional circulation models (RCMs) developed under the EURO-CORDEX initiative (Jacob et al., 2014), with the past CO_2 concentration data and two future scenarios of representative concentration pathways (RCPs, Moss et al., 2010). All these daily meteorological model datasets are available from 1961 to 2005 (for current climatic scenario) and from 2005 to 2098 (for future climates scenarios). We selected the EUR-11.SMHI.CNRM-CERFACS-CNRM-CM5 (CM5 in the following) as warm and wet RCM (optimistic) and EUR-11.SMHI.MOHC-HadGEM2-ES (HadGEM in the following) as warm and dry RCM (pessimistic). Regarding future RCPs, the RCP4.5 scenario considers an increase of CO_2 concentration of 650 ppm with a 1.0–2.6°C increase by 2100, and corresponds to the SRES B1 scenario (Nakićenović and Swart, 2000). The RCP8.5 scenario considers an increase of CO_2 concentration of 1,350 ppm CO_2 with a 2.6–4.8°C increase by 2100, and corresponds to the A1F1 SRES scenario (van Vuuren et al., 2011; Harris et al., 2014; IPCC, 2014). To avoid potential biases due to differences between WATCH and EURO-CORDEX datasets, we compared the simulations run on each future EURO-CORDEX scenario to their current EURO-CORDEX reference. The two current climate datasets (CM5_hist and HadGEM_Hist) and the four future climate datasets (CM5_RCP4.5, CM5_RCP8.5, HadGEM_RCP4.5, and HadGEM_RCP8.5) were corrected for bias and downscaled using the R package "meteoland" (De Caceres et al., 2018), and considering the WATCH dataset as reference data.

2.3. Soil Data

To account for the variability of soil water capacity across Europe, we used (1) the European Soil Database to obtain data on the soil depth reached by the roots; (2) the SoilGrids 250 m database to obtain data on bulk density and clay, silt, sand and coarse fragments contents; and (3) the 3D soil hydraulic database to obtain data on soil water content at field capacity and at wilting point (Hiederer, 2013; Hengl et al., 2017; Tóth et al., 2017). All these data were aggregated from 1 × 1 km resolution to 0.5° × 0.5° (WGS84) resolution using the R package "raster" (Hijmans et al., 2015). Then, we extracted the mean value of each parameter at each grid point. A summary table of the values of the climate and soil variables is available in the **Supplementary Table 1**.

2.4. Management Practices

Four silvicultural systems (SS) were modeled on the basis of locally prescribed management practices inventoried in (Härkönen et al., 2019):

- SS1, "No management": no thinning nor regeneration cuts were applied.
- SS2, "Even-aged forest management with shelter-wood": intermediate cuts depend on tree height, stand basal area, and/or age. The last thinning is a shelter-wood cut, removing

the overstory and coinciding with the recruitment of young seedlings (typically 10 years old). The age of the shelter-wood and intermediate cuts are specific of each species and each ecoregion. Trees that do not meet the criteria are not cut.
- SS3, "Even-aged forest management with clear-cut": intermediate cuts depend on tree height, stand basal area, and/or age. After clear-cut, a new stand is planted the following year. Simulation starts when the trees reach breast height, which takes different lengths of time depending on the ecoregion and the species.
- SS4, "Short rotation": there are no thinnings applied, and an integral final cut is done at an early age, followed by planting.

These silvicultural systems were only applied to the main target tree species, and were assumed to be constant over the simulated period. Thinning rules were adapted from Härkönen et al. (2019) and determined the reduction in stand density according to stand age, and eventually to stand height and/or basal area (**Supplementary Table 2**). These thinning rules varied among the five species and the four main ecoregions (North, Central East, Central West, South; **Supplementary Figure 3**). At each grid point, the shares of the four possible silvicultural systems was derived from Cardellini et al. (2018) (**Supplementary Table 3**). For some countries, the share values of silvicultural systems were not available, and computed as the average of the percentage of each silvicultural systems from the closest ecoregion to the country. **Supplementary Figure 4** shows the distribution of silvicultural systems across the simulated area.

2.5. Simulation Design

We first considered three past climatic scenarios (WATCH, CM5_Hist, HadGEM_Hist) and four future climatic scenario (CM5_RCP4.5, CM5_RCP8.5, HadGEM_RCP4.5, HadGEM_RCP8.5), without management. For each species and climatic scenario, we ran one CASTANEA simulation at each of the 3,411 grid points (i.e., inside and outside the current species distribution range). At each grid point, one average, even-aged stand was simulated (hence, one average tree), with fixed soil properties. For all simulations, we considered the same average starting tree, with an initial age of 8 years and a diameter at breast height of 5 cm. All species-specific parameters are available in **Supplementary Appendix 1**. In total, we ran 119,385 CASTANEA simulations (5 species × 7 climates × 3,411 grid points) without management (**Supplementary Table 4**).

Secondly, we considered the management practices locally prescribed for each species. Additional scenarios with silviculture were simulated only at the grid points where at least another silvicultural systems than SS1 was identified (**Supplementary Table 3**). At each of these grid point, up to three additional CASTANEA simulations were run (if SS2, SS3, and SS4 were all locally applied), with the same conditions as above. In total 71,695 additional simulations with silviculture were run (**Supplementary Table 4**).

The entire set of simulated points under WATCH climate was used to evaluate model predictions (see next section). The simulated points within current observed species range were used to investigate the risk of mortality and its variation between climate and silviculture scenario (**Supplementary Figure 1**—shape of species distribution is obtained from http://www.euforgen.org/species/). Note that the length of the simulated period varied among current and future scenarios (30 years for WATCH, 45 years for CM5_hist, and HadGEM_Hist, and 94 years for CM5_RCP4.5, CM5_RCP8.5, HadGEM_RCP4.5, and HadGEM_RCP8.5). Moreover, the silvicultural cycle of SS2 and SS3 most often require one hundred years to be completed. To be able to check the influence of climate change and silviculture on mortality risk and not an age effect, we compare the LAI, DBH, and stand density between WATCH, historical climate, and future climate at 2050 and 2100 years.

2.6. Model Evaluation

CASTANEA has already been evaluated at stand scale for the five species (Davi et al., 2006a; Delpierre et al., 2012). We re-evaluated the model on a series of CO_2 flux measurements at five sites. Three of these datasets were obtained from the FLUXNET2015 (Pastorello et al., 2020), database CZ-BK1 for *P. abies*; FR-LBr for *P. pinaster*; NL-Loo for *P. sylvestris*. The two others came from the ICOS dataset, FR-Hes for *F. sylvatica* and FR-Fon for *Q. petraea*, see **Supplementary Appendix 3** for details.

To evaluate the validity of CASTANEA large-scale simulations, we used a similar approach as Cheaib et al. (2012) using "R" (R Development Core Team, 2013). We investigated the model's ability to predict species range based on thresholds values of NPP and ring widths (rw), below/above which the species is considered as absent/present. The optimal thresholds minimizing the difference between the predicted and observed distribution were selected using an iterative procedure and three statistics used in SDM evaluation: the Area Under the receiver operating Curve (AUC) and the True Skill Statistic (TSS), two classical statistics (Fourcade et al., 2018); and also the Boyces index (BI), another statistic recently proposed and non correlated with classical metrics (Konowalik and Nosol, 2021).

First, AUC represents the rate of true positives (fraction of presences that are actually detected) vs. the rate of false positives (fraction of absences that are incorrectly detected as presence). It is independent from the threshold value used to convert probabilities of presence per pixel into presence-absence data (Elith and Graham, 2009). An AUC-value of 1 means a perfect fit between the predicted and observed distribution; an AUC-value of 0.5 corresponds to random prediction of a species presence and an AUC-value value of 0 means that the prediction is always wrong. To calculate the AUC we used the "PresenceAbsence" package (Freeman, 2012). Second, the TSS compares the number of correct predictions, minus those attributable to random guessing, to that of a hypothetical set of perfect predictions (sensitivity plus specificity −1) and varies between −1 (poor fit) and 1 (perfect fit). TSS normalizes the overall presence-absence by the presence-absence that might have occurred by chance alone and is not influenced by the distribution size. To calculate TSS, we converted the net primary production and ring width simulated into presence-absence data by using a threshold value maximizing sensitivity and specificity as recommended by Liu et al. (2013). Finally, the BI only requires presences and measures how much model predictions differ from random distribution of the observed presences across the prediction gradients (Boyce et al., 2002). It varies between −1 and +1. Positive values indicate that the model's predictions are consistent with the distribution of presences, values close to zero mean that the model is not different from a random model, negative values indicate counter predictions, i.e., poor ability to predict areas where presences are more frequent (Hirzel et al., 2006). We used the "ecospat" package to calculate the BI (Broennimann et al., 2021).

Finally, we also evaluated the effects of CO_2 enrichment under future climate of the main output variables simulated by CASTANEA. To quantify and standardize CO_2 effects across variables and varying ranges of $[CO_2]$ (Walker et al., 2021) proposed a relativized β factor:

$$\beta = \frac{log(\frac{Y_e}{Y_a})}{log(\frac{CO_{2\ e}}{CO_{2\ a}})} \tag{5}$$

where Y_a and Y_e are the values of any response variable at lower CO_2 concentration (CO_2,a) and higher CO_2 concentration (CO_2,e), respectively.

We computed the beta growth primary production (β_{GPP}), β_{WUE}, and β_{BG} simulated by CASTANEA for *F. sylvatica*, using simulations between 1975 and 2005 under the HadGEM_Hist scenario (ambient CO_2) on the one hand, and between 2070 and 2098 under the HadGEM_RCP8.5 scenario (elevated CO_2) on the other hand. Then, we compared these simulated values to the observations compiled in Walker et al. (2021).

2.7. Computation of the Risk of Mortality

Note that we did not directly simulate mortality due to drought and frost damage with CASTANEA because the thresholds in PLC, NSC, and FD triggering mortality are unknown. Instead, to evaluate the risk of mortality, and compare it between scenarios and species, we computed the relative values of three CASTANEA output variables over all the simulated period, as in Petit-Cailleux et al. (2021).

First, the relative percent loss of conductivity (*rPLC*) was computed as a proxy of the risk of mortality due to hydraulic failure:

$$rPLC = \begin{cases} \frac{PLC_{mean}}{PLC_{species\ threshold}} & if\ PLC_{mean} < PLC_{species\ threshold} \\ 1 & if\ PLC_{mean} > PLC_{species\ threshold} \end{cases} \tag{6}$$

where PLC_{mean} is the mean of yearly PLC-values over the simulated period, and $PLC_{species\ threshold}$ is the species-specific PLC-value above which mortality occurs (88% for deciduous and 50% for coniferous species; Brodribb, 2009; Urli et al., 2013). Hence, *rPLC* varied between 0 and 1, and increased with the risk of hydraulic failure.

Because *rPLC* is computed from the mean PLC value over the simulated period, it is expected to buffer the effect of extreme climate events such as intense drought. To overcome this limitation, we also computed $rPLC_{max}$ by considering instead the maximum PLC-value over the simulated period (i.e., replacing PLC_{mean} by PLC_{max} in Equation 3).

Second, the relative non-structural carbohydrate content (*rNSC*) was computed as a proxy of the risk of mortality due to carbon starvation:

$$rNSC = \begin{cases} 1 - \frac{mean(NSC_{frac\ n})}{NSC_{species\ threshold}} & if\ NSC_{mean} < NSC_{species\ threshold} \\ 0 & if\ NSC_{mean} > NSC_{species\ threshold} \end{cases} \tag{7}$$

where $NSC_{frac\ n}$ is the average fraction of NSC biomass over the biomass of all the other compartments at a given year n, and $NSC_{species\ threshold}$ the threshold in NSC-value above which mortality through carbon starvation is unlikely. $NSC_{species\ threshold}$ was arbitrarily set at the CASTANEA initial NSC concentration value ($g_C.g_C{}^{-1}$) that corresponds to the average measured value for each considered species (see references in **Supplementary Appendix 1**). Hence *rNSC* varied from 0 to 1, increasing values indicating an increasing risk of carbon starvation.

We also computed $rNSC_{max}$ considering instead the minimum NSC-value over the simulated period (i.e., replacing NSC_{mean} by NSC_{min} in Equation 4). Taking the average measured NSC value as a threshold value below which starvation risk occurs may seem too severe, but in reality, when carbon starvation occurs, the NSC drop quickly and we verified that the choice of the threshold had little impact.

Thirdly, the level of frost damage *(rFD)* was computed as a proxy of the risk of mortality due to frosts. The FD_{yearly} index described in equation (2) is already relative and varies from 0 to 1, increasing values indicating an increasing risk of frost damage. *rFD* was thus computed as the mean of FD_{yearly} values over the simulation period, and rFD_{max} as the maximal FD value over the simulation period.

Note that for scenarios with silviculture, there were possibly up to four simulations, and hence four values of PLC, NSC, or FD at a given grid point. In these cases, we computed a ratio taking into account the share of each silvicultural systems *j* at each grid point *i*:

$$Ratio_{ij} = \frac{share_{ij}}{(\sum_{j=1}^{N} share_{ij})} \tag{8}$$

where $share_{ij}$ is the share of each silvicultural system *j* at grid point *i*, and *N* is the number of different silvicultural systems at point *i*. The different *PLC*, *NSC*, or *FD* values for each silvicultural system *j* were weighed by $Ratio_{ij}$.

Finally, we computed a composite risk index of mortality *(CRIM)* combining rPLC, *rFD*, and *rNSC* with an identical weight. Annual *CRIM* values were computed as:

$$CRIM_n = rFD_n + (1 - rFD_n) * rPLC_n + (1 - rFD_n) \\ *(1 - rPLC_n) * rNSC_n \tag{9}$$

The mean *CRIM* value was then averaged across the simulated period. *CRIM* can vary between 0 (minimal risk of mortality) and 1 (maximal risk of mortality) and $CRIM_n$=1 as soon as either rFD_{max}, *rPLC* or rNSC = 1. A similar $CRIM_{max}$ value was calculated by combining $rPLC_{max}$, $CRIM_{max}$, and rFD_{max}.

TABLE 1 | Model evaluation based on the prediction of species distribution.

Species	Variable	TSS	AUC	BI	Threshold
F. sylvatica	rw (mm)	0.62	0.86	0.94	2.64
	NPP (gC.m^{-2})	0.63	0.86	0.97	449.35
Q. petraea	rw (mm)	0.69	0.92	1	3.70
	NPP (gC.m^{-2})	0.72	0.93	1	692.66
P. pinaster	rw (mm)	0.18	0.60	0.64	0.87
	NPP (gC.m^{-2})	0.32	0.64	0.81	334.61
P. abies	rw (mm)	0.12	0.56	-0.08	0.23
	NPP (gC.m^{-2})	0.15	0.55	-0.03	153.67
P. sylvestris	rw (mm)	0.06	0.60	-0.76	0.79
	NPP (gC.m^{-2})	0.07	0.62	-0.31	287.08

Both the Net Primary Production (NPP) and ring width (rw) simulated by CASTANEA were used to predict species distribution, based on a threshold value above/below which the species was predicted as present/absent. To select this threshold value and evaluate the quality of the prediction we used three statistics (AUC, TSS, and BI, see text for details).

3. RESULTS

3.1. Model Evaluation

We obtained a high, positive correlation of GPP, the net ecosystem exchange and ecosystem respiration between measures and simulations for broadleaved species and *P. sylvestris* ($r \geq 0.74$; **Supplementary Appendix 3.2**). For *P. abies* and *P. pinaster*, the correlation between measures and observations was high for GPP and the ecosystem respiration, but low for net ecosystem exchange.

We determined a species-specific threshold for ring widths and NPP-values maximizing the agreement between observed and predicted distributions for the TSS calculation. The current distribution ranges of broadleaved species were predicted with high TSS-values, high AUC-values and high BI-values; for *F. sylvatica* (TSS $\geq$ 0.62, AUC $\geq$ 0.86, and BI $\geq$ 0.94); and for *Q. petraea* (TSS $\geq$ 0.69, AUC $\geq$ 0.92, and BI = 1; **Table 1**). By contrast, the distribution ranges of coniferous species were poorly predicted: for *P. abies* TSS $\leq$ 0.15, AUC $\leq$ 0.56, and BI $\leq$ -0.03; and for *P. sylvestris* TSS $\leq$ 0.07, AUC $\leq$ 0.61 and with a negative correlation according to BI $\leq$ -0.31. For *P. pinaster*, the evaluation is contrasted between indices, with a poor TSS $\leq$ 0.32 and AUC $\leq$ 0.64, but a rather good prediction according to BI $\geq$ 0.64.

CASTANEA simulated a strong positive effect of increased CO_2 on Gross Primary Production (GPP), Water Use Efficiency (WUE), and biomass growth (BG). for *F. sylvatica* between HadGEM_Hist and HadGEM_RCP8.5 scenario. Simulated β_{GPP} was 0.71; β_{WUE} was 0.64 and β_{BG} reached 0.91.

3.2. Variations of the Risk of Mortality Over Species Realized Range Under Current Climate

Under the WATCH climatic scenario, the mean *CRIM* simulated from 1979 to 2008 was 0.13 for *F. sylvatica*, 0.25 for *Q. petraea*, 0.25 for *P. pinaster*, 0.28 for *P. abies*, and 0.34 for *P. sylvestris*, within their respective realized niche (**Figure 1**, **Supplementary Table 5**). For broadleaved species, the highest *CRIM*-values occurred in the eastern Mediterranean region, in mountainous areas and in the eastern part of their distribution. For *P. abies* and *P. sylvestris*, the highest *CRIM*-values occurred in the northern and eastern parts of their distribution. For *P. pinaster*, the highest *CRIM*-values occurred in the southern part of its distribution. When considering $CRIM_{max}$ to better account for the effect of extreme climatic events on the risk of mortality, mean $CRIM_{max}$ values were much higher for all species: 0.69 for *P. pinaster*, 0.48 for *F. sylvatica*, 0.83 for *P. abies*, 0.72 for *Q. petraea*, and 0.84 for *P. sylvestris* (**Figure 2**, **Supplementary Table 5**). The spatial variations of $CRIM_{max}$-values were similar to that of *CRIM*-values, except that high $CRIM_{max}$ values were also observed at the southern part of *P. abies* and *P. sylvestris* distributions (**Figure 2**).

The processes contributing to the risk index of mortality varied among species and spatially (**Figures 1**, **2**, **Supplementary Table 5**). For *Q. petraea* and *P. sylvestris*, *CRIM* was mostly driven by the risk of hydraulic failure ($rPLC = 0.18$ for both species), and $CRIM_{max}$ by both the risk of hydraulic failure ($rPLC_{max} = 0.6$ and 0.63, respectively) and frost damage ($rFD_{max} = 0.52$ and 0.57, respectively). The highest rPLC-values occurred in the Mediterranean region and in Eastern Europe for these two species (**Figures 1**, **2**). For *P. abies*, the risk of frost damage drove both the *CRIM*-value ($rFD = 0.19$) and the $CRIM_{max}$-value ($rFD_{max} = 0.76$). The highest *rFD*-values occurred in Northern and Eastern Europe for this species. For *P. pinaster*, the risk of carbon starvation drove the *CRIM*-value ($rNSC = 0.13$), while the three risks contributed equally to $CRIM_{max}$. For this species, the highest rNSC-values occurred along the coastline. Finally for *F. sylvatica*, *CRIM* was driven both the risk of hydraulic failure (rPLC = 0.07) and late frost ($rFD = 0.05$), while the three risks contributed equally to $CRIM_{max}$ ($CRIM_{max} = 0.21$, $rPLC_{max} = 0.23$, and $rFD_{max} = 0.30$). For a given risk, the highest values did not occur in the same place for different species. For instance, for broadleaved species, the highest *rFD*-values mainly occurred at high altitudes (Meseta, Alps, Carpathian mountains), while for the coniferous species, the highest high *rFD*-values occurred in northern Europe. For a given species, the contributions of the physiological processes to the risk of mortality varied across its range. For instance considering $CRIM_{max}$ and *Q. petraea*, in the eastern continental part of the range all three risks were high, in the Alps the risk of frost was predominant, in Northern Europe (Finland) the risks of hydraulic failure and frost damage were the highest, while in the Southern part of the range (Iberian peninsula) the risk of carbon starvation was predominant.

3.3. Evolution of the Risk of Mortality Between Current and Future Climates

The variation of the risk of mortality (estimated by *CRIM* and $CRIM_{max}$) between current (CM5hist and HadGEM_hist) and future (CM5_RCP4.5, CM5_RCP8.5,HadGEM_RCP4.5, HadGEM_RCP8.5) climatic scenarios differed between species (**Figures 3**, **4**, **Supplementary Figure 5**). In average over all pairwise comparisons, the risk of mortality increased for *P.*

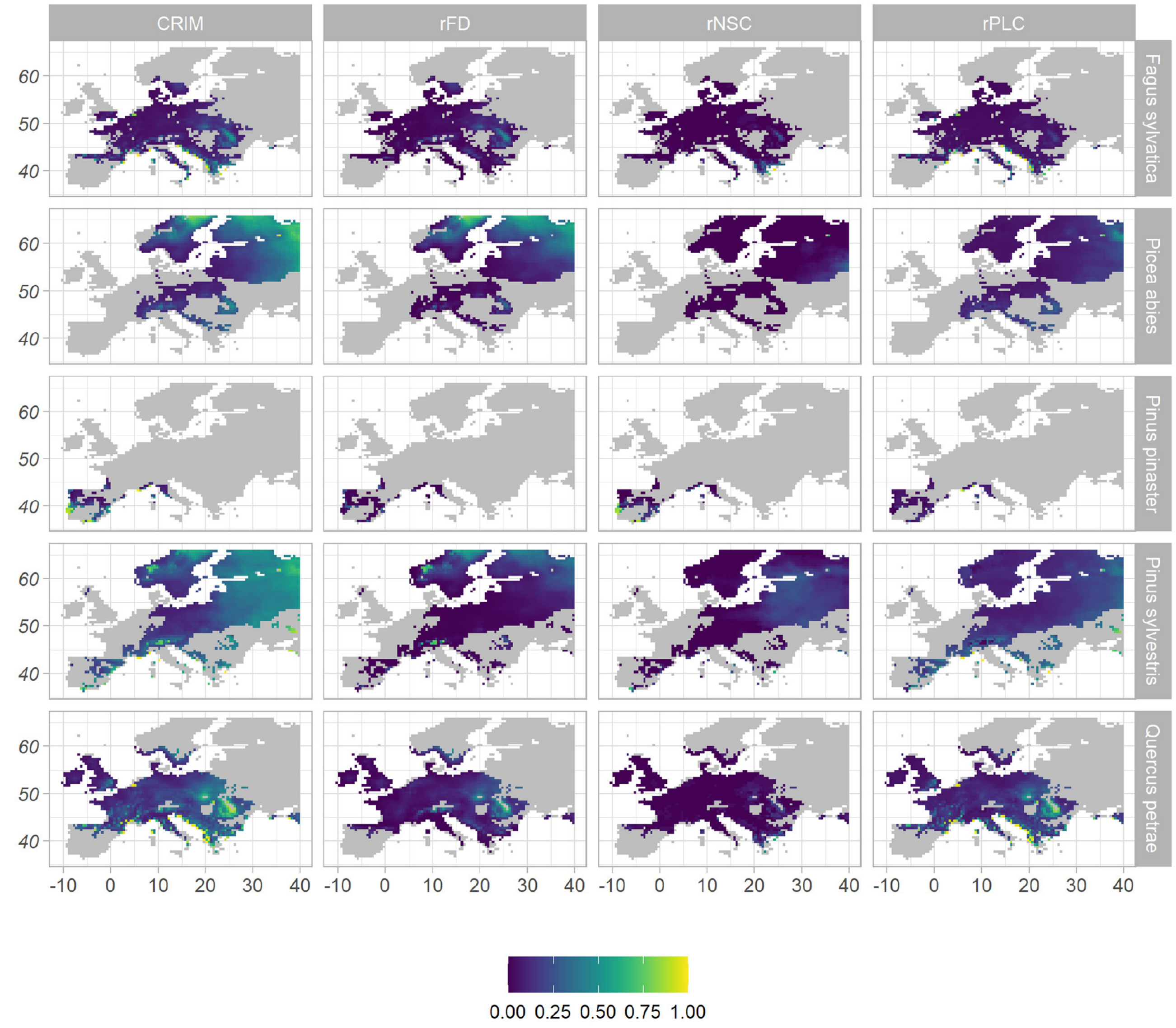

FIGURE 1 | Spatial distribution of mean values of mortality risk indices under WATCH current climate, across species' distribution range. The composite risk index of mortality (*CRIM*), given in the first column, is the combination of the three indices displayed on the other columns: the frost damage index *(rFD)* as a proxy of the risk of mortality due to frost; the relative non-structural carbohydrate content *(rNSC)* as a proxy of the risk of carbon starvation; the relative percent loss of conductivity *(rPLC)* as a proxy of the risk of hydraulic failure. All indices vary from 0 (purple, low risk) to 1 (yellow, high risk).

pinaster (mean Δ $CRIM = 0.10$; mean Δ $CRIM_{max} = 0.17$), and this was mainly due to increasing risks of frost damage (mean Δ $rFD = 0.04$; mean Δ $rFD_{max} = 0.40$) and carbon starvation (mean Δ $rNSC = 0.04$; mean Δ $CRIM_{max} = 0.08$). By contrast, the risk of mortality markedly decreased in the future for *F. sylvatica* (mean Δ $CRIM = -0.13$; mean Δ $CRIM_{max} = -0.17$), *Q. petraea* (mean Δ $CRIM = -0.21$; mean Δ $CRIM_{max} = -0.07$), and *P. abies* (mean Δ $CRIM = -0.17$; mean Δ $CRIM_{max} = -0.01$). This decrease was due to decreasing risks of frost damage (e.g., for *Q. petraea*; mean Δ $rFD =$ mean; Δ $rFD_{max} = -0.06$) and hydraulic failure (e.g., for *Q. petraea*, mean Δ $rPLC =$ mean Δ $\mathrm{rPLCD}_{max} = -0.08$). Finally, the variation of the risk of mortality was negligible for *P. sylvestris* (mean Δ $CRIM = 0.01$; mean Δ $CRIM_{max} = 0.2$). Note however that the risk of carbon starvation due to extreme climatic events increased for all species (from Δ $rNSC_{max} = 0.07$ for *Q. petraea* to Δ $rNSC_{max} = 0.35$ for *P. abies*). Spatial variations in Δ *CRIM* and Δ $CRIM_{max}$ are shown on **Supplementary Figure 14**.

The maximum value of $CRIM_{max} = 1$ was reached in many locations particularly for all conifers (**Figures 2**, **4**). The risk of mortality estimated with both *CRIM* and $CRIM_{max}$ tended to be lower for the "optimistic" CM5 RCM compared to the "pessimistic" HadGEM RCM for the coniferous species. For all species except *P. abies*, the *CRIM*-values were similar for the

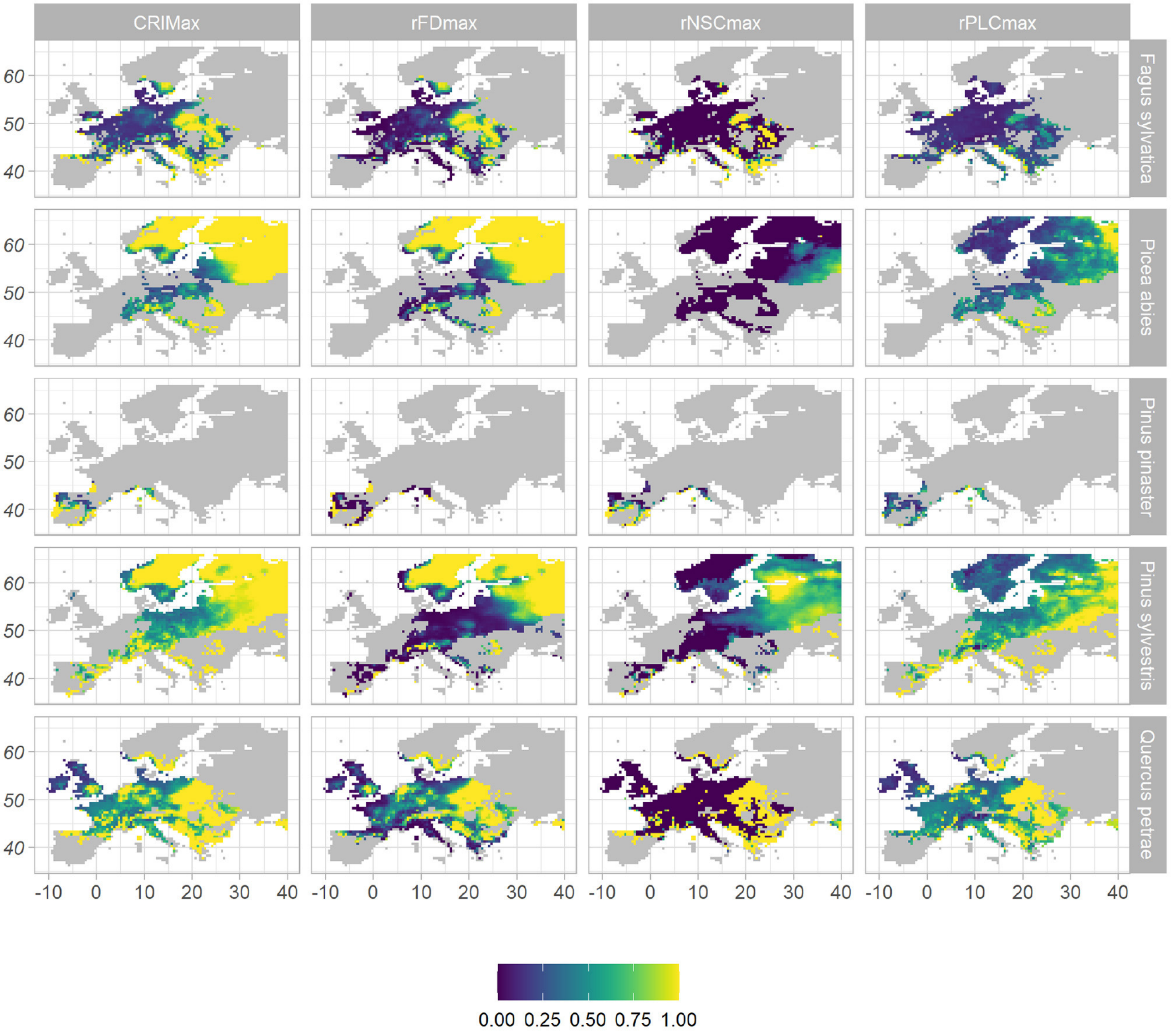

FIGURE 2 | Spatial distribution of maximum values of mortality risk indices under WATCH current climate, across species' distribution range. The risk index of mortality ($CRIM_{max}$), given in the first column, is the combination of the three indices displayed on the other columns: the frost damage index (rFD_{max}) as a proxy of the risk of mortality due to frost; the relative non-structural carbohydrate content ($rNSC_{max}$) as a proxy of the risk of carbon starvation; the relative percent loss of conductivity ($rPLC_{max}$) as a proxy of the risk of hydraulic failure. All indices vary from 0 (purple, low risk) to 1 (yellow, high risk).

RCP 4.5 and RCP 8.5 scenarios whereas, for all species, $CRIM_{max}$ tended to be higher for the RCP 8.5 scenarios (**Figure 4**).

To verify whether the observed changes in risks between present and future climatic scenarios could be due to the shorter simulation period for the present climatic scenario (45 years) than for the future (94 years), we also analyzed the mortality risk under future climate at the 2050 date (i.e., over a 45-year period): for each climate change scenario, the risks predicted at this intermediate date did not differ in any major way from those based on the entire simulation period (**Supplementary Table 5**, **Supplementary Figures 6–9**). Mean DBH slightly increased and tree density slightly decreased in 2050, and these changes were much more pronounced in 2100 for broadleaved species only (**Supplementary Figures 10**, **11**).

3.4. Effect of Silviculture on the Risk of Mortality

In average, silviculture had contrasting effects on the risk of mortality under current climate depending on the species (**Figure 5**, **Supplementary Table 5**). Under HadGEM current climate, *CRIM* and $CRIM_{max}$ decreased by 0.02 and 0.01, respectively for *P. sylvestris* between scenario SS1 (no sylviculture) and scenarios mixing SS1–SS4 (with silviculture).

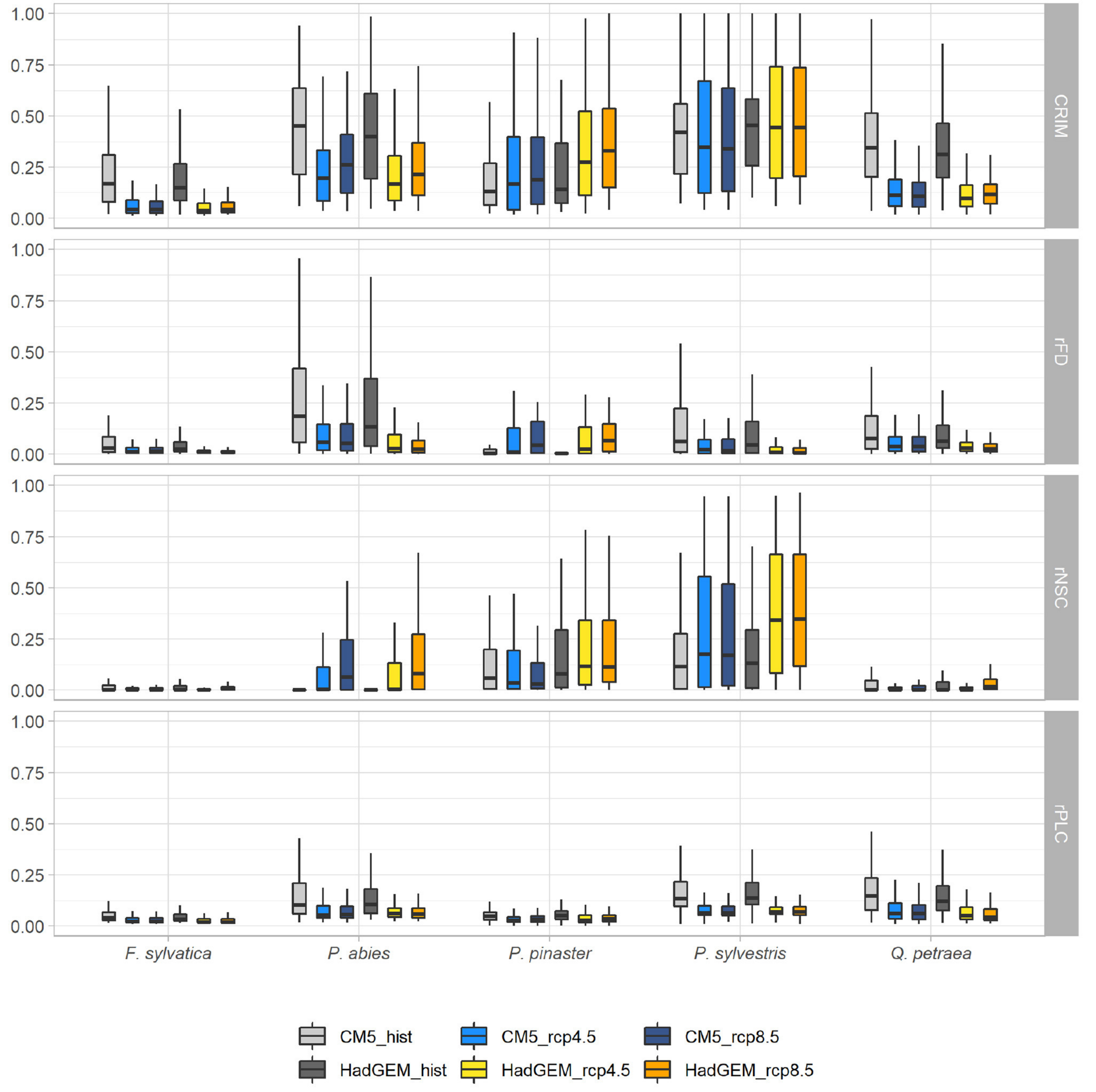

FIGURE 3 | Variation of the mean values of mortality risk indices (*CRIM*, rFD_{max}, *rNSC*, and *rPLC*) under two current and four future climatic scenarios. Each whisker box represents the distribution of risk indices values across the simulated range (with the median as the horizontal line, the interquartile range as the box, and the minimal and maximal values at the ends of the vertical lines). Each future climatic scenario (in blue for the CM5 RCM and in orange for the HadGEM RCM) can be compared to their historical reference (in light and dark gray for the CM5 and HadGEM RCMs, respectively). Simulations were run without management (SS1).

This decrease was driven by a decreased risk of carbon starvation (Δ *rNSC* = −0.12; Δ $rNSC_{max}$= −0.13), despite an increased risk of hydraulic failure. However, *CRIM* and $CRIM_{max}$ increased by 0.05 and 0.04, respectively for *P. abies*. Silviculture had no effect on the risk of mortality for *P. pinaster*, *F. sylvatica*, and *Q. petraea* (**Figure 5**, **Supplementary Table 5**). Under current climatic conditions, the local impacts of management practices on the different risks were globally uniform and low all over species' range, except for *P. sylvestris* in which case silviculture tends to reduce the risk of carbon starvation in the north-eastern part of the range, i.e., precisely where this risk is higher (**Supplementary Figure 12**).

Applying today's silviculture rules under future climatic scenario resulted in increasing *CRIM*-values as compared to the

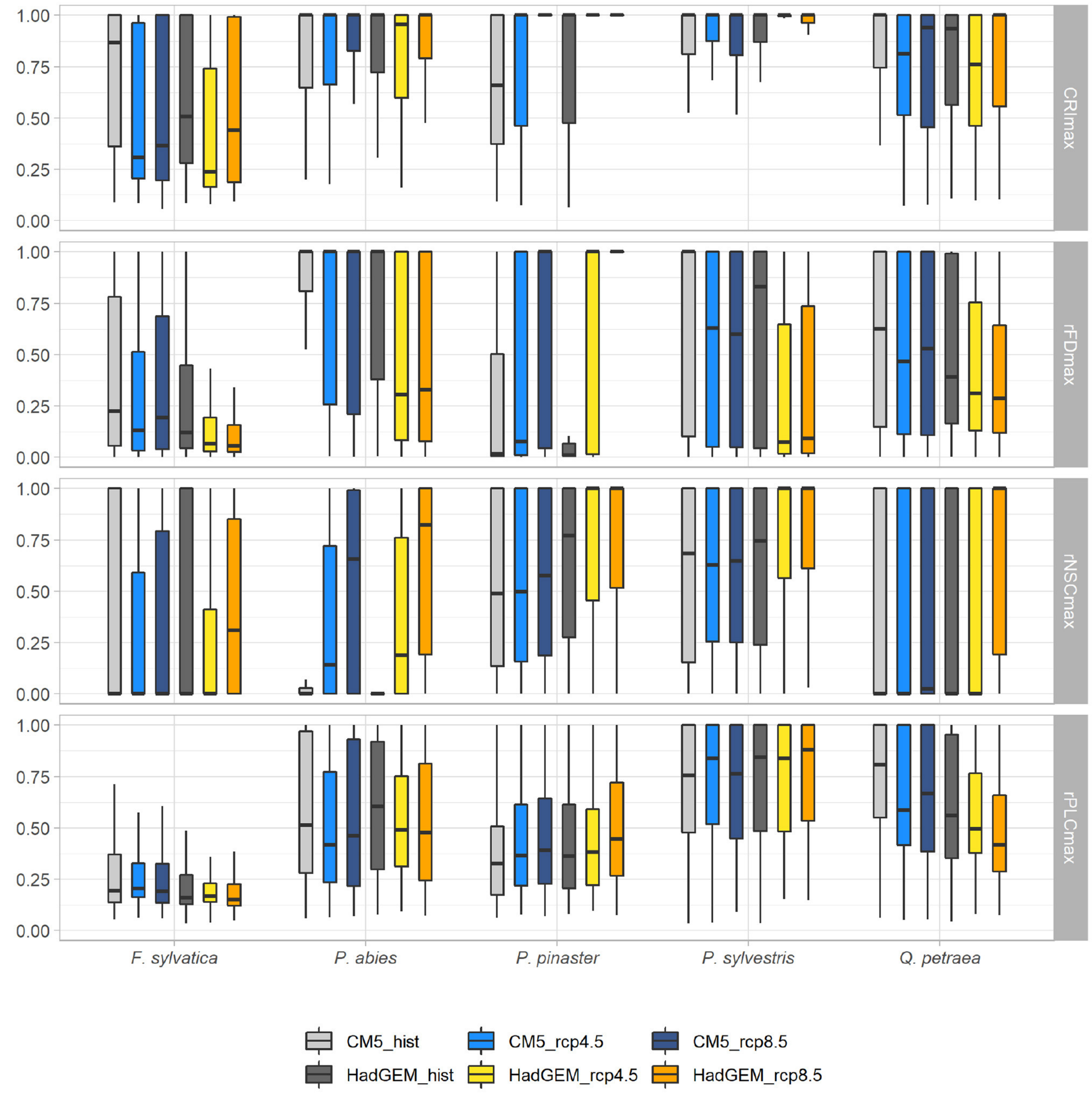

FIGURE 4 | Variation of the mean values of mortality risk indices ($CRIM_{max}$, rFD_{max}, $rNSC_{max}$, and $rPLC_{max}$) under two current and four future climatic scenarios. Each future climatic scenario (in blue for the CM5 RCM and in orange for the HadGEM RCM) can be compared to their historical reference (in light and dark gray for the CM5 and HadGEM RCMs, respectively). Simulations were run without management (SS1). See legend of **Figure 3** for whisker boxes.

baseline scenario without silviculture (hist) for *P. abies* (mean Δ *CRIM* = 0.04) and *P. pinaster* (mean Δ *CRIM* = 0.03). This increase in *CRIM* was mostly driven by increasing risk of hydraulic failure (mean Δ *rPLC* = 0.03 and 0.01 for *P. abies* and *P.pinaster*, respectively) and carbon starvation (mean Δ *rNSC* = 0.01 and 0.04 for *P. abies* and *P. pinaster*, respectively). By contrast, silviculture was always associated to decreasing *CRIM* and rNSC-values for *P. sylvestris* (mean Δ *CRIM* = 0.10 and mean Δ *rNSC* = −0.22). However, $CRIM_{max}$-values increased for all species, including *P. sylvestris*, between scenarios without vs. with silviculture under future climates (mean Δ $CRIM_{max}$ = 0.05 over the five species). This increase in $CRIM_{max}$ was mostly driven by increasing risk of carbon starvation (mean Δ $CRIM_{max}$ = 0.15 over the five species) (**Figure 6**, **Supplementary Table 5**).

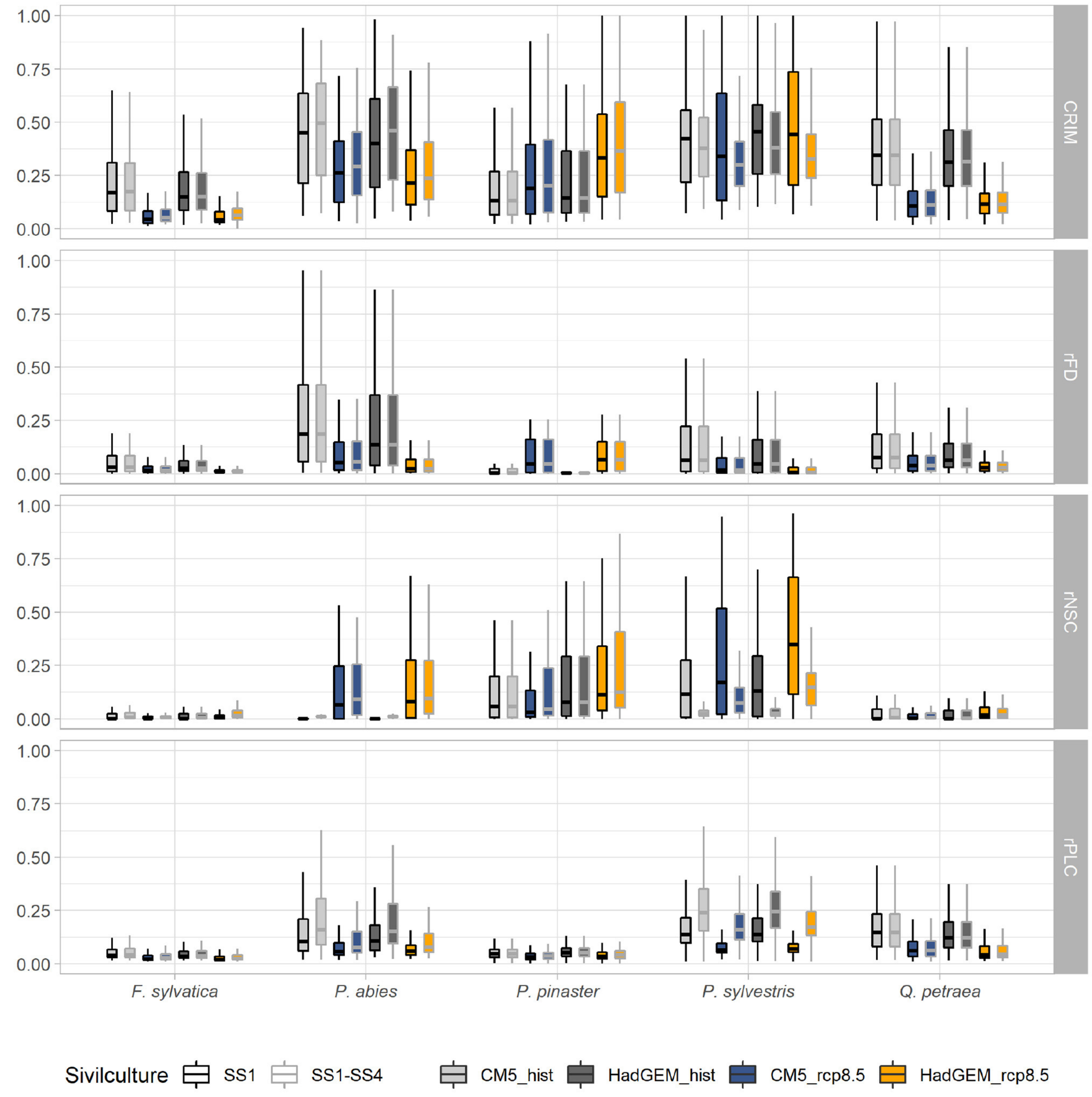

FIGURE 5 | Variation of the mean values of mortality risk indices (*CRIM*, rFD_{max}, *rNSC*, and *rPLC*) under two current (CM5-hist in light gray and HadGEM-hist in dark gray) and two future (CM5-8.5 in blue and HadGEM-8.5 in orange) climatic scenarios. Each scenario with locally prescribed silviculture (i.e., four possible silvicultural systems) is represented with gray whisker box contouring, and can be compared to its reference without management (i.e., SS1), with black contouring. See legend of **Figure 3** for whisker boxes.

These changes in $CRIM_{max}$ were associated to changes in tree density and LAI. In average, silviculture (SS1–SS4) was associated to lower LAI and density per hectare in *P.abies* and *P.sylvestris*. Silviculture was associated to lower LAI only for *F. sylvatica* and to lower density per hectare only for *P. pinaster*, while it has no effect on LAI and density per hectare of *Q. petraea* (**Supplementary Figures 11**, **13**, **14**).

3.5. The Risk of GCU's Extirpation

We used the value of $CRIM_{max} = 1$, i.e., predicted occurrence of mortality of the simulated stand during a period of time, as a criterion of threat of extinction. Under the most severe climate change scenario (HadGEM_rcp8.5), from 38% (*F. sylvatica*) to 90% (*P. pinaster*) of the GCUs are at threat of extinction in 2100 assuming that they are not managed, and these values are slightly

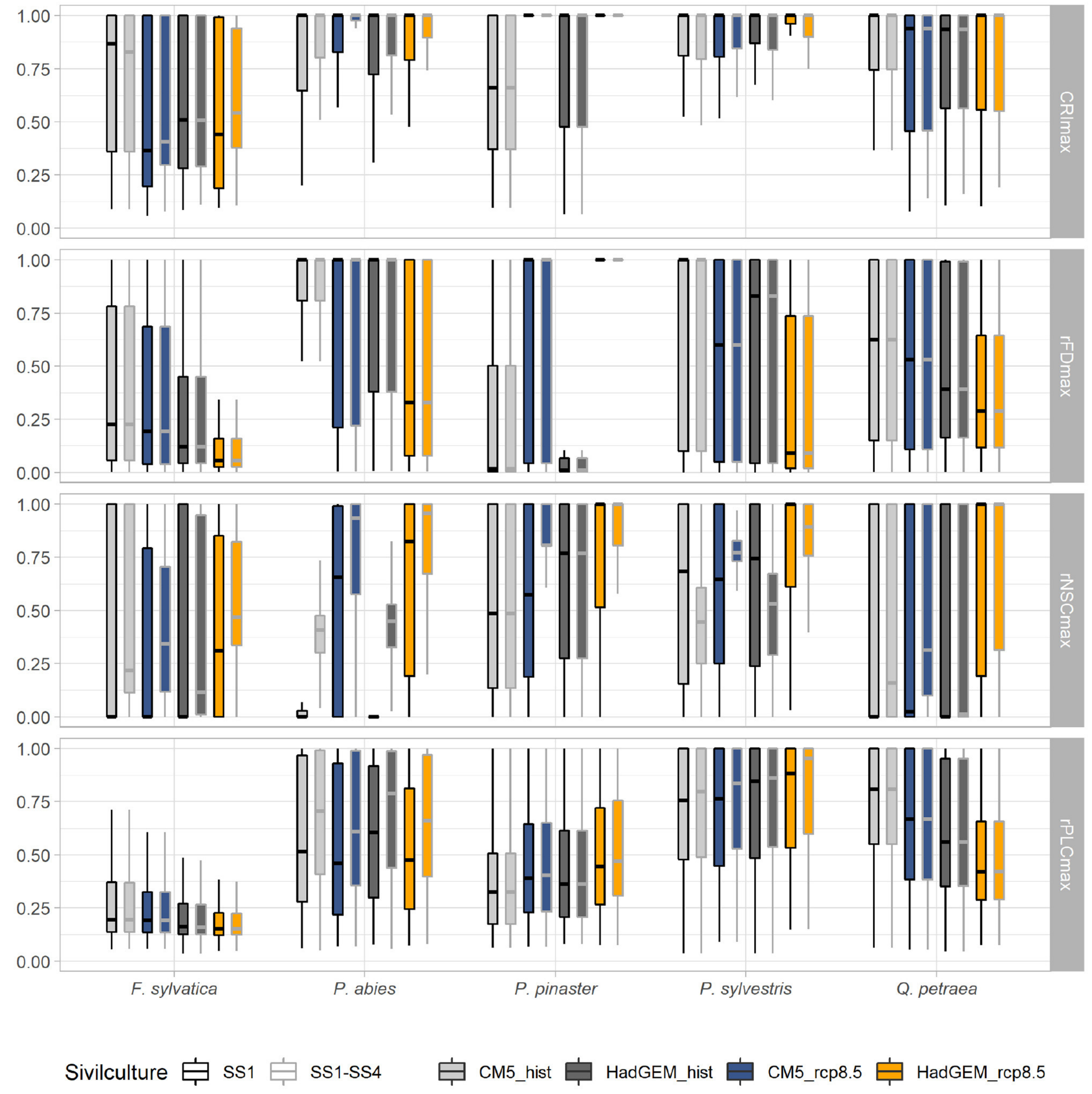

FIGURE 6 | Variation of the mean values of mortality risk indices (*CRIM*$_{max}$, *rFD*$_{max}$, *CRIM*$_{max}$, and *rPLC*$_{max}$) under two current (CM5-hist in light gray and HadGEM-hist in dark gray) and two future (CM5-8.5 in blue and HadGEM-8.5 in orange) climatic scenarios. Each scenario with locally prescribed silviculture (i.e., four possible silvicultural systems) is represented with gray whisker box contouring, and can be compared to its reference without management (i.e., SS1), with black contouring. See legend of **Figure 3** for whisker boxes.

higher if we assume they are managed following the current local silvicultural practices (**Table 2**), from 40% (*F. sylvatica*) to 98% (*P. pinaster*) in this case. The evolution of the index of mortality risk (*CRIM*$_{max}$) between current and 2100, under the harshest climate change scenario (HadGEM_rcp8.5), is highly variable among species: for *F. sylvatica* the risk will increase in 19% and decrease in 60% of the GCUs, whereas for *P. pinaster* the risk will increase in 48% and decrease in 2% of the GCUs (**Table 2**).

4. DISCUSSION

In this study, we used the process-based model CASTANEA to simulate spatial and temporal variation in mortality risks due

TABLE 2 | Variation of GCU extirpation threat between species under HadGEM RCP 8.5 future climatic scenario.

Species	Management	Total	0.75≥ $CRIM_{max}$	Increased $CRIM_{max}$	Exceeding 0.75	Decreased $CRIM_{max}$	Falling below 0.75	No $CRIM_{max}$ change
F.sylvatica	SS1	526	201 (38%)	98 (19%)	28 (5%)	316 (60%)	139 (26%)	112 (21%)
P.abies	SS1	658	422 (64%)	217 (33%)	75 (11%)	224 (34%)	82 (12%)	217 (33%)
P.pinaster	SS1	61	55 (90%)	29 (48%)	19 (31%)	1 (2%)	0	31 (51%)
P.sylvestris	SS1	412	323 (78%)	157 (38%)	37 (9%)	71 (17%)	18	184 (45%)
Q.petraea	SS1	282	184 (65%)	75 (27%)	39 (14%)	104 (37%)	60	103(37%)
F.sylvatica	SS1–SS4	526	212 (40%)	143 (27%)	31 (6%)	278 (53%)	133 (25%)	105 (20%)
P.abies	SS1–SS4	658	490 (74%)	263 (40%)	96 (15%)	178 (27%)	69 (10%)	217 (33%)
P.pinaster	SS1–SS4	61	60 (98%)	29 (48%)	24 (39%)	1 (2%)	0	31 (51%)
P.sylvestris	SS1–SS4	412	393 (95%)	213 (52%)	91 (22%)	52 (13%)	15 (4%)	147 (36%)
Q.petraea	SS1–SS4	282	179 (63%)	75 (27%)	39 (14%)	104 (37%)	65 (23%)	103 (37%)

For each species, under contrasted management scenarios (i.e., without or with management), we computed the number and percentage of CGUs with a high CRIM in 2100 (≥0.75); the number of CGUs where the $CRIM_{max}$ increases between current and 2100; the number of CGUs where the $CRIM_{max}$ exceeding 0.75 after increases; the number of CGUs where the $CRIM_{max}$ decreases; the number of CGUs where the $CRIM_{max}$ falling below 0.75 after decreases; the number of CGUs where no change of $CRIM_{max}$ were observed. The third column gives the total number of GCUs per species (as available in June 2017).

to hydraulic failure, carbon starvation and frost damage. These risks were assessed in five major European tree species across their distribution range, as a function of variations in climate, soil properties and management practices. We focused on the risk of mortality associated with droughts and frosts (winter, spring, and fall frosts with varying frost resistance across season), two major risks likely to increase in the future (Augspurger, 2013; IPCC, 2014; Charrier et al., 2018).

4.1. The Impacts of Drought and Frost Vary Between Species and Across Distribution Range

Considering the current climate, our results show that the physiological processes driving the risk of mortality differ among species. Carbon starvation drives the mean mortality risk (*CRIM*) for *P. pinaster*; frost damage drives the *CRIM* for *P. abies*; hydraulic failure drives the *CRIM* for *Q. petraea* and *P. sylvestris*; and a combination of hydraulic failure and frost damage drives the *CRIM* for *F. sylvatica*. When considering extreme climatic events with $CRIM_{max}$, the risk is higher and the contributions of the three focal physiological processes are more balanced. The rank of simulated species-specific risks of hydraulic failure or frost damage were not necessarily those expected from physiological or phenological observations. Indeed, deciduous broadleaves have a narrower safety margin for hydraulic failure as compared to evergreen conifers (Choat et al., 2012; Martin-StPaul et al., 2017). Late-leafing species such as *P. abies* have a higher safety margin for frost damage as compared to early-leafing species (Bigler and Bugmann, 2018). The low contribution of carbon starvation to the mean risk index is consistent with current ecophysiological knowledge (Martínez-Vilalta et al., 2016). However, the fact that simulations are initiated with small trees (diameter 5 cm) probably contribute to explain this result. Simulations run with bigger and older trees on average may show higher carbon starvation risk. We also find that the physiological processes driving the risk of mortality vary across species distribution ranges. The highest risk of hydraulic failure is found under Mediterranean and continental climates in Eastern Europe, associated to long and severe droughts, which is consistent with other studies based on PBMs or cSDMs (Gárate-Escamilla et al., 2019). As expected, the places the most vulnerable to frosts are located at high latitude and altitude.

Secondly, our results highlight that the evolution of mortality risk under future climate by 2100 differs between species. *CRIM* markedly decreases for broadleaved species and *P. abies*, and slightly decreases for *P. sylvestris*. This decrease is driven by decreasing risks of hydraulic failure and frost damage, which compensates for the increasing risk of carbon starvation for coniferous species. Broadleaved species remain at a low risk of carbon starvation under future climate, which can be due to their higher stomatal sensitivity to CO_2. Indeed, Klein and Ramon (2019) showed that conifers will need as much water as they currently do to complete their photosynthesis under future climate, while angiosperms will need less water for the same amount of CO_2 to complete their photosynthetic cycles. In contrast, for *P. pinaster*, the *CRIM* increases due to increasing risk of frost damage and carbon starvation. For the broadleaved species and *P. abies*, our model predicts a marked reduction of *CRIM* between current climatic conditions and future RCP 4.5 scenario, but not so much changes between RCP 4.5 and RCP 8.5 scenarios. This singular pattern suggests a non linear beneficial effect of CO_2 which compensates for the other harmful effects of climate change.

The evolution of mortality risk under future climate by 2100 also differs through space. Overall, for coniferous species, the risk of carbon starvation increases everywhere except in areas where it was already high and in mountainous areas. The risk of frost damage decreases or remains stable in most of Europe, which may be due to less severe winters; however it increases for *P. pinaster* in the Iberian Peninsula, likely due to earlier budburst and late frost in this area (Vitasse et al., 2014). The risk of hydraulic failure tends to decrease slightly throughout Europe between the current and future climate, except in a few patches mainly due to soil characteristics.

4.2. The Impact of Current Management Practices on the Risk of Mortality Under Current and Future Climate Varies Between Species

In our simulations, considering the current management practices has an ambivalent effect on the risk of mortality. Under current climate conditions, local forest management practices decrease in average the mean risk of mortality (*CRIM*) for *P. sylvestris*, slightly increase it for *P. abies* and has no impact on the other species. Under future climate conditions, the same local forest management practices still decrease the *CRIM* for *P. sylvestris*, slightly increase it for *P. abies* and *P. pinaster* and has no impact for the other species. Moreover, for all species, silviculture increases the risk of mortality due to carbon starvation when considering extreme drought events ($rNSC_{max}$).

Our results are thus at odds with previous studies showing that forest thinning could mitigate drought impacts (Elkin et al., 2015; Sohn et al., 2016). The simulated management practices reduce the average density of forest stands in coniferous species. This leads to a decrease of the average tree biomass and thereby its respiration. But the leaf area index (LAI) and thus the photosynthesis are also reduced by thinning. Hence, the effect of management practices on the risk of carbon starvation simulated by CASTANEA depends on the respective effects of forest thinning on respiration on the one hand, and photosynthesis on the other hand. For *P. sylvestris* this effect is always stronger on respiration and therefore management practices decreases the carbon starvation risk under current and future climates. But for *P. abies* and *P. pinaster*, management practices have the opposite effect in the future and increase the risk of carbon starvation.

The leaf area index decrease should also mitigate the risk of hydraulic failure by decreasing evapotranspiration (in average by 6% in our simulations, see **Supplementary Table 5**). That is why the increase in *rPLC* with silviculture for some species is quite unexpected. In these cases, the decrease in leaf area index is greater than the decrease in transpiration (data not shown), because leaf area index is quite high. The leaf midday water potential that determines the risk of cavitation is not calculated from the total tree transpiration, but from the transpiration per m_2 of leaf. Physiologically, the higher the flux at leaf level, the greater the risk of cavitation. When the canopy is dense there are more leaves and therefore the flux is distributed over more surface, which explains why in these cases, *rPLC* is finally lower without silviculture.

This study is among the first attempts to simulate the large-scale effects of management practices with an ecophysiological PBM (see also Härkönen et al., 2019). Our simulations suggest that the impact of silviculture on the risk of mortality might not be so obvious and depend on species, the sites and the climatic scenarios considered. In particular for broadleaved species, the impacts of silviculture on the risks of mortality are uniformly low over species' distribution range. To improve these predictions, future simulations should take into account the variations in age and size class distribution at initialization.

4.3. The Threat of GCU Extirpation Under Climate Change Differs Among Species

Under the harshest climate change scenario, our projections of mortality risk in the five *in situ* conservation networks predict that 38–90% of the GCUs are at threat of extinction in 2100, depending on the species. These PBM-based projections are more pessimistic than earlier BNM-based projections predicting that 33–65% of the GCUs will be at the limit or outside their current climatic niche (Schueler et al., 2014). This unexpected contrast between PBM and BNM predictions has two main explanations. First, in contrast to Schueler et al. (2014) assumption that 95% of the species' current climatic niche is considered to be riskless, our $CRIM_{max}$ predictions indicate that most of the CGUs are already in a high mortality risk zone under current climate. This is consistent with the policy of choosing some GCUs located in areas that are already experiencing climate-related selection pressures. There are few GCUs (from 5 to 31%) shifting from low $CRIM_{max}$ (<0.75) in the current climate to high $CRIM_{max}$ in the future climate (>0.75); by contrast, 12–51% of CGUs shift from high $CRIM_{max}$ to low $CRIM_{max}$. Secondly, and contrasting with the line of previous studies (Morin and Thuiller, 2009; Cheaib et al., 2012), we used the maximal and not the mean risk index of mortality to predict the threat of GCU extirpation. We considered spatio-temporal patterns of mean *CRIM* variation useful to disentangle how hydraulic failure, carbon starvation and frost damage respectively contribute to the risk of mortality; however, we argue that realistic predictions of the extirpation threat should rather account for extreme climatic events triggering maximal physiological risks of mortality. Doing so,we may overestimate this threat. In particular, because of the coarse spatial resolution of our simulation grid ($0.5 \times 0.5°$), the local climates at actual CGUs location may differ from the average climate at the grid point.

Our projections also show that traditional management systems would not help to reduce the mortality risk in those areas, and that risk reduction would require other specifically dedicated management practices. Our PBM approach lies on the pessimistic side of the projections because it does not account neither for the within-stand diversity of the response to climate, which is a factor of resilience of the populations facing disturbance since not all trees are equally threatened at the same time, nor for the evolutionary potential of each forest stand, which is a factor of adaptation from one generation of trees to the next. However, in the harshest situations, silvicultural interventions and natural evolution might not be sufficient to conserve the local population *in situ*, and *ex situ* conservation strategies, either dynamic or static, should be considered.

The EUFORGEN program has developed an operational decision support tool for the management of GCU based on demographic, genetic and disturbance indicators that can be measured by different verifiers, and recommended actions depending on the levels of these indicators (Rudow et al., 2020). A combined index of mortality risk such as $CRIM_{max}$ could be used as a verifier to inform the risk of population loss.

4.4. Future Direction for PBM Improvements

The growth and NPP simulated with CASTANEA across the whole Europe (i.e., potential niche) under current climate were consistent with the realized distribution range of broadleaved species, but less so for coniferous species. Three hypotheses might explain why NPP variations may less correctly predict the realized distribution of coniferous species: (1) their distribution is rather determined by biotic interactions and management practices rather than by climate and soil conditions; (2) the coarse climatic grid does not correctly represent local climate conditions in mountainous areas where *P. sylvestris* and *P. abies* are located; (3) the realized distribution is not limited by survival at adult stage, but by reproduction or survival at seedling stages (Niinemets and Valladares, 2006). In addition, for *P. abies*, in the comparison with the CO_2 flux measurements, we may underestimate the GPP if the average value of Vcmax used for the simulations and obtained from the literature underestimate photosynthesis (Walker et al., 2014), which can lead to too low values especially at the northern and eastern boundaries. The large-scale validation of CASTANEA needs to be improved for some species to better predict mortality. Two approaches, out of the scope of the current study, can be used. The first approach would be to simulate mortality at stand scale and compare it with mortality observations at European scale, as done in Petit-Cailleux et al. (2021) at local scale. A second one would be to compare NPP simulated with those measured from satellite data. These two approaches would additionally require to account for the variations in age and size classes for forest stand across the simulated area.

CASTANEA simulated a strong positive effect of increased CO_2 on Gross Primary Production (GPP), Water Use Efficiency (WUE) and biomass growth (BG). The simulated β_{GPP} is close to average value obtained across FACE experiments (β_{GPP} = 0.73, 11 sites, 45 species). The simulated β_{WUE} is a bit lower than the observed increase in ecosystem-scale plant WUE from Duke and ORNL FACE experiments (0.76 and 1.1, respectively). Finally, the simulated β_{BG} is higher than the estimated β_{BG} (between 0.49 and 0.56) from FACE experiments (Walker et al., 2021). However, CASTANEA does not take into account the possible acclimation of photosynthesis to rising CO_2 concentration and temperatures neither that of respiration to rising temperatures and water stress. Yet, in C3 plants, the maximum carboxylation rate and the maximum rate of electron transport were significantly reduced at elevated CO_2 (Ainsworth and Rogers, 2007). Most species can also shift their thermal optimum of photosynthesis upward in response to warming (Crous, 2019). Similarly, temperature acclimation of respiration involves a change in respiratory capacity and/or the sensitivity of respiration rate to temperature (Atkin et al., 2008). These acclimation processes would need to be accounted for in future simulation studies.

We also only partially accounted for interspecific variability in thresholds to mortality (e.g., the PLC value leading to mortality differed among broadleaved and conifer trees), and not at all for intra-specific variability in vulnerability. Yet, local adaptation is widespread in tree populations throughout their distribution ranges (Benito Garzón et al., 2011; Alberto et al., 2013). For example, Anderegg et al. (2016) demonstrated a genetic differentiation of xylem resistance traits in several species. For *F. sylvatica*, Kreyling et al. (2014) found genetic differentiation of frost resistance parameters, particularly in marginal populations. These patterns of intra-specific variability and differentiation of adaptive traits involved in response to drought and frost would be interesting to consider in future simulations.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories at: doi: 10.5281/zenodo.5160130.

AUTHOR CONTRIBUTIONS

SO-M, HD, FL, and BF initiated the study. SO-M, ML, and PV reviewed the silvicultural management across Europe. CP-C, HD, and SO-M upgraded and ran the PBM. CP-C, SO-M, and FL created the post processing method. CP-C drafted the manuscript. All authors contributed to its improvement and approved its final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.706414/full#supplementary-material

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Future Representation of Species' Climatic Niches in Protected Areas: A Case Study With Austrian Endemics

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Climate driven species' range shifts may interfere with existing protected area (PA) networks, resulting in a mismatch between places where species are currently protected and places where they can thrive in the future. Here, we assess the climate-smartness of the Austrian PA network by focusing on endemic species' climatic niches and their future representation within PAs. We calculated endemic species' climatic niches and climate space available in PAs within their dispersal reach under current and future climates, with the latter represented by three climate change scenarios and three time-steps (2030, 2050, and 2080). Niches were derived from the area of occupancy of species and the extent of PAs, respectively, and calculated as bivariate density kernels on gradients of mean annual temperature and annual precipitation. We then computed climatic representation of species' niches in PAs as the proportion of the species' kernel covered by the PA kernel. We found that under both a medium (RCP 4.5) and severe (RCP 8.5) climate change scenario, representation of endemic species' climatic niches by PAs will decrease to a sixth for animals and to a third for plants, on average, toward the end of the century. Twenty to thirty percent of Austrian endemic species will then have no representation of their climatic niches in PAs anymore. Species with larger geographical and wider elevational ranges will lose less climatic niche representation. The declining representation of climatic niches in PAs implies that, even if PAs may secure the persistence of a part of these endemics, only a small portion of intraspecific diversity of many species may be represented in PAs in the future. We discuss our findings in the context of the varied elevational gradients found in Austria and suggest that the most promising strategies for safeguarding endemic species' evolutionary potential are to limit the magnitude of climate change and to reduce other pressures that additionally threaten their survival.

Keywords: conservation, dispersal, habitat suitability, niche modeling, range, range-restricted species

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INTRODUCTION

Economic growth, increasing resource consumption, land use change, pollution, and over-harvesting have led to a biodiversity crisis (Díaz et al., 2019; Dasgupta, 2021) that may well develop into a sixth global mass extinction (Barnosky et al., 2011). Across Europe, natural landscapes have been transformed and almost all natural and semi-natural habitat types have been subject to loss, degradation or fragmentation during the last decades (Ellis et al., 2013; Watson et al., 2016). Area-based conservation measures are pivotal to prevent further loss of habitats and associated species (Watson et al., 2014). By and large, protected areas (PAs) have been successful in safeguarding biodiversity within their boundaries, with species richness being mostly higher within than outside PAs (Thomas and Gillingham, 2015). In the future, however, climate change and associated range shifts of species may interfere with the effectiveness of the existing PA networks, resulting in a mismatch between places where species are currently protected and places where they can thrive under future climatic conditions not encompassed by PAs (Lawler et al., 2015; Elsen et al., 2020).

Whether PA networks will support the protection of species under a changing climate will depend on their spatial configuration. For instance, large, continuous PAs may allow poleward range shifts and tracking of suitable climates during climate warming. Longer elevational gradients within PAs provide access to a higher variety of future climates, including analogues to current ones, within short distances (Elsen et al., 2018), and may also offer a variety of micro-refugia (Scheffers et al., 2014). PAs may also serve as stepping stones for species tracking their climatic niches, so that in larger and sufficiently connected PA networks losses of populations in one PA may be offset by establishment in others (Hole et al., 2011; Thomas and Gillingham, 2015).

Yet, the functioning of such relocation processes relies on range characteristics and the dispersal abilities of species, and may be futile for many endemics. Their defining feature—a narrow geographic range—often is a consequence of limited dispersal ability, be it for the particular traits of these species (Dullinger et al., 2012a) or because the habitats or climatic conditions they are adapted to are geographically isolated (Ohlemüller et al., 2008; Flantua et al., 2020). As a consequence, many endemic species may be too slow to track their climatic niches (Loarie et al., 2009) even within a continuously protected habitat irrespective of its size, or they may get further trapped in increasingly fragmented habitats (Dobrowski and Parks, 2016). Endemics may moreover be ecologically highly specialized and hence have particular problems to cross an impermeable matrix between PAs and use them as stepping stones during migration (Dullinger et al., 2015; Wessely et al., 2017). Hence, lack of sufficient, continuous and reachable climate space may render current PA networks ineffective for narrow-range species when the climate is changing (Araújo et al., 2011; Lawler et al., 2015; Batllori et al., 2017). This is particularly problematic as PA networks arguably have a special responsibility for those species which are endemic to their spatial domain.

Whether a PA network is "climate-smart" (Maxwell et al., 2020) has so far mostly been evaluated by comparing its extent to the projected geographic distribution of its target features (e.g., species or habitats under protection) under future climatic conditions (Hole et al., 2009; Araújo et al., 2011; Ayebare et al., 2018; Fuentes-Castillo et al., 2019). Unfortunately, occurrence data for endemic species are often sparse, and dispersal limitations interfere with ecological requirements in determining species' geographic distributions (Early and Sax, 2014). As a consequence, geographic projections of suitable ranges are difficult to calculate for many endemics, especially for those restricted to very small areas (Scherrer et al., 2019).

Moreover, apart from the size of the climatically suitable area that remains protected, a potentially important additional criterion for assessing the climate smartness of PA networks is whether and to which extent they will cover the ecological niches of target species in the future. In fact, changes of the overlap between species and PAs in geographical and ecological space are not necessarily correlated. When geographical ranges of species shift from smaller, but climatically diverse PAs to larger, but climatically monotonous ones, the suitable area under protection might increase while the protected part of the climatic niche might decrease. In topographically diverse areas, correspondence between changes in geographical and climatic representation of species in PA networks are particularly hard to predict because they depend on the configuration or shape of the mountains which can vary considerably (Elsen and Tingley, 2015; García-Rodríguez et al., 2021).

Taking changes of climatic niche representation within PAs into consideration is important because the species' climatic niches are abstractions resulting from aggregations of ecotypes with diverging specializations (Clark et al., 2011). For instance, the climatic niche of a single species may entail a suite of ecotypes with somewhat different niches, which may lose protection if this part of the niche is no longer represented in PAs. Focusing on the overarching species niches and their representation in geographic space may thus result in massive underestimation of hidden, intraspecific biodiversity loss (Bálint et al., 2011) even at phylogenetic and functional levels (Hidasi-Neto et al., 2019; Prieto-Torres et al., 2021). As evolutionary lineages within species may partition niche space while sharing geographic space, predictions of change in available niche space are likely more indicative of threats to intraspecific diversity than predictions of change in available geographic area. In addition, a broader niche space will, by trend, be associated with larger genetic diversity and hence a higher potential of species to adapt to a changing climate (Cotto et al., 2017). For these reasons, we argue that assessing climate-smartness of PA-networks should pay more attention to the target species' climatic niche space (Hanson et al., 2020) and its future representation within PAs.

On a global scale, the representation of vertebrates' climatic niches in PAs under current climate has recently been shown to be insufficient (Hanson et al., 2020). Here, we demonstrate how such an assessment can be conducted on a regional scale for range-restricted endemic plants and invertebrates, and how the evaluation of climatic representation under current climate can be projected onto future climates. As a case study, we use the national PA network of Austria and the endemic species it harbors. Due to its biogeographical location, topography and glacial history, the Austrian flora and fauna is relatively rich in endemic species (Rabitsch and Essl, 2009). In our analysis, we focus on 530 endemic plant and invertebrate species and ask how the representation of their climatic niches within PAs would change over the 21st century under three different climate change scenarios. We understand the study as an evaluation of the Austrian PA network's climate smartness, a basic challenge for area-based conservation in the 21st century (Maxwell et al., 2020). We expect that this smartness will decrease with the magnitude of climate change, i.e., that PAs will represent species' niches less in the future, the more pronouncedly the climate changes. We have no specific assumptions on whether endemic plants and invertebrates differ in their respective sensitivity. We expect, however, that across taxonomic groups the future mismatch of the (current) PA network and the niches of species will be more pronounced, in the case study region and perhaps generally, for species with smaller ranges and narrower niches because their chance to find analogue climates in geographically proximate PAs should be lower, on average.

MATERIALS AND METHODS

Species' and PAs' Occupancies

We extracted range maps of 530 Austrian endemic species (including sub-endemics, i.e., species with >75% of their known distribution in Austria) of vascular plants and a number of invertebrate taxa (insects, crustaceans, mites, spiders, springtails, millipedes, and snails), hereafter divided into plants and animals, respectively, from Rabitsch and Essl (2009). The maps represent the species' extents of occurrence in 3 × 5 arcmin grid cells (c. 35 km^2) across the country's domain. As many of the species are cryptic and likely understudied, the published range maps may underestimate the actual distribution. To compensate for that, we assumed that each species occurs not only in the mapped grid cells, but also in a one-cell buffer around them. We refer to the mapped cells plus the buffer as species' range in the following (cf. **Figure 1**).

Point occurrence data for most of these species are rare or lacking completely and parameterizing species distribution models (at finer scales) is hence barely possible. However, apart from the range maps, Rabitsch and Essl (2009) deliver information about each species' upper and lower elevational range margins. We used this information to further constrain each species' range. We therefore overlaid the species ranges by a 100 m × 100 m (= 1 ha) digital elevation model (EU-DEM[1]) and assumed the species' occupancy in all cells within their reported elevational range (**Figure 1**). Species with published elevational ranges narrower than 100 m (i.e., the difference between lower and upper elevation limits) were excluded, as we assumed these species to be studied incompletely.

On the part of the PAs, we used the IUCN protected areas categories Ia (Strict Nature Reserve), Ib (Wilderness Area), II (National Park), III (Natural Monument or Feature), and IV (Habitat/Species Management Area) available from the IUCN (UNEP-WCMC and IUCN, 2021), and the Austrian Natura 2000 network (DG ENV[2]). We then overlaid the PA network with each species' range and defined, for each species, the PAs within its range as being within reach given the species' assumed dispersal capacities and hence relevant for the respective species until the end of the century (cf. **Figure 1**). In other words, we assumed that each species can reach all suitable future climatic space within the 3 × 5 arcmin cells it currently occupies plus the one-cell buffer, but is not able to migrate beyond this range.

Climatic Data and Scenarios

For calculating climatic niches of the species and climatic spaces of their associated PAs, we overlaid the species' range and PA maps (at 1 ha scale, see above) with climatic raster maps of current and future climates (as calculated by climate change scenarios). Predictions of monthly time series of mean temperature and precipitation sums for the 21st century were extracted from the Cordex data portal.[3] The CORDEX experiment provides regional climate change simulations for Europe using various regional climate models at a resolution of 0.11°. In this study, we used predictions calculated by Météo-France/Centre National de Recherches Météorologiques using the CNRM-ALADIN53 regional climate model, fed by output from the global circulation model CNRM-CM5 (Tramblay et al., 2013).We selected projections based on CNRM-ALADIN53 because they predict "mean" temperature and precipitation trends for the study area, i.e., neither particularly strong nor particularly weak changes. We included predictions for three IPCC scenarios from the Representative Concentration Pathways-family representing mild (RCP 2.6), medium (RCP 4.5), and severe (RCP 8.5) climate change to consider the uncertainty in climate predictions. The RCP 2.6 scenario assumes that radiative forcing reaches nearly 3 $W\ m^{-2}$ (ca. 490 ppm CO_2 equivalent) mid-century and will decrease to 2.6 $W\ m^{-2}$ by 2080. Average temperature rise thereby is predicted to increase by 1.46°C in the study area compared to the year 2000. The RCP 4.5 scenario assumes an increase of 4.5 $W\ m^{-2}$ (ca. 650 ppm CO_2 equivalent) until 2100. Temperature is predicted to increase by ca. 2.3°C in the study area. The RCP 8.5 scenario assumes radiative forcing to continuously rise throughout the 21st century and reaches >8.5 $W\ m^{-2}$ (ca. 1370 ppm CO_2 equivalent) at the end of the century (Moss et al., 2010) which translate to an increase of temperature by 3.7°C.

We statistically downscaled the 0.11° resolution time series to match the resolution of the 1 ha species distribution maps. Downscaling was done using the delta method by (a) calculating differences ("deltas") between future values and hindcasted values (i.e., current climatic conditions; mean 1970–2005) at the original spatial resolution of 0.11°; (b) spatially interpolating these differences to a resolution of 1 ha using cubic splines; and (c) adding them to fine scaled maps of current climate (Karger et al., 2017) separately for each climatic variable (for more details on the delta method see e.g., Zimmermann et al., 2009; Dullinger et al., 2012a). From the resulting annual time series of monthly temperature and precipitation from 2011 to 2100 we calculated average values of mean annual temperature (Tmean) and annual precipitation (Prec) in 20-year intervals centered on 2020, 2030, 2050, and 2080 for every RCP scenario. We acknowledge that mean annual temperature and annual precipitation sums are coarse descriptors of climatic niches and may not adequately

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[1] https://www.eea.europa.eu/data-and-maps/data/copernicus-land-monitoring-service-eu-dem

[2] https://www.eea.europa.eu/data-and-maps/data/natura-11

[3] http://cordex.org

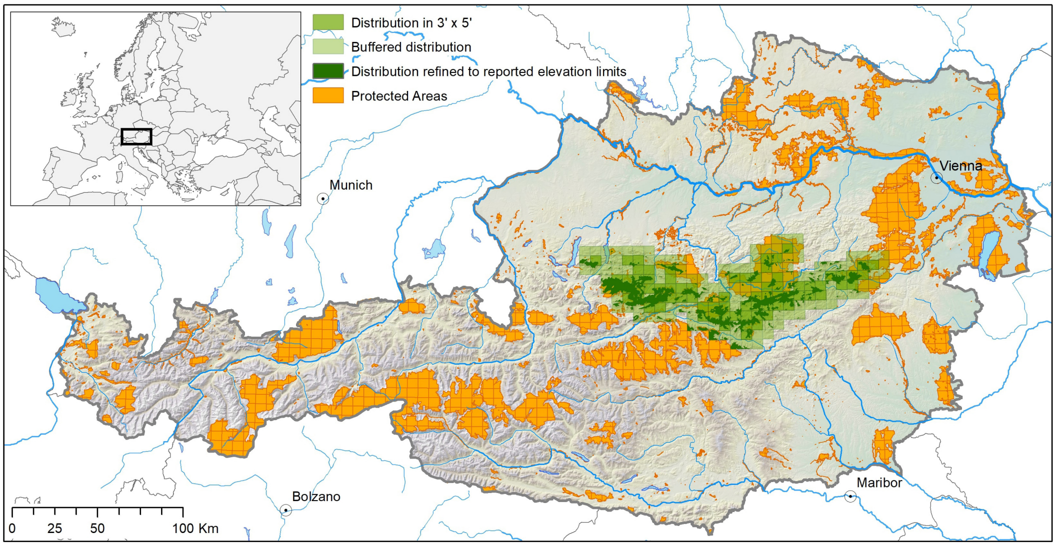

FIGURE 1 | Derivation of species distribution from 3′ × 5′ raster maps and information on elevational range limits illustrated for the vascular plant species *Achillea clusiana*. The light green area describes the range extent at the 3′ × 5′ raster-scale, and the dark-green area the assumed occupancy within this extent at the 1 ha scale. For more details see text. Country borders are adaped from GADM (https://gadm.org/); rivers are adaped from OSM (www.openstreetmap.org).

describe the more specific climatic requirements of many individual species (Körner and Hiltbrunner, 2018). However, as more detailed information on each of the 530 species' climatic needs is missing, and these variables are often closely correlated with other climatic descriptors at regional scales, we consider our variable selection a reasonable simplification.

Since climate projections are modeled data each with characteristic boundary conditions they deviate slightly from climate data produced by interpolation of climate station data (like e.g., Worldclim, Fick and Hijmans, 2017) even in overlapping regions. In order to ensure that current (2020) and future (2030, 2050, and 2080) climate data represent a consistent time series, we used long term means/hindcasts calculated from the climate projections to describe the current climate.

Climatic Niche Construction

Our aim was to quantify the proportion of each species' climatic niche that overlaps with the climatic conditions offered by the PAs situated within its range under current and future climates. For each species and associated PA, we therefore constructed climatic niches and climatic space offered by the PA, respectively, following the approach of Broennimann et al. (2012) via the function ecospat.grid.clim.dyn of the ecospat package in R (Di Cola et al., 2016; R Core Team, 2017). This method creates bivariate density kernels from the above described mapped climatic data (Tmean, Prec), i.e., from the grid cells occupied by a species, or covered by a PA, standardized by the density of the same climatic variables in a background area. The bivariate kernels are thus three-dimensional histograms which describe the empirical density of combinations of two variables [instead of the density of one variable in a conventional histogram, see Broennimann et al. (2012) for details] and represent the species' climatic niche and the PAs' climatic space in the two dimensions considered (mean annual temperature and annual precipitation). For our calculations we defined the species range (mapped 3 × 5 arcmin cells + buffer) as the background area. We used the current climatic conditions (2020) as the climate of this background area in all calculations because comparing volumes of bivariate kernels as defined here (see below) requires a common extent of the climatic data, i.e., a common value range or interval over which the kernels are calculated.

We derived the species' climatic niches from the overlay of their current occupancy (at the 1 ha scale) and the current climatic maps (2020). For calculating the species' niches' representations in PAs under future climates, we only considered those parts of their niches which will still be available in the future within their ranges (3 × 5 arcmin scale). To do so, we truncated their niches by excluding the combinations of Tmean and Prec no longer realized within a species' range in the future from the bivariate kernels. Because this potentially shrinks species' niches in the future, and one and the same PA may represent a larger proportion of a species' niche when the species' total niche is smaller, the calculation of the change in niche representation in PAs is potentially conservative. However, as unavailable climatic space can neither be part of a species' realized niche nor protected by PAs, we nevertheless consider this a sensible approach. We moreover emphasize that this approach assumes that the species are able to colonize their future climatic niche in geographical space completely, corresponding to a "full dispersal" scenario, which is, however, constrained to their current range extent (**Figure 1**).

On the part of the PAs, we calculated their currently available climate space similarly as for the species, i.e., from the overlay of their geographic extent and the current climatic maps. For future scenarios, however, we assumed that PA locations will remain unchanged. With respect to PAs our approach hence corresponds to a "no dispersal" scenario. For calculating the future climatic space offered by the PA network within a species range we hence overlaid its current extent with the maps of the future climate and re-calculated the bivariate kernels. We then excluded non-analogue climates from the calculation of the PA climate space in the future, i.e., those cells within its extent that would have a climate in the future which is not realized within the species' range (mapped 3 × 5 arcmin cells + buffer) currently. As long as we assume that the species' ecological niche will stay the same and not evolve, this truncation of the future PA climate space does not affect, but technically facilitates the computation of the species niche's representation in the PA (see below).

Climatic Niche Representation

To determine each species' climatic niche's representation within its associated PA's climate space, we calculated the proportion of its bivariate density grid covered by the PA's density grid. We therefore overlaid the density grids of associated species and PAs, set the densities in the PA-grid to zero where the density in the species' grid was zero, calculated the volume of this reduced PA climatic space as the sum of the remaining non-zero values, and divided this sum by the volume of the species niche. A value of 1 hence indicates full representation of the species' niche, and a value of 0 means that no part of the species' niche is represented by its associated PAs. The calculation was done separately for each combination of time steps and climate scenarios. These calculations were done in R (R Core Team, 2017), and scripts to repeat the analysis may be requested by the corresponding author.

Presentation of Results

To summarize the temporal trend of the representation of climatic niches in PAs across time steps and scenarios and over all species, we applied a generalized linear mixed effect model with climatic niche representation as response and species as random factor via the package glmmTMB in R (Brooks et al., 2017; R Core Team, 2017). We assumed the response to follow a beta distribution and hence applied the beta-family in the generalized model. Eighteen species (3.4% of all species) had no climatic niche representation in their affiliated PAs at one or several time-steps, i.e., the data contained zeroes. As the range of values over which the link function of the beta distribution is defined does not include zero (or one, but note that the climatic representation never reached one), we applied the lemon squeezer transformation of Smithson and Verkuilen (2006) prior to modeling [value * (n - 1) + 0.5)/n], which basically moves all values slightly toward 0.5 without changing relative differences. For our full model, we used the thus transformed climatic niche representation as response variable, and the combination of time step and scenario (as one factor variable, i.e., time step/scenario combination, for instance 2050-RCP4.5 or 2080-RCP8.5) together with the taxonomic group (plants, animals) as interactive fixed-effects predictor variables to test whether plants' and animals' climatic representations react differently to climate change. To account for the usage of the same species across time steps and scenarios (pseudo-replication) we moreover estimated random intercepts for each species. To test whether the interaction between time step, scenario and taxonomic groups was significant, we compared the full model to the corresponding additive model by means of a likelihood ratio test. Finally, we performed Tukey-corrected pair-wise comparisons across all factor levels in the final model to test whether the climatic scenarios and/or the taxonomic groups differ statistically significantly in terms of niche representation, taking pair-wise contrasts as significantly different with $p < 0.05$.

In addition to test for differences in the niche representation across time, scenarios and taxonomic groups, we graphically evaluated the relationship between the change of niche representation in the future and some attributes of the species, namely their current occupancies, their current mean elevations, as well as the widths of their current elevational ranges. For this purpose, we scaled the niche representation such, that a value of −1 means complete loss of representation, zero means no change, and a value of 1 means a doubling of representation.

RESULTS

Under current climate, i.e., in 2020, the climatic niches of 18 (or 3.4%) of the 530 species considered here have no representation of their climatic niches within their associated PAs (see **Supplementary Table 1** for results of each species). None of these 18 species will gain representation under future climates in any scenario, even though PAs are situated within their range (3 × 5 arcmin scale and buffer). In contrast, 77 species (or 14.5%) had more than 90% of their climatic niches represented within their associated PAs under current climate. Under future climates, all of them are expected to experience representation losses at some point, with 29 species completely losing representation until 2080.

A total of 256 species (or 48%) experienced increases of their climatic niche representation in PAs at some time-step and climate change scenario. However, these increases were generally small, most frequent during the first time-step under the RCP 2.6 and RCP 4.5 climate change scenarios, and usually offset by subsequent decreases in later time-steps (**Supplementary Table 1**). For instance, under RCP 4.5, 158 species gained representation until 2030. However, only 12 of these species could sustain these increases while the majority of these species (129) experienced decreases, with 17 species experiencing a complete loss of representation until 2080.

At the end of the period considered (year 2080) under the RCP 8.5 scenario, the climatic niches of 152 species (or 28.7%) have no representation in their associated PAs. This number of unrepresented species was lower for the two less severe scenarios, namely 103 (or 19.4%) and 25 (or 4.7%) for RCP 4.5 and 2.6, respectively (for a visualization of this result, compare the increase in the number of -1 values in RCP 4.5 and 8.5 across **Figures 3–5**).

The full model (including an interaction between the predictor variables time-step, scenario and taxonomic group) was the most appropriate to summarize future trends of climatic niche representation across all species (likelihood ratio test, interaction vs. additive model, $p < 0.00001$). All scenarios and time-steps

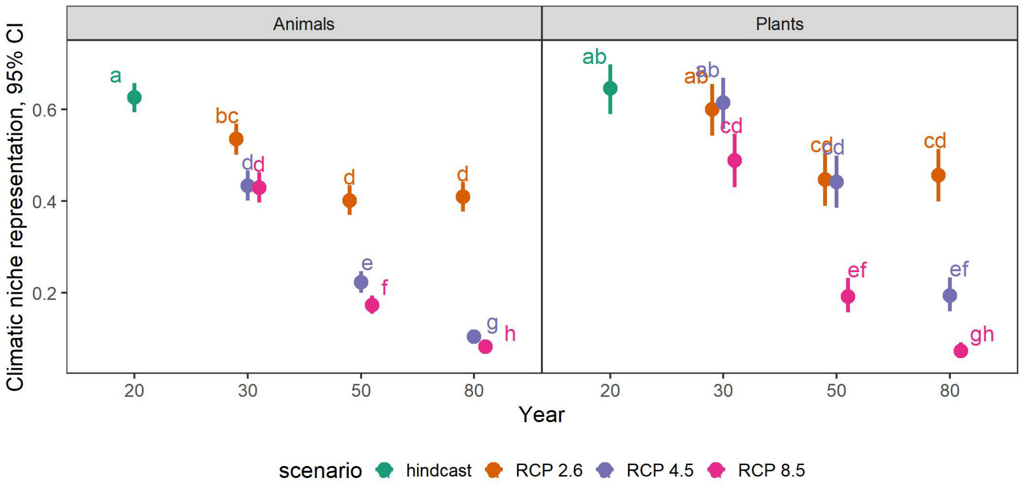

FIGURE 2 | Proportional representation of climatic niches in PAs across all 530 endemic plant and animal species considered in this study. Shown are estimates and 95% confidence intervals (CI) from a generalized linear mixed effects model including a significant interaction between time-step, scenario and taxonomic groups. Please note that all data presented here come from a single model, even though the taxonomic groups are displayed in two separate panels for overview. The different colors represent the climatic scenarios RCP 2.6, RCP 4.5, and RCP 8.5, while the hindcast represents the current climate (i.e., year 2020). Numbers on the x-axis refer to the modeled year with 20, 30, 50, and 80 referring to the years 2020, 2030, 2050, and 2080, respectively. Pair-wise contrasts (Tukey-method corrected) are statistically significant at $p < 0.005$ (letters).

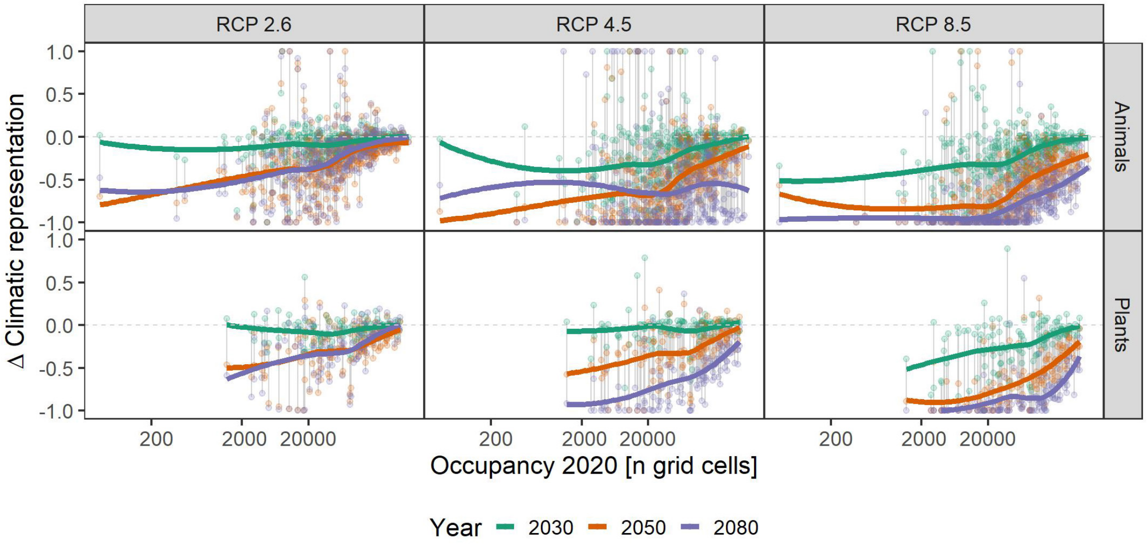

FIGURE 3 | Relationship of species' assumed area of occupancy and their respective gains and losses of climatic representation in the future under climate change scenarios RCP 2.6, RCP 4.5, and RCP 8.5. Colored, bold lines represent splines within each time-step (colors) and scenario (panels) for overview. Gray vertical lines connect data points belonging to one species. A value of -1 means complete loss of representation, and a value of 1 means a doubling of representation. Please note that some species had a relative change >1, and that for overview, we set those to 1. See **Supplementary Table 1** for details.

had statistically significantly different representations of species' climatic niches in PAs, and plants and animals also differed in this respect (Tukey-corrected pair-wise comparisons $p < 0.05$, for details see **Figure 2**).

Under current climate, an average of 62.6 and 64.6% of the species' climatic niches across animals and plants, respectively, were represented in their associated PAs. This value, however, decreased rapidly with each time-step of the future scenarios, reaching levels as low as 8.2 and 7.3% in 2080 under RCP 8.5 (**Figure 2**). Under RCP 2.6, years 2050 and 2080 were not significantly different from each other for both taxonomic groups, i.e., the initial decrease of representation halted after 2050 under RCP 2.6, while the decrease continued until 2080 under the other scenarios. For animals in the year 2030, representation

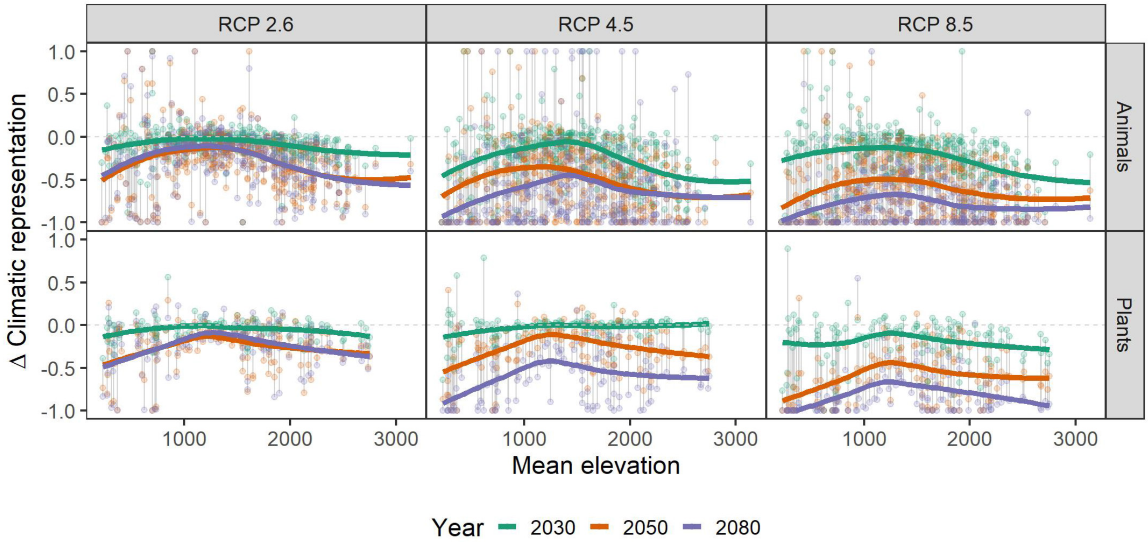

FIGURE 4 | Relationship of mean elevation (meters) of the species' assumed area of occupancy and their respective gains and losses of representation in the future under climate change scenarios RCP 2.6, RCP 4.5, and RCP 8.5. Colored, bold lines represent splines within each time-step (colors) and scenario (panels) for overview. Gray vertical lines connect data points belonging to one species. A value of -1 means complete loss of representation, and a value of 1 means a doubling of representation. Please note that some species had a relative change >1, and that for overview, we set those to 1. See **Supplementary Table 1** for details.

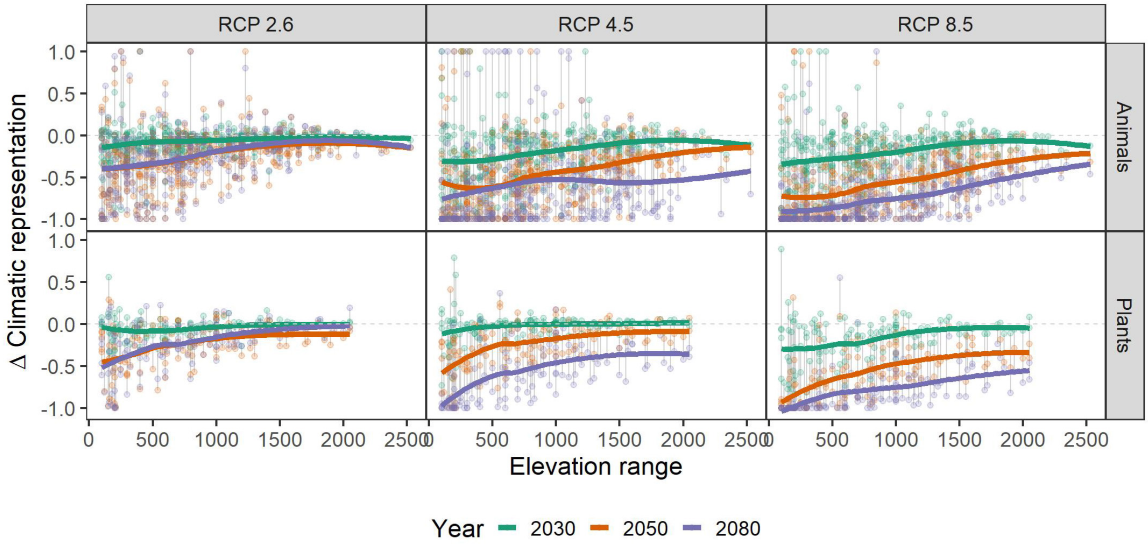

FIGURE 5 | Relationship of the species' elevational range (in meters) and their respective gains and losses of representation in the future under climate change scenarios RCP 2.6, RCP 4.5, and RCP 8.5. Colored, bold lines represent splines within each time-step (colors) and scenario (panels) for overview. Gray vertical lines connect data points belonging to one species. A value of -1 means complete loss of representation, and a value of 1 means a doubling of representation. Please note that some species had a relative change >1, and that for overview, we set those to 1. See **Supplementary Table 1** for details.

was almost equal between RCP 4.5 and 8.5, i.e., the trajectories of representation loss were more or less similar between these scenarios until 2030, after which they furcated. For plants, this was the case in years 2030 and 2050 for scenarios RCP 2.6 and RCP 4.5, respectively.

Independent of scenario or taxonomic group, species with small range sizes (at the 1 ha occupancy scale), experienced higher loss of climatic niche representation than more widespread ones. This difference became more pronounced over time, i.e., in 2050 and 2080 the loss of representation is particularly biased toward small-range species, especially in the RCP2.6 and 4.5 scenarios (**Figure 3**). Across the elevational gradient, species from intermediate elevations were predicted to lose less climatic representation in PAs than those from higher and lower ones, with these differences somewhat more pronounced in plants than in animals (**Figure 4**). Finally, the elevational range of a species, as an indicator of its climatic niche breadth, was negatively related to loss rates (**Figure 5**), a result consistent with higher loss rates found for species with narrower geographical range (**Figure 3**). As in the case of geographical range size, this trend was consistent across scenarios and taxonomic groups, but became more pronounced over time, especially in the scenarios RCP4.5 and 8.5.

DISCUSSION

The protection of rare endemic species is arguably an important asset of PAs, and with regard to this criterion we conclude that the Austrian PA network is unfit for climate change under two of the three climate scenarios tested here (i.e., RCP 4.5 and RCP 8.5). Under these scenarios, until 2080 the representation of currently realized climatic niches of the 530 endemic species in PAs drops to below 20%, on average. A sizeable portion of 20–30% of these species will even completely lose access to their climatic niches, or exclusively find suitable climate space outside PAs where colonization and establishment are less likely (Thomas et al., 2012). These findings generally underpin other warnings that climate change may significantly reduce the efficiency of current PA-networks in the future (Araújo et al., 2011; Nori et al., 2016; Batllori et al., 2017; Hidasi-Neto et al., 2019; Elsen et al., 2020; Prieto-Torres et al., 2021) if they remain static and their extent is not adapted to mitigate climate change impacts.

It has been argued that the world is not currently on track to the RCP 8.5 scenario but rather to an RCP 4.5 climate change-future (Hausfather and Peters, 2020). However, differences between the RCP 8.5 and the RCP 4.5 scenario were quantitatively small in the case of animals, each leading to a ca. 6-fold decrease of climatic niche representations of endemics in their associated PAs. In case of plants, the two scenarios differed more strongly, but climatic niche representation in 2080 still dropped to ca. 30% of its current value under the RCP 4.5 scenario. We don't know the reason for the differences between plants and animals, but we hypothesize that the peculiar distribution patterns of species in relationship with associated PAs is the main driver. Even under the very stringent RCP 2.6 scenario, which inspired the Paris climate agreement, endemics would face an approximate 30%-loss of climatic niche representation according to our calculations. Nevertheless, as the climate stabilizes after 2050 in this scenario, adapting spatial distributions to the changed suitability patterns is probably much easier for most species than under the continued or even accelerating change predicted by the RCP 4.5 and 8.5 scenarios. We add, however, that our calculations were only based on predictions of one particular global circulation model. The use of other models may have added additional variability to our results. However, the effect of varying R on species' range shift projections is usually more pronounced than the effect of GCMs (Thuiller et al., 2019). We hence believe that the general pattern of a massive loss of species' niche representation in PAs, especially in the more pronounced climatic scenarios, is most likely robust.

A major reason why the Austrian PA falls short of protecting endemics in the future is the assumed lack of dispersal capabilities of these species, i.e., the restriction of the calculations to the current extent of species' ranges. While this assumption might not be true in each single case, the majority of these endemics has been shown by previous studies to have narrow ranges precisely because of their limited dispersal abilities (Essl et al., 2011; Dullinger et al., 2012b). With respect to the subset of species that are sufficiently mobile, climate smartness of the Austrian PA network might, however, score differently. Indeed, several studies have shown that bird and well flying insect species may remain represented within larger PA networks because they can more easily track their niches to PAs outside the extent of the current ranges (Hole et al., 2009; Thomas and Gillingham, 2015). However, while these highly mobile animal groups may be able to migrate through fragmented landscapes or pass landscapes with unsuitable climates that separate individual PAs, this is less likely for plants and many other invertebrate groups, be they endemic or not (Wessely et al., 2017). Consequently, our approach may easily represent an overestimation of the study species' future climatic representation within PAs, because many of them might not even be able to reach nearby PAs (Prieto-Torres et al., 2021).

Our calculations suggest that species with larger distribution areas and wider elevational ranges will lose less climatic niche representation in their associated PAs. These two factors are correlated (**Supplementary Figure 1**), however, it is beyond the scope of this study to determine their relative contribution to the loss or gain of climatic niche representation. In any case, high values in any or both of these factors may be a result of larger climatic niches and hence increase the likelihood of representation by the PA network now and in the future. Hence, our results support the general notion that smaller range sizes lead to higher extinction risk (Manne and Pimm, 2001), even within the group of narrow-range species studied here.

We found that species from intermediate elevations (i.e., with their occurrence at a mean elevation of around 1,000–1,500 m) have lower loss of climatic niche representation than species occurring in lower or higher elevations. These species live at elevations low enough to allow tracking climatic niches via the assumed short distance dispersal along topoclimate gradients (Ackerly et al., 2010). Additionally, the presence of PAs is larger at higher elevations, mainly because competing interest from other land-use is lower (cf. **Figure 4**). As a corollary, a warming climate will shift the climatic niches of these mid-elevation species "into PAs." Species from lowest elevations may profit less from this PA pattern, because they may be geographically separated from mountainous areas and have no access to topoclimate gradients. Moreover, these lowland endemics of Austria often are specialists of peculiar, rare and isolated habitat types (Rabitsch and Essl, 2009), and hence often have particularly small ranges and narrow climatic niches. Small ranges and narrow niches, in turn, reduce the likelihood that PAs with appropriate environmental conditions are within reachable distance of a species. On the other end of the elevation spectrum, species may already occupy the highest elevations available and hence have little scope to shift ranges when climate warms, as no higher elevations can be reached (Dirnböck et al., 2011). We emphasize, however, that the microclimatic variation is often particularly pronounced at highest elevations, and that the respective microrefugia could not be accounted for in our analyses. Climatic representation of alpine and sub-nival species in these microrefugia may hence buffer future loss of meso-climatic representation to a certain extent (Scherrer and Körner, 2011).

Low representation of endemics' climatic niches by PAs implies that, even if PAs secure the persistence of populations of these species in geographic space, only a small portion of intraspecific genetic diversity may be represented in that space. As a result, the ability of species to overcome the shrinking representation of their climatic niches in PAs by phenotypic plasticity or genetic adaptation, i.e., by shifting their niche instead of their distribution, may also shrink (Barrett and Schluter, 2008; Salamin et al., 2010). Little is known about the intraspecific diversity of these endemic species, but as most of them have probably undergone severe demographic bottlenecks during Pleistocene climatic fluctuations (Rabitsch and Essl, 2009), the level of this diversity might often be low (Ellegren and Galtier, 2016) and its further reduction particularly critical. For the endemic species considered here, this risk might be higher for plants than for many of the animals, because plants are mostly long-lived, and the odds of evolutionary rescue decreases with the species lifespan (Cotto et al., 2017). However, all species are likely to face severe loss of ongoing diversification processes when just small fractions of their climatic niches will be conserved in the future.

Our niche calculations of endemic species are based on the simplifying assumption that species (a) occupy all geographic space within reported elevational range limits and (b) may freely disperse across the whole suitable climatic space within their ranges. This is certainly not true because occupancy is additionally determined by factors other than climate, for instance by resource availability (e.g., water and nutrients in case of plants, host plants or other food resources in case of invertebrates) or dispersal capabilities (Pagel et al., 2020; Treurnicht et al., 2020), and the distribution of the species will hence be patchy rather than continuous within their elevational limits. Further, dispersal and incidence across the climatically suitable space of a species may likewise be constrained by biotic factors not considered here such as the presence and abundance of competitors and mutualists (Estrada et al., 2016). The area of occupancy that we derived for the study species is hence rather a potential area and almost certainly overestimates real occupancy. In addition, it may also overestimate niche breadth, and hence niche representation in PAs, because reported elevational range limits neither distinguish source from sink populations nor account for mismatches between niches and distribution that are due to other reasons such as persistence of long-lived species at sites no longer suitable to them (Pagel et al., 2020). Alternative approaches, such as those that directly measure demographic rates along environmental gradients (Treurnicht et al., 2020) could deliver more accurate niche characterizations. However, these approaches require considerable measurement effort and appear unfeasible for large sets of rare species as those modeled here, despite recent efforts to compile available demographic information (Salguero-Gómez et al., 2015, 2016). For such sets, the approach taken here should provide a reasonable approximation of the climatic niche because elevation is closely correlated to climate, especially to temperature, and elevational limits are hence a reasonable indicator of (realized) niche boundaries. If the focus is on climatic niches only, our simplified rectilinear envelop approach may even have advantages as it abstracts from other abiotic or biotic constraints on species' distribution that may confound the derivation of species climatic niches from occurrence records. In general, however, the estimation of the species' realized niche is certainly less accurate with such an approach, as also illustrated by comparisons of various niche modeling algorithms (Zimmermann et al., 2010; Blonder, 2018). For species with sufficient documentation of real occupancy, using this more precise information for determining niches is hence clearly preferable. In addition, information on functional traits has demonstrated potential to improve the characterization of species' niches and their ability to respond to climatic changes (Estrada et al., 2016; Treurnicht et al., 2020). However, trait information is usually least available for narrow-range species, and in many invertebrate groups modeled here the relevance of particular traits for niche characterization is yet little explored.

Taken together, our results suggest that under a set of climate change scenarios, the Austrian PA-network will perform poorly in safeguarding its endemic species, i.e., the group of species for which it has a particular responsibility. In order to conserve species' climatic niches, and thereby intraspecific diversity and evolutionary potential, expansions of PAs based on prioritization of climatic conditions should be considered (Hanson et al., 2020). In Austria, land-use and its associated threats to biodiversity are less intense at higher elevations also outside of PAs. Therefore, the survival of high-elevation species tracking their climatic niches during climate change may depend less on the presence of PAs, as unprotected land may still offer intact suitable habitats. In contrast, the survival of lowland species tracking their niches may depend more strongly on the presence of PAs if suitable habitat outside of PAs is scarce due to human pressures. However, despite a general decrease of land use intensity, human pressure can be considerable even at high elevations, e.g., from tourism, energy production or resource extraction, and conflicts between conservation and competing interests are frequent in various parts of the Alps.

Increasing the elevational gradients covered in PAs is a suggested strategy to adapt PA networks to a warming climate (Elsen et al., 2018). However, there are obvious limits to this strategy for species that already now live close to the highest elevations in their surroundings. As endemism in the European Alps is spatially biased toward marginal areas that have not been glaciated during the Last Glacial Maximum (Schönswetter et al., 2005; Dirnböck et al., 2011), and as these marginal parts of the Alps are mostly lower than the more central ones, scope for securing the protection of endemics through upward expansion of PAs appears indeed restricted. The most promising strategies are hence to limit the magnitude of climate change as far as possible, and to effectively reduce other pressures than climate change that additionally impact endemic species.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

PS, SS, FE, and SD designed the study. DM compiled species range and climate data. JW and AG provided future climate data maps. PS performed climatic niche representation calculations and all other analyses and wrote the text with further input from all authors. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.685753/full#supplementary-material

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Broadening Predictive Understanding of Species' Range Responses to Climate Change: The Case of *Aloidendron dichotomum*

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Concerns have been raised about attribution of species range shifts to anthropogenic climate change. Species paleo-range projections are emerging as a means to broaden understanding of range shifts and could be applied to assist in attribution. Apparent recent range contraction in the Quiver Tree (*Aloidendron dichotomum* (Masson) Klopper and Gideon F.Sm) has been attributed to anthropogenic climate change, but this has been challenged. We simulated the paleo- and future geographic range of *A. dichotomum* under changing climate using species distribution models (SDMs) to provide a broader perspective on its range dynamics. Ensemble modelling of the Last Glacial Maximum (LGM), mid-Holocene, current, and projected 2070 time periods simulates a paleo-historical poleward expansion of suitable bioclimatic space for this species under natural climate change post-LGM, and projects an eastward shift towards 2070. During the LGM, suitable bioclimatic space for *A. dichotomum* was simulated to be restricted to the equatorward part of its current range. During the Pleistocene/mid-Holocene climate transition period, the species' range is predicted to have expanded significantly polewards at an average rate of 0.4 km per decade, assuming constant tracking of its optimal climatic niche. By 2070, suitable bioclimatic space is projected to expand further eastward into the summer rainfall region of South Africa, and contract in its equatorward reaches. Simulated post-LGM shifts roughly match expectations based on preliminary phylogenetic information, further supporting the attribution of current population declines to anthropogenic climate change drivers. Equatorward populations are required to migrate south-eastwards at a rate roughly 15 times faster than that calculated for the LGM/mid-Holocene climate transition period to avoid local extirpation. A preliminary analysis of range-wide genetic variation reveals a cline of variation, with generally higher levels in the central and more northerly part of the species distribution, as expected from the proposed paleo-range of the species. A more detailed analysis of the species' phylogeographic history could be used to test the proposed paleo-range dynamics presented here, and if confirmed, would provide strong support for the use of this species as an indicator of anthropogenic climate change and a powerful case study for testing the implementation of conservation actions.

Keywords: climate change, Last Glacial Maximum, mid-Holocene, migration, range dynamics, species distribution modelling, genetic variation

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INTRODUCTION

African terrestrial surface air temperatures have warmed by roughly double the rate (Engelbrecht and Engelbrecht, 2015) of the global surface air temperature rise of between 0.8 and 1.2°C since the preindustrial era (IPCC, 2014). There is high certainty that this warming will continue into the future (IPCC, 2018) with increases in Africa projected to exceed 5°C century^{-1} in the dry subtropical regions (Engelbrecht and Engelbrecht, 2015). A large body of research and observation work shows that biological systems and species are already responding to anthropogenic climate change (Parmesan, 2006; IPCC, 2014), but the study locations have a strong northern hemisphere bias. A common prediction for plants is that they will shift their geographic ranges in response to warming, either poleward or upward in elevation (Parmesan and Yohe, 2003; Parmesan, 2006; Midgley and Thuiller, 2007; Chen et al., 2011; Midgley and Thuiller, 2011; Manes et al., 2021), with many plant species already having undergone such changes (Chen et al., 2011; Feeley and Rehm, 2012; Telwala et al., 2013).

Range shifts are a well-known response of species to changes in regional and global climates in the distant geological past (Hewitt, 2004; Urrego et al., 2010; IPCC, 2014). Nonetheless, certain plant functional types have shown the early signs of adverse impacts as a result of recently accelerated anthropogenic climate change (Allen et al., 2015). Among these, trees are arguably the most vulnerable, with mortality potentially resulting in rapid and long term alterations of ecosystem types and associated ecological processes (Breshears et al., 2005), and with long generation times slowing the establishment rate of new populations (Pitelka, 1997). Globally, trees are critical for maintaining the climate regulating service of carbon sequestration (Canadell and Raupach, 2008). They typically also play keystone roles in the structuring and functioning of many habitats by providing habitat, shelter, food and mutualistic relationships with many animal, plant, and microbial species (Aitken et al., 2008). The responses of long-lived trees to past changing climates are therefore extremely important for ecological understanding of the systemic impacts of future projected climate change, and the accurate attribution of climate-driven impacts on these long-lived sentinels can support the development of appropriate conservation responses.

Over the past two decades, the Quiver Tree (*Aloidendron dichotomum (Masson), formerly Aloe dichotoma*), an iconic long-lived stem succulent of the arid western regions of southern Africa (**Figure 1**), has undergone substantial demographic change (Foden et al., 2007; Hoffman et al., 2010; van der Merwe and Geldenhuys, 2017). Population surveys have shown enhanced mortality of established individuals in the warmer parts of its range (central and equatorward populations), and enhanced population recruitment in the cooler parts (generally the more poleward populations) (Foden et al., 2007; Midgley et al., 2009; Hoffman et al., 2010; van der Merwe and Geldenhuys, 2017). Repeated observations of *A. dichotomum* population status over several decades, analysis of demographic patterns in relation to expected climate drivers, and consideration of alternative explanations (i.e., protocols meeting the requirements of attribution of range changes to anthropogenic climate change; see Taheri et al., 2021) strongly supports attribution of current population dynamics of *A. dichotomum* to anthropogenic climate drivers (see Foden, 2002; Foden et al., 2007; van der Merwe and Geldenhuys, 2017). Coupled with projected south and south-easterly range expansion in cooler parts of its range (Foden, 2002; Guo et al., 2016), these observations may suggest that a range shift is underway, although this interpretation has been contested (Jack et al., 2016).

Multiple lines of evidence indicate that *A. dichotomum* is sensitive to changes in climate (Foden et al., 2007; Hoffman et al., 2010; Guo et al., 2016; van der Merwe and Geldenhuys, 2017). Observations indicate that many populations have not had significant recruitment in the last 50 years, and at sites where limited recruitment has occurred, the timing of seedling establishment correlates with timing of rare favourable climatic windows (Foden, 2002; Hoffman et al., 2010). Further, Guo et al. (2016) the geographic range of *A. dichotomum* is constrained by temperature-based variables, indicating the potential vulnerability of this species to changing climate conditions, while the range of the species appears insensitive to rainfall seasonality, with positive population growth rates in both the winter-rainfall and summer-rainfall zones of south-western Africa (Foden et al., 2007; van der Merwe and Geldenhuys, 2017).

Further evidence for the species sensitivity to climate change can be gained through insight into the role of glacial-interglacial climate changes and the corresponding range shifts. Past climatic conditions are known to have affected speciation, extinction, and migration dynamics. Quaternary glacial and interglacial cycles have been shown to have caused drastic shifts in species distributions (Graham et al., 1996; Hewitt, 1996; Riddle, 1998; Avise, 2000; Bellard et al., 2012; Lyam et al., 2020; Łabiszak et al., 2021). Using both molecular and paleo-climatic data, Łabiszak et al. (2021) propose that the European peat bog pine (*Pinus uliginosa*) underwent a significant range contraction during the Last Glacial Maximum (LGM), reflected by a substantial reduction in genetic diversity during this period. Similar trends have been inferred for sub-Saharan savanna trees, with *Senegalia Senegal* proposed to have undergone a range reduction during the LGM and subsequently expanding its range out of climatic refugia through the mid-Holocene, to its current wider distribution (Lyam et al., 2020).

In many cases, geographic processes have led to distinct signals of past distributional changes through the patterning of genetic differentiation across populations, subspecies, and species (Comes and Kadereit, 1998; Hewitt, 2004; Habel et al., 2005; Łabiszak et al., 2021). In general, however, southern Africa has only sparse paleo-environmental archives to provide a basis for understanding how climates and vegetation have interacted. Development of Global Climate Models (GCMs), which enable reconstruction of past environmental conditions and prediction of future conditions, provide the potential for insight into the temporal distribution of vegetation types (Svenning et al., 2011). Additionally, the use of species distribution modelling (SDMs) (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005), provides an effective way of reconstructing the likely spatial extent of species' ranges during glacial periods. And

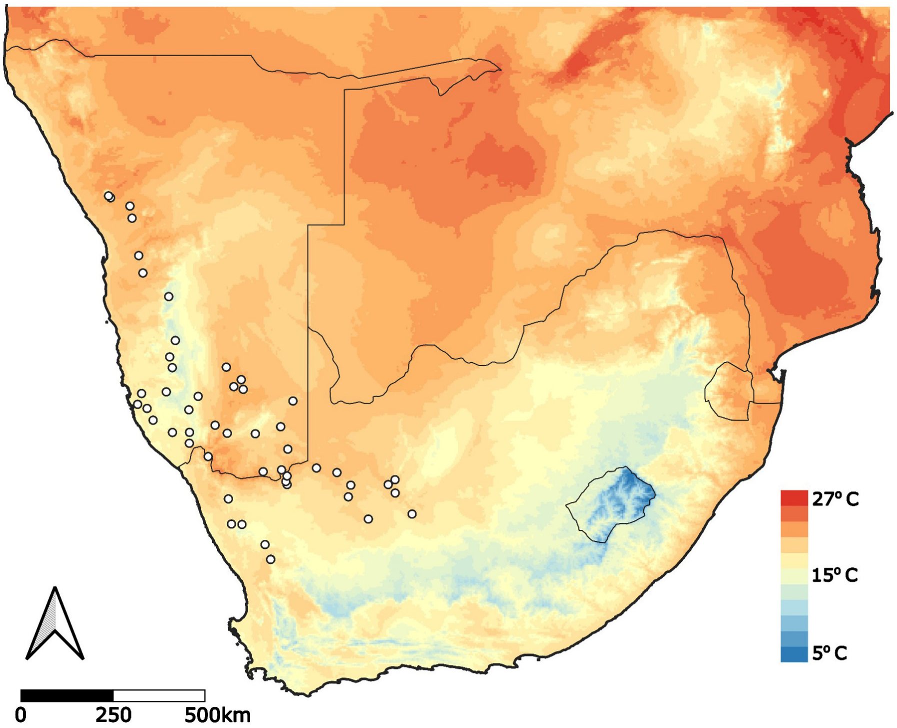

FIGURE 1 | Geographic range of *Aloidendron dichotomum*. Presence localities obtained from Foden et al. (2007) Diversity and Distributions, Foden (pers. obs.) and the Global Biodiversity and Information Facility (GBIF). Mean annual temperature (mean of all monthly temperatures) was obtained from WorldClim (Hijmans et al., 2005) at 2.5-min resolution.

the combined use of SDMs and population genetic methods, broadens our understanding of past and current population dynamics, providing a stronger base for both modelling and interpreting future projected population responses to climate change (Łabiszak et al., 2021).

The primary aim of this study was to reconstruct the paleo-historical macroclimate of southern Africa to determine regions in which *A. dichotomum* may have persisted during natural cycles of climate change to broaden our predictive understanding of how it may respond to future projected anthropogenic climate change. The objective of this approach is to establish the potential value of this species as an indicator (sentinel) for anthropogenic climate change, and as a subject for considering, developing and testing pragmatic conservation solutions to conserve genetic diversity under anthropogenic climate change. Our hypothesis is that the reconstructed macroclimate would reflect a poleward shift of suitable bioclimatic space for *A. dichotomum* post-LGM, from a more equatorward distribution during the late Pleistocene. Further, we predict that the current geographic patterns of genetic variation will reflect higher genetic diversity in the regions that remained climatically suitable for the persistence of *A. dichotomum* during the LGM, with relatively lower variation outside of this space. We predict that in response to future warming, suitable habitat of *A. dichotomum* will shift further polewards as surface air temperatures increase in southern Africa. We finally predict that the migration rate required to keep pace with optimal climate space under anthropogenic climate change would exceed the rate needed to track post-LGM climate change (e.g., see IPCC, 2014).

MATERIALS AND METHODS

Species and Climate Data

Species Occurrence Data

To construct a distribution data set for *A. dichotomum*, three separate data sources were used for presences, including data from Foden et al. (2007), occurrence points documented by W. Foden in March 2018, and presence localities from the Global Biodiversity and Information Facility Database (GBIF[1]). All presence data were collated into a single presence dataset with any duplicate or outlier coordinates removed. The final dataset consisted of 367 presences (**Figure 1**).

Climate Data

Nineteen bioclimatic variables were obtained from WorldClim[2] (version 1.4; Hijmans et al., 2005) at 10 min resolution. The variables consisted of summary statistics for temperature and rainfall at different temporal resolutions, and which represent average climatic conditions from the period of 1950–2000, interpolated from weather station data. These data were used

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[1] http://www.gbif.org

[2] http://www.worldclim.org

as "current" climate data to develop the SDM for the species (Hijmans et al., 2005).

The palaeoclimatic datasets (Last Glacial Maximum and mid-Holocene) and future climate scenario (2070) were also obtained from WorldClim, downscaled data from Global Climate Models (GCMs). Ten-minute spatial resolution datasets were used for the Last Glacial Maximum (22,000 years ago), the mid-Holocene (6,000 years ago) and 2070. For both the LGM and mid-Holocene, the Community Climate System Model (CCSM4) (Gent et al., 2011), the Max-Planck-Institute Earth System Model (MPI-ESM) (Giorgetta et al., 2013) and the Model for Interdisciplinary Research on Climate (MIROC-ESM) (Watanabe et al., 2011) are used. These GCM models are used as they are the three GCM's available on Worldclim for all three time periods (LGM, mid-Holocene, and 2070). All three models were used in the SDM simulations to allow for comparison between models and to assess the agreement in the species ranges predicted. The climate dataset used to represent the future scenario in 2070 are the same GCMs as used for the past reconstructions, taken from the IPCC 5th Assessment Report climate projections (IPCC, 2014), using the representative concentration pathway (RCP 4.5) scenario. The RCP 4.5 is an intermediate "stabilisation pathway" in which radiative forcing is curbed at 4.5 W/m^2 after 2100 where CO_2 levels stabilise at 650 ppm (Clarke et al., 2007; Moss et al., 2008). The pathway was used as it represents a mid-range global mitigation response (Thomson et al., 2011).

WorldClim data show western reaches of southern Africa as arid during the LGM while robust proxies (Stuut and Lamy, 2004) strongly suggest an increase in rainfall during this time, caused by a northern displacement in the westerly winds. As a consequence, we focused primarily on temperature predictors due to uncertainty relating to rainfall reconstruction for the LGM, and incorporated precipitation only via composite bioclimatic variables. Temperature variables are known to be important from previous work that has shown that temperature plays an important role in limiting *A. dichotomum* distributions (Foden et al., 2007; Guo et al., 2016). The final variables were selected using principal components analysis (PCA), visualised using correlation circle plots and informed by Pearson's correlations between pairs of variables. The variables selected were those which both minimised the correlation coefficient and have been identified as biologically important for the species (Guo et al., 2016).

Variables selected included temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean temperature of the wettest quarter, mean temperature of the driest quarter, mean temperature of the warmest quarter, mean temperature of the coldest quarter and precipitation of the coldest quarter.

Modelling Framework for Current Climate

Simulations of the distribution of *A. dichotomum* were conducted using an Ensemble Platform for Species Distribution Modelling, "Biomod2" in R version 3.5 (Thuiller et al., 2016, 2009; R Core Development Team, 2018). Four algorithms were used including three regression models (generalised linear model, GLM; generalised additive models, GAM; and generalised boosted model, GBM) as well as a tree-based method (Random Forest, RF). The GLM was run with quadratic terms and first order interactions, the GAM was run using the mgcv package (Wood, 2017), and the GBM was limited to 1000 trees. The models were calibrated using 80% of the presence data and then evaluated on the remaining 20% (Araújo and New, 2007). In addition, 2000 pseudo-absences were used, and a threefold cross validation was done to yield an average model for each algorithm (4 model algorithms, 3 cross-validations, and 4 repetitions). Therefore, in total, 48 model simulations were run.

The models were then evaluated according to two metrics, namely the area under the Receiver Operating Characteristic (ROC) Curve and the True Skill Score Statistic (TSS) (Allouche et al., 2006). Models are considered to be credible when ROC scores > 0.8 (Swets, 1988) and TSS scores > 0.65. TSS scores varying between 0.4 and 0.8 are considered as fair to good performances (Li et al., 2016; Shrestha et al., 2018). Sensitivity and specificity were also calculated to assess predictive accuracy of the models. Sensitivity is the proportion of observed presences that are predicted as presences and specificity is the proportion of observed absences that are predicted as absences (Allouche et al., 2006). The models were calibrated onto "current" conditions using the same environmental predictors that were used to build the models. Binary (presence/absence) projections were made using the threshold that maximises the ROC score, providing a process which allows the projections to be mapped onto the African climate.

Models often yield different predictions and may vary depending on the differing scenarios. A solution for this variation is the use of multiple models within an ensemble approach, which may then allow a consensus scenario to be achieved (Araújo and New, 2007; Marini et al., 2009). Ensemble models were conducted using two methods, namely committee averaging (CA) and weighted means (WM). These models incorporate all algorithms, all pseudo-sampling and all cross-validations, subsequently producing a coefficient of variation in order to demonstrate whether or not the predictions are consistent. Ensemble models allow for better informed projections to be made when compared to a single model (Araújo and New, 2007). The ensemble models were then projected onto the current African climate which produces both continuous projections (habitat suitability) and binary projections. The ensemble models were also evaluated using TSS and ROC scores and the values were found to be higher in the ensemble modelling in comparison to the individual models (**Tables 1**, **2**).

Palaeoclimate Reconstruction and Future Climate Projections

For the past and future distributional projections, the WorldClim paleo- and future climate data were sourced (version 1.4; Hijmans et al., 2005; see text footnote 2). In order to delineate the range changes of the *A. dichotomum* at each time period an ensemble approach was used. The ensemble models that were calibrated under the current conditions were then projected to the LGM, mid-Holocene and 2070 using the nine bioclimatic predictors from the three GCMs. These models incorporated the GLM, GAM, and RF, in addition to all pseudo-absence sampling and all cross-validations. The models were evaluated using the ROC score and were only kept if the score > 0.8. Two types of ensemble models were used, as above, namely CA and WM. From the models, binary projections were created. This allows for a visualisation of the presence and absence of *A. dichotomum* across the range (**Figure 2**). From this we can determine where range was lost and gained at each time projection.

All SDM predictions were visualised in Quantum-GIS 3.2.1[3] (QGIS). To calculate migration rate, coordinates were obtained from the centroid position of each range for each GCM at each time frame. Range shifts were calculated as the distance between current centroid and centroid of projected range (LGM, mid-Holocene, or 2070) and subsequently, migration rates were estimated. Migration rates were estimated using the distance between centroids as a function of the difference in time between current (present) and the other modelled time periods (LGM/mid-Holocene/2070).

Sample Collection and Amplified Fragment Length Polymorphisms Analysis

To generate a preliminary assessment of genetic variation in *A. dichotomum* and test concordance with models of the species' past distribution, we sampled multiple localities across the species range allowing for inference of broad-scale patterns (detailed in Foden et al., 2007). Thinly sliced sections from the tips of young leaf samples were taken from 3 to 5 adult plants per sampling locality and collected into silica gel for drying prior to DNA extraction. Total genomic DNA was extracted using a standard CTAB extraction method for plant material (Doyle and Doyle, 1987) after grinding the dried sample to a fine powder with liquid nitrogen. A final total of 57 individuals from 17 localities were included in the analysis (**Table 4**).

Amplified fragment length polymorphisms (AFLP) reactions were performed following the general method of Vos et al. (1995) using the Applied Biosystem AFLP Plant Mapping Kit Protocol. Approximately 100 ng of DNA from each sample was used in the AFLP reactions. After digestion with *Eco*R1 and *Mse*1, adaptors were ligated on to both ends of the DNA fragments and a two-step selective amplification was carried out. We tested four primer combinations for the final selective amplification. Reactions were repeated 3–5 times for five test samples to assess the number, quality, and reproducibility of AFLP fragment peaks. Final analysis of samples was based on amplification with *Eco*R1-ACA/*Mse*1-CAT (FAM). The amplified products were run with GeneScan 500 ROX size standard on an ABI 377 Genetic Analyzer (Applied Biosystems) and analysed using GeneScan v3.2 software (Applied Biosystems).

The genetic diversity estimators% polymorphic fragments (P) and Nei's gene diversity (h) (Nei, 1973) were calculated in Genalex v6 (Peakall and Smouse, 2006) and AFLP-SURV v1.0 (Vekemans et al., 2002). The 5% criterion was applied before analysis; loci with fragment frequencies of >95% and <5% were removed. Nei's h was then mapped to the sampling area, interpolating values onto the map space between geographical sampling locations using inverse weighting of the distance to the three nearest neighbour geographical centres in ArcView GIS (ESRI). Known populations (from Foden et al., 2007) are indicated on **Figure 3**.

RESULTS

Climatic Variable Selection

The current distribution of *A. dichotomum* could be modelled using nine bioclimatic variables selected through PCA and correlation coefficients. The relative importance of climate variables was evenly spread for the GLM, GAM, and the RF algorithms (**Figure 4**). "Mean temperature of the coldest quarter" and "Temperature seasonality" were important in all three of these models. The GBM, however, was heavily driven by one variable, namely "mean temperature of the coldest quarter," with only "minimum temp of the coldest month," and "temperature seasonality" having some importance (**Figure 4**).

Current Climate Projections Using Individual Models and Model Performance

Results of the independent models had high congruence. All ROC and TSS values were found to be above 0.8 and 0.65, respectively (**Table 1** and **Supplementary Figure 1**). TSS scores indicate that GAM and RF are the models that have the highest accuracy and ROC scores indicate that GBM and RF are the most accurate. The TSS score is often seen as a more practical and realistic method of evaluating the accuracy of SDM methods (Shabani et al., 2018). However, ROC scores were used as their accuracy result was found to be higher than the TSS score.

The realised current distribution of *A. dichotomum* was generally well predicted by the models, except for the GBM. Mapping the current model projections using ROC scores (to align with most previous work published for southern Africa) showed that the GBM model significantly overestimates the potential current distribution of *A. dichotomum* (**Figure 5**), likely the due to the severe overestimation of the range, as a result of being dominated by only two bioclimatic variables, while the RF

TABLE 1 | Statistical validation of the four models using two metrics: Area under the ROC curve (ROC) and True Skill Statistic (TSS).

Model	ROC score		TSS score	
	Average	Range	Average	Range
GLM	0.956	0.907–0.989	0.905	0.818–0.949
GAM	0.974	0.966–0.992	0.92	0.875–0.960
GBM	0.987	0.977–0.990	0.904	0.869–0.95
RF	0.993	0.988–0.999	0.925	0.887–0.965

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[3] http://download.qgis.org

model is more constrained. The GBM was thus removed from further analysis.

Current Climate Projections Using Ensemble Models

Models with ROC scores of > 0.8 were used to build ensemble models using committee averaging (CA) and weighted mean (WM) from h. Model evaluation scores for both CA and WM were >0.98 and thus performed better than the individual models in projecting the current distribution of *A. dichotomum* (**Table 2**), noting some apparent range overestimation in the southern and eastern ranges of the species relative to recorded presences at these areas (**Figure 2**). Distant disjunct bioclimatic conditions identified by the ensemble model with no known occurrence data for the species were not considered further.

Palaeoclimatic Distribution

Using the ensemble model predictions, suitable bioclimatic space for *A. dichotomum* was modelled for LGM climate, and found to be strikingly different from the current modelled distribution. More than 90% of the species' current range was excluded as bioclimatically suitable, suggesting a significant poleward latitudinal shift for this species since the LGM informed by modelled bioclimatic suitability (extending to 5.8 degrees south of LGM modelled range). During the LGM, models predict that 69% of suitable habitat was outside the current range, mostly inside Namibia (**Figure 2**). Using an average latitudinal distance from the centroid of the current projected range, suitable bioclimatic space for *A. dichotomum* was around 650 km to the north of the current modelled range and around 320 km to the west (**Table 3**). This implies that, provided the species has tracked changes in climate suitability, *A. dichotomum* has migrated 650 km in the poleward direction in the last 18,000 years. As such, its poleward migration rate since the LGM has been *ca.* 0.4 km/decade.

The mid-Holocene model predicts that suitable bioclimatic space for *A. dichotomum* was also contracted in comparison to the current range (≈62%). When comparing modelled shifts in climate suitability between the LGM and mid-Holocene, it is clear that suitable habitat for the species shifted significantly poleward (5.9°S) subsequent to the end of the LGM (**Table 3**). In comparison to the current range, suitable habitat for *A. dichotomum* during the mid-Holocene, despite contracting, is suggested to be found in similar locations and predicted to be on average only 40 km north and 52 km to the west of the current range.

Future Distribution

By 2070 suitable bioclimatic space for *A. dichotomum* is projected to shift 191 km (average of the three GCMs) eastwards (**Table 3**). The northern reaches (above 23.7 degrees) of the current range are expected to become unsuitable in the future and this range will likely be lost. Populations to the west of 14.7 degrees are also projected to be lost (**Figure 2**). The models differed slightly in the latitudinal shift with the CCSM4 and MIROC-ESM models projecting a poleward range shift, whereas MPI-ESM projection suggests a slight equatorward shift (**Table 3**). Nevertheless, on average, the distance that the species will be required to migrate

TABLE 2 | Evaluation scores of the two ensemble models (CA: committee averaging and WM: Weighted Mean) based on ROC scores.

Ensemble model	Testing data	Cut-off	Sensitivity	Specificity
CA	0.976	677	99.455	98.258
WM	0.971	514	99.455	98.258

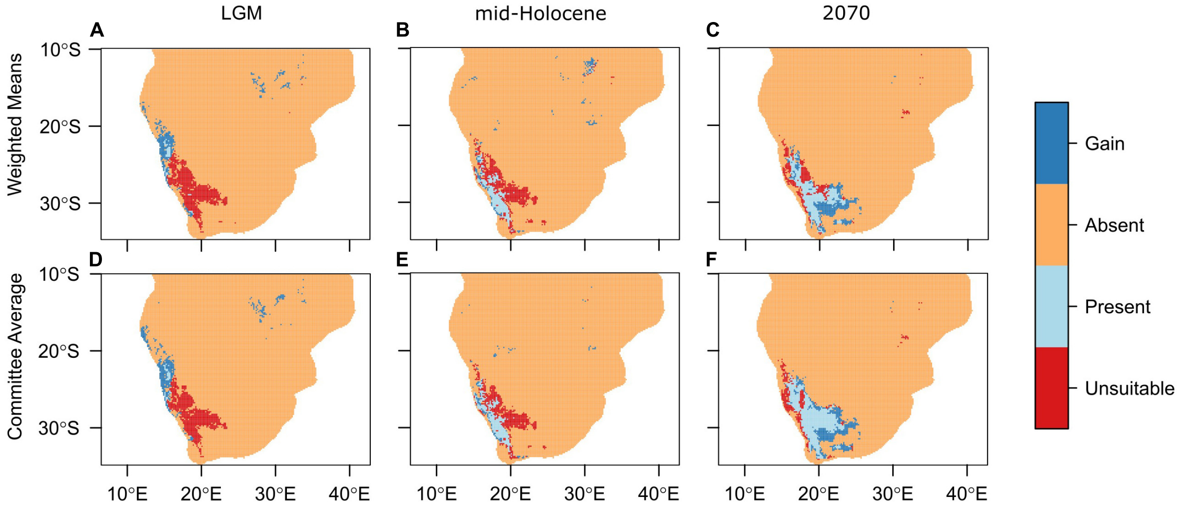

FIGURE 2 | Projected ranges of *Aloidendron dichotomum* for the **(A,D)** Last Glacial Maximum (22,000 years BP), **(B,E)** mid-Holocene (6,000 years BP), and **(C,F)** 2070. Ensemble models were computed using the **(A–C)** weighted means and **(D–F)** committee averaging methods using the CCSM4 global circulation model. Orange regions denote areas where the species is absent; dark blue where it has gained range; light blue where it has remained present when compared to current range projections; and red where range is unsuitable when compared to current range.

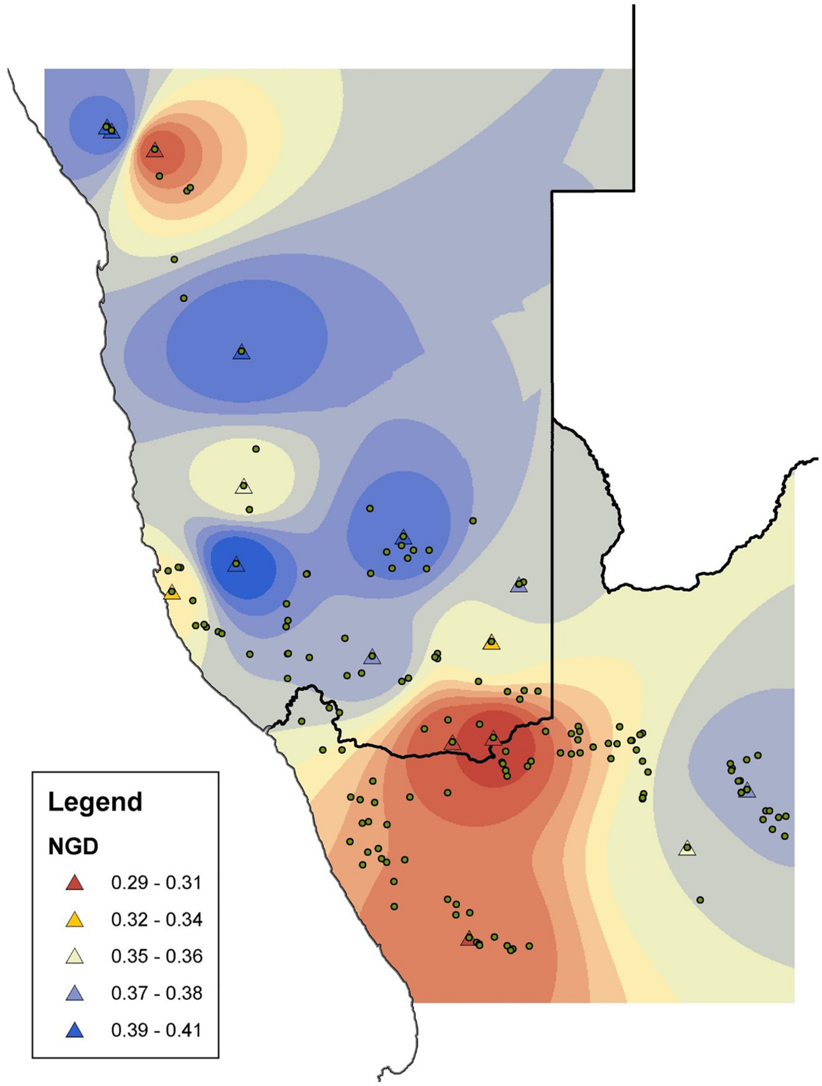

FIGURE 3 | The distribution of genetic variation in *Aloidendron dichotomum* based on Nei's gene diversity *h* (NGD) calculated from amplified fragment length polymorphisms (AFLPs). Triangles represent genetic sampling locations; circles represent known populations surveyed in Foden et al. (2007).

is 42 km in a 70-year period. This implies that the migration rate required for *A. dichotomum* to reach its predicted optimal range by 2070 is 6 km per decade.

Spatial Patterns of Genetic Variation

The final data set comprised 251 AFLP loci analysed as a binary matrix. Mean% polymorphic loci (*P*) across the data set was 39.8% (std. dev. ± 13.3; range 17.1–65.7%) and mean Nei's *h* was 0.36 (std. dev. ± 0.03; range 0.29–0.41) (**Table 4**). The spatial representation of Nei's *h* indicates generally higher levels of genetic variation in the central and more northerly (equatorward) part of the species distribution, with lower levels characterising the more southern and south-easterly regions (**Figure 3**). At the most northerly extent of the species range, individuals at higher altitude on the Brandberg Massif in Namibia support greater levels of genetic variation as measured by Nei's *h*, than their nearest neighbour counterparts on the lower lying plains.

DISCUSSION

Unequivocal attribution of observed range shifts to anthropogenic climate change is rare, as pointed out by Taheri et al. (2021). An argument has been made that agreement between model predictions and observation is now sufficient to support high confidence in the conclusion that anthropogenic climate change is driving species range shifts (Parmesan et al., 2013). However, the incidence of false attribution for individual studies due to range shifts that mimic anthropogenic climate as a driver (Hockey and Midgley, 2009) is not known. In long-lived species, for example, the legacy of historical climatic, or other

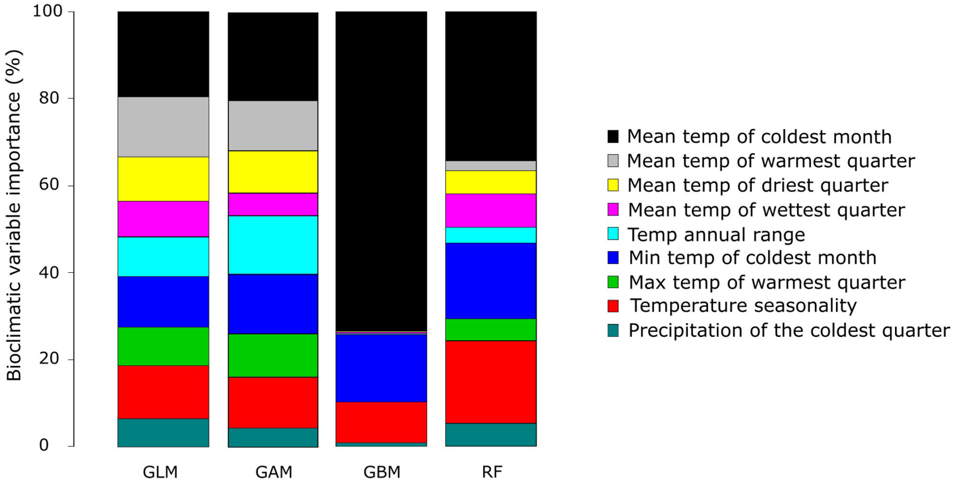

FIGURE 4 | The relative importance of the nine bioclimatic variables for each model algorithm used to model the current distribution of *Aloidendron dichotomum*. The four algorithms used include the generalised linear model (GLM), generalised additive model (GAM), generalised booted model (GBM), and random forest (RF).

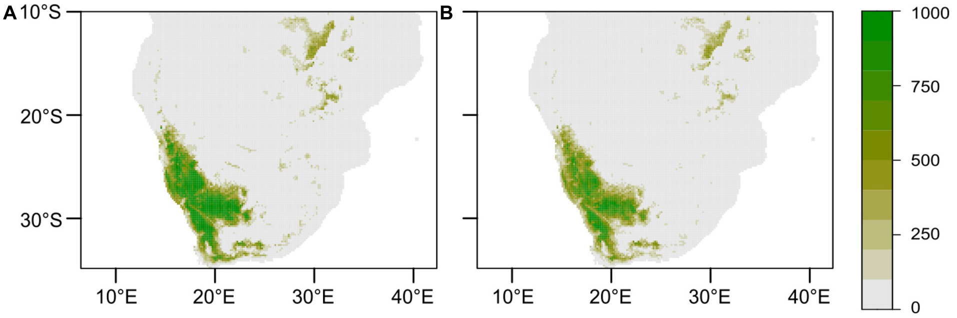

FIGURE 5 | Current modelled geographic range of *Aloidendron dichotomum*. Ensemble models of the generalised linear, generalised additive, and random forest models were computed using the **(A)** committee averaging and **(B)** weighted means methods. Colour scale indicates density estimates.

non-anthropogenic, events can be used as evidence for their influence and challenge the attribution of observed population trends to anthropogenic climate change. For *A. dichotomum*, matching of demographic rates for multiple populations with observed climate shifts (e.g., Foden et al., 2007) in addition to observed geographical patterns of mortality serves to reduce uncertainty in attribution, but nonetheless alternative explanations for these patterns have been proposed (Jack et al., 2014). Understanding and predicting species' responses to ongoing and future climate change can be enhanced through an understanding of species' biological responses to deeper historical climatic trends (Savolainen et al., 2007; Lawing and Polly, 2011). It is therefore extremely useful to use the example of *A. dichotomum* to develop a paleo-historical view on recent observed demographic changes, and ongoing and potential range shifts.

During periods of glaciation, exemplified most recently by the Last Glacial Maximum (LGM; approx. 18,000–22,000 years BP), it has now been well established that species ranges across the world shifted and/or contracted equatorwards, persisting in areas now often referred to as climatic refugia (e.g., Stewart et al., 2010; Lyam et al., 2020). Range expansions occurred in many species when temperatures warmed rapidly (e.g., during the end Pleistocene, 18,000–9,000 years BP) and more slowly towards the mid-Holocene thermal optimum (approx. 6,000 years BP) (Hewitt, 1999; Lyam et al., 2020). While studies investigating the role of the palaeoclimatic oscillations in shaping modern geographic and genetic patterns are generally biased towards the Northern hemisphere (Rödder et al., 2013; Roces-Díaz et al., 2018; Łabiszak et al., 2021), patterns that they identify indicate the general evolutionary fingerprint that may be left by paleo-range shifts. For example, Łabiszak et al. (2021) attribute current phylogenetic patterns of *P. uliginosa* to an ancient bottleneck event that took place around 26,400 years ago as a result of a range contraction during the LGM. Roces-Díaz et al. (2018) showed that *Castanea sativa* contracted its range to Western Europe during the LGM, followed by a subsequent expansion during the mid-Holocene, a shift that was corroborated by phylogeographic analysis.

In southwestern Africa, surface air temperatures likely rose by about 5°C over 10,000 years during glacial to interglacial

TABLE 3 | *Aloidendron dichotomum* latitudinal range shift values for the Last Glacial Maximum (LGM), mid-Holocene, and 2070, in relation to the current range.

		Current	**LGM**			**Mid-Holocene**			**2070**		
			CC	**MR**	**ME**	**CC**	**MR**	**ME**	**CC**	**MR**	**ME**
Centroid Coordinates	X:	18.5	14.9	16.0	14.9	17.3	17.5	17.6	19.9	19.9	20.1
	Y:	–28.1	–21.7	–23.4	–21.6	–27.8	–28.1	–28.3	–28.3	–28.9	–28.1
Latitudinal (Y) distance from current centroid (km)		0.0	708.9	530.3	718.6	67.1	25.8	29.2	–94.2	–25.7	–2.9
Longitudinal (X) distance from current centroid (km)		0.0	–365.3	–250.6	–344.2	25.7	38.5	92.9	131.3	134.1	152.2
Total range lost (%)		0.0	93.2	91.0	92.0	56.5	66.7	61.8	29.8	29.1	26.7
Total range gained (%)		0.0	66.5	99.8	40.5	26.8	13.0	28.8	70.3	50.7	59.1

For each time period (with the exception of current) three Global Circulation Models were used for comparison: CCSM4 (CC), MIROC-ESM (MR), and MPI-ESM (ME). The range loss/gain percentages were calculated from the ensemble model using committee averaging.

TABLE 4 | Sampling locations and estimates of genetic diversity across the range of *Aloidendron dichotomum*.

Population	**Latitude (South)**	**Longitude (East)**	**% Polymorphic loci (*P*)**	**Nei's Gene Diversity (*h*)**
Tantalite Valley, Namibia	28.715973	18.783005	25.8	0.3
Onseepkans, Namibia	28.666712	19.282172	17.1	0.29
C11A, Namibia	27.494788	19.257486	36.6	0.37
C11B, Namibia	27.492297	19.26062	29.5	0.34
Aroab, Namibia	26.793133	19.59336	45	0.37
Tses, Namibia	26.212531	18.186431	54.2	0.4
Uis, Namibia	21.488667	15.15805	38.2	0.31
Brandberg Plains, Namibia	21.261693	14.630877	65.7	0.41
Brandberg Mountain, Namibia	21.209864	14.575819	54.6	0.39
Remshoogte Pass, Namibia	23.951194	16.214	53.8	0.4
Vergenoeg, Namibia	25.593291	16.239861	23.1	0.35
Tweikoppen, Namibia	26.88367	15.366742	34.3	0.34
Namib-Naukluft National Park, Namibia	26.543601	16.14727	23.5	0.41
Canyon Lodge, Namibia	27.670343	17.80606	49.8	0.38
Strondberg, South Africa	30.004857	21.644551	46.6	0.36
Koegas, South Africa	29.297265	22.374613	31.4	0.38
Nieuwoudtville, South Africa	31.105833	18.985667	47.8	0.31

warming at the end of the Pleistocene (Potts et al., 2013), and there is evidence for regional drying associated with the poleward retreat of rain-bearing westerlies (Stuut and Lamy, 2004). These significant changes in bioclimatic conditions likely had significant impacts on the regional semi-arid winter-rainfall flora, as revealed by phylogenetic evidence for the widespread species *Elytropappus rhinocerotis* (Bergh et al., 2007), palynological evidence (Scott, 1994; Scott et al., 2018) and are also thought to have driven a poleward expansion of woody vegetation in the summer rainfall sub-tropics (Scott, 1999). However, most palynological studies in the region have been point based and have not reconstructed individual species' range shifts. A study that investigated the impact of palaeo-climatic changes on a southern African savanna tree species, *S. Senegal*, also suggests that the patterns of range contractions during the LGM, followed by range expansions through the mid-Holocene until current observed distributions seen for Northern Hemisphere species are likely to have also occurred for Southern Hemisphere species (Lyam et al., 2020).

There is strong bioclimatic modelling evidence that the current geographic range of *A. dichotomum* is limited by air temperature variables (Guo et al., 2016), and our modelling focussing on temperature as the primary driving variable showed the likely importance of low temperature limits to range edges in the southerly (poleward) and easterly reaches of *A. dichotomum*'s range (**Figure 4**). According to our SDM, areas of suitable climatic conditions for the persistence of *A. dichotomum* are projected to have contracted equatorward during the LGM when air temperatures would have decreased significantly in this region (**Figure 2**), thereafter, suitable climatic space is projected to have shifted southwards at the end of the LGM and into the mid-Holocene when temperatures became more favourable (**Figure 2**). Indirect evidence of this pattern can be seen in preliminary observations of geographic disparities in the genetic diversity of the northerly and southerly ranges of *A. dichotomum* (**Figure 3**). A general cline in variation characterises the species contemporary range, with northerly populations supporting, on average, higher levels of genetic diversity than populations in the southern and south-eastern regions.

When viewed together, these independent lines of evidence support the hypothesis of a glacial contraction to a northerly refugial state during the LGM (Stewart et al., 2010). Similar patterns have been found for Chinese pine (*Pinus tabulaeformis*), where ecological niche modelling and the presence of glacial lineages provide evidence for post-glacial spread from LGM refugia (Hao et al., 2018). Midgley et al. (2005) suggested that Pleistocene glacial cycles have played an important role in the creation of species clines, and in the current geographic patterns of high endemic richness of clades with low dispersal ability in the winter-rainfall western areas of southern Africa. Huntley et al. (2016) invoked a similar explanation for current geographic patterns of bird species richness in this region, and more broadly in southern Africa. Certainly, the impact of changing climate patterns through the LGM and mid-Holocene until the present day has been important for current geographic distributions and spatial patterns of genetic diversity for multiple long-lived tree species globally (Hao et al., 2018; Lyam et al., 2020; Yannic et al., 2020; Łabiszak et al., 2021).

What insights can be gained for conservation of *A. dichotomum* in the face of projected climate change? Modern plant taxa have persisted since at least the Pleistocene by both *in situ* adaptation and geographic range shifts in response to climate change related to glacial-interglacial cycles (Dawson et al., 2011), with evidence in the winter rainfall region of southern Africa for range shifts in *E. rhinocerotis* (Bergh et al., 2007). The past changes in climatic suitability projected by this study suggests that *A. dichotomum* may also have shifted its range since the LGM. There are four potential responses for plant species under climate change, namely persistence through migration to new ecological niches that are more favourable, persistence through *in situ* adaptation by genetic changes, persistence through *in situ* acclimation by phenotypic plasticity, or local extinction (Aitken et al., 2008; Feeley et al., 2012).

While species with shorter generation times are likely to be able to adapt via evolutionary processes (Lustenhouwer et al., 2018), it has been suggested that long-lived trees with extended juvenile phases are unlikely to be able to match the rate of anthropogenic climate change through *in situ* adaptation alone (Nathan et al., 2011; Kremer et al., 2012). Feeley et al. (2012) even suggest that, due to the high rates of projected anthropogenic climate change, adaptation to climate change by long-lived tree species may even be ruled out altogether. It is believed that migration is the most important autonomous response to climatic change for tree species (Feeley et al., 2012), allowing them to remain within their inferred climatic niche (Pitelka, 1997). However, the response of long-lived species to changing climates is projected to be characterised by significant lags, with species only reaching equilibrium with suitable climate hundreds of years after climate stabilisation (Kuparinen et al., 2010; Moran and Ormond, 2015). It is therefore likely that species will have to simultaneously shift range and adapt and acclimate to new local climatic conditions (Feeley et al., 2012; Moran and Ormond, 2015). Further, it has been suggested that adaptation may become important for long-lived tree species as climate-induced mortality of mature trees increases (Kuparinen et al., 2010). With the observed increase in mortality of mature *A. dichotomum* individuals in warmer populations (Foden et al., 2007; van der Merwe and Geldenhuys, 2017), and with its inherent long generation time, it is possible that evolutionary adaptation may be important to consider in future projections of changes for this species. Shifting range may therefore be only one part of the whole response for *A. dichotomum* to future projected changes in climate, with local adaptation and acclimation playing an important role as well. The ability of *A. dichotomum* to adapt to these changes *in situ*, will require genetic diversity within populations, where some individuals carry genes allowing them to better cope with extreme climatic conditions (Foden et al., 2019).

From the modelling conducted in this study, it can be inferred that a significant pre-Holocene range contraction likely occurred for *A. dichotomum*. For the LGM period, the ensemble models showed spatial agreement of the distribution of *A. dichotomum* during this time (**Figures 2A,D** and **Table 3**). Mid-Holocene projections showed congruent patterns across ensemble models, with the area of suitable climatic space for *A. dichotomum* projected to have been almost 6° south of that during the LGM (**Figures 2B,E** and **Table 3**). The models therefore suggest that, if *A. dichotomum* did indeed track these changes in climate suitability, the past range of *A. dichotomum* would have been found significantly equatorward (650 km north) of its current range and that the species was non-existent in South Africa at this time, with the only suitable habitat located in the higher latitudes of Namibia (North of 27°S).

Range expansions in this species are likely to be caused by rare long distance dispersal events of its wind dispersed seed, followed by exponential population growth (Hampe and Petit, 2005) and potential founder effects. Signatures of this process are predicted to include generally lower levels of genetic diversity in the poleward direction (**Figure 3**). The latitudinal trend in genetic diversity of *A. dichotomum* (**Figure 3**) supports our current conclusion of a paleo-historical poleward range shift from more spatially stable equatorward populations, into novel geographic locations when temperatures warmed significantly at the end of the Pleistocene (Potts et al., 2013). This pattern of genetic diversity may also allude to the importance of microclimatic refugia during the LGM, for example the Brandberg Massif in Namibia which currently supports higher genetic variation than the surrounding lowlands (**Figure 3**). Similar patterns of higher genetic variation at higher elevations have been found for Chinese pine (*P. tabulaeformis*) across the Loess Plateau in northern China as a result of persistence of the species in mountains surrounding the plateau during the LGM, and subsequent recolonisation of surrounding areas from local refugia (Hao et al., 2018).

A concern for slow-growing and long-lived tree species is whether they will be able to shift range fast enough to keep pace with the ever-increasing rates of anthropogenic climate change (Feeley et al., 2012), and the likelihood of significant lags of range shifts behind changing climates (Moran and Ormond, 2015). The projected post-glacial increase in climatic suitability in the poleward direction and the present pattern of populations isolated from each other by many tens of kilometres suggest that long-distance dispersal and establishment is possible for *A. dichotomum* at least on a century time scale. From the modelled climatically determined southern range limit at the LGM, it is possible to calculate a hypothetical migration rate of 0.4 km per decade to permit the current range extent, assuming range expansion in response to warming post-LGM. This rate is far lower than the average rate of ∼2 km/year suggested for other long-lived tree species (Settele et al., 2014), thus plausibly supporting a post-LGM range expansion of this magnitude for this species. However, this hypothetical rate is 15 times slower than the migration rate required for the species to track its optimal climatic space by 2070, as modelled in this study.

Models developed here using mainly temperature controls only were able to project the current range extent of *A. dichotomum* with acceptable accuracy (**Figure 5**), but it must be noted that the poleward range extent was slightly overestimated when compared to current observations of *A. dichotomum* populations (see **Figure 1**). It may therefore be that the more southerly reaches highlighted by the models may be suitable for *A. dichotomum* establishment, but that there is an inherent dispersal lag behind increased climate suitability (Moran and Ormond, 2015), and the species may currently be undergoing a range-filling process (Schurr et al., 2007) in these southern sites where high recruitment rates have been recorded. Understanding ongoing shifts in range at this southerly range edge will be vital in interpreting and monitoring range expansion and correctly attributing observed changes for further learning about autonomous climate change responses in this species. It will therefore be important to conduct empirical studies to pinpoint the role of low temperature relative to other controls on at least the southerly range edge of the species.

Current demographic trends across the species' range have also been used to infer an incipient range shift (Foden et al., 2007). The southern and eastern populations show high population growth rates (Foden et al., 2007; Hoffman et al., 2010; van der Merwe and Geldenhuys, 2017) while northern and central populations (equatorward) tend to have higher mortality rates and low recruitment rates (Foden et al., 2007). These patterns have been attributed to warming and drying trends (Foden et al., 2007), but the attribution was subsequently challenged by an analysis of demographic patterns that split populations by arbitrarily defined climatic zones (Jack et al., 2016), thus making a direct test of the findings of the original attribution study unclear.

The modelled LGM to mid-Holocene (**Figure 2**) and then to current (**Figure 5**) range shifts of *A. dichotomum* align with initial observations of geographic disparities in the distribution of genetic variation in the more northerly and southerly populations, with a general decline in genetic diversity in the poleward direction (**Figure 3**). The palaeogeographic modelling, together with this preliminary genetic data, suggest that the northern populations are highly likely to be older and, as such, acted as the source region for the species' southward range expansion (Hampe and Petit, 2005). A more detailed and densely sampled phylogeographic analysis of the species will allow a robust test of this hypothesis, providing an opportunity to reconstruct both the fine-scale and regional genetic structure of the species, and estimate historical migration rates across the distribution. The linkage between historical climatic events and the current pattern of genetic variation suggests that the phylogeographic history of *A. dichotomum* has likely played an integral part in shaping the current population demographics. A more nuanced understanding of this history will provide valuable insight for its importance to the species in a future of substantial environmental change.

What might be projected for the next few decades to centuries for this species? Surface air temperatures are projected to continue to increase across southern Africa over the next decades, with likely increases of 1–2°C along coastlines and 2–3°C in the interior (Department of Environmental Affairs, 2017), with extreme increases of up to 4–6°C over the western region under high emissions scenarios (Engelbrecht et al., 2011). Warmer temperatures will result in increased evaporation and therefore decreased water availability, especially if rainfall amounts are reduced (Schulze et al., 1993; MacKellar et al., 2014). Model projections to 2070 were consistent across ensemble models (**Figures 2C,F** and **Table 3**), and broadly consistent with previous distribution modelling for the species (Foden et al., 2007; Guo et al., 2016), in projecting significant loss of bioclimatic space in the equatorward parts of the range. However, this study suggests, in concurrence with Foden et al. (2007) and Guo et al. (2016), that the majority of the current poleward range will remain within the optimal climatic niche for *A. dichotomum* at least during this century, but in contrast to Foden et al. (2007), that additional bioclimatic space would become available towards the east (**Figures 2C,F**). The projected persistence of climatic suitability in some equatorward parts of its range into the future may be due to climatic buffering provided by the prominent elevational gradients in these regions (Foden et al., 2007) and could potentially conserve unique genetic variation harboured by these populations (**Figure 3**).

If successful conservation plans and strategies are to be developed to support natural adaptation to climate change, it will be important to firstly understand what capacity these organisms have to adapt on their own, and then subsequently to anticipate biological impacts on such organisms, in order to make the best use possible of natural processes to enhance species, community, and ecosystem resilience. While the models are able to predict the optimal niche space for *A. dichotomum* in the future, it is critical to take into account its life history traits, such as the fact that the species is very slow growing and is slow to reach sexual maturity (Kaleme, 2003). This will provide further insight as to whether the species will be able to migrate to this optimal niche space in time to track the changing climate, which is dependent on its dispersal capability (Foden et al., 2019).

The iconic desert tree succulent *A. dichotomum* provides a powerful test of the theory behind plant species responses to climate change, and its application to conservation action into the future. While poleward populations occupy a part of the potential range which we project to remain suitable in 2070, slow migration rates in potential expansion zones in the south and east (leading range edges), coupled with projected loss of climatic suitability in the north (trailing range edges), will likely narrow the geographic range of *A. dichotomum* (**Figure 1**). The generally lower levels of genetic variation of poleward populations may also be important in limiting the species' potential to survive and adapt to a novel climate (Foden et al., 2019). With our preliminary genetic analyses suggesting higher genetic diversity in the trailing edge populations, they may become disproportionately important for the longer-term conservation of the phylogeographic history and adaptive capacity of the species, warranting a higher level of conservation priority in the near future (Hampe and Petit, 2005).

Further research will also expand our current understanding of both the large and fine scale drivers of genetic structuring of *A. dichotomum* across its geographic range. This could provide invaluable insights into the effects of historical and ongoing climate change on current genetic structuring of the species (Avise, 2000; Byrne, 2007) and strengthen a predictive framework for understanding the future response of *A. dichotomum* to anthropogenic climate change (Gavin et al., 2014). In particular, SDM-based efforts for reconstructing the paleo-range for this species could be improved through the inclusion of credible paleo-historical rainfall patterns that concur with empirically based reconstructions (Stuut and Lamy, 2004), at the local scales necessary to construct SDM projections. Finally, empirical observations and experimental work on this species holds promise for testing SDM assumptions and attributing local scale changes in recruitment and mortality of this species in response to ongoing observed changes in climate.

CONCLUSION

The link between past, present, and future may be extremely valuable when investigating climate change risks to species under anthropogenic climate change. While developing such information for all species, or even several species, is an impossible task, information for selected species in multiple areas may add significantly to an understanding of risks and potential adaptive responses. This longer-term perspective is especially important for understanding the range dynamics of a long-lived sessile organism. The preliminary population genetic data, combined with range modelling in this study suggests that the range of *A. dichotomum* was likely limited to northern (equatorward) reaches relative to its current distribution during the LGM and subsequently expanded polewards into the Holocene. Model projections to 2070 showed a predominantly eastward as opposed to the hypothesised poleward range shift, and diverged from those previously projected (e.g., Foden et al., 2007). Overall, the outlook for the persistence of this species in the wild is positive, as most of its current range appears to remain habitable into the future. However, the northerly (equatorward) populations appear to be at risk of local extirpation, as the calculated migration rate of the species is unlikely to permit them to track the projected warming rate over the next few decades. If this occurs, valuable adaptive genetic diversity of populations possibly selected under warmer and drier conditions may be lost. Beyond 2070, if emissions continue to rise and climate to warm, populations in easterly and poleward reaches of the range may be at risk that would be exacerbated due to their lower genetic diversity.

We would propose that proactive *ex situ* efforts could be made to ensure safeguarding of this genetic diversity, such as through carefully considered assisted colonisation informed by work that elaborates on this study. The findings presented here add to the growing literature on this iconic species that will inform conservation responses not only for this species, but potentially also for a wide range of endemics and near endemics of this species-rich region.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

LB and GM designed the study. LB led species distribution modelling. JB led the genetic analysis. K-AG led manuscript preparation. All authors contributed to writing.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.715702/full#supplementary-material

Supplementary Figure 1 | Projections of the current distribution of *Aloidendron dichotomum* in southern Africa using the **(A)** generalised linear model, **(B)** generalised additive model, **(C)** generalised boosted model, and **(D)** random forest algorithms. Colour scale indicates density estimates (see **Supplementary Data Sheet 1**).

Supplementary Data Sheet 1 | Locality data (X:Y latitude:longitude decimal degrees) for *Aloidendron dichotomum* used for distribution modeling in this paper.

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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

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> *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? 2. Are rare plant species more limited by genetic variation? 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? 4. Do small-ranged species show greater signals of extinction dept?	1. Assume small ranges are most vulnerable to climate change. 2. Assume range size is influenced by myriad factors, including niche-breadth, species' age, niche availability, range position, and mating system. 3. Promote strong protection and conservation status for endemic, rare, and small-ranged species. 4. Promote connectivity and gene flow for large-range species. Engage relevant stakeholders in the discussion.	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

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. *xantiana* (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. *xantiana* (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.

Conclusions, Future Directions, and Conservation Applications

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.

Conclusions, Future Directions, and Conservation Applications

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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Managing Uncertainty in Scots Pine Range-Wide Adaptation Under Climate Change

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Forests provide important ecosystem services and renewable materials. Yet, under a future climate, optimal conditions will likely shift outside the current range for some tree species. This will challenge the persistence of populations to rely on inherent plasticity and genetic diversity to acclimate or adapt to future uncertain conditions. An opportunity to study such processes is offered by Scots pine (*Pinus sylvestris* L.), a forest tree with a large distribution range including populations locally adapted to a wide variety of environments, which hinders a range-wide assessment of the species to climate change. Here we evaluate tree height growth uncertainty of Scots pine marginal populations in Spain and the Nordic countries linked to their genetic adaptation promoted by different climatic drivers. Our aims are to: (i) review the main climatic drivers of Scots pine adaptation across its range; (ii) undertake provenance-based modeling and prediction of tree height under current and future climate scenarios including four representative concentration pathways (RCPs) and five general circulation models (GCMs) at two extremes of its climatic niche; (iii) estimate uncertainty in population tree height linked to the main drivers of local adaptation that may change among RCPs and GCMs in the Nordic countries and Spain. Our models revealed that tree height adaptation is mostly driven by drought in Spain and by photoperiod in the Nordic countries, whereas the literature review also highlighted temperature as a climatic driver for the Nordic region. Model predictions for the Nordic countries showed an overall increase in tree height but with high uncertainty in magnitude depending on the RCPs and GCMs whereas predictions for Spain showed tree height to be maintained in the north and reduced in the south, but with similar magnitudes among RCPs and GCMs. Both models predicted tree height outside the data range used to develop the models (extrapolation). Predictions using higher emission RCPs resulted in larger extrapolated areas, constituting a further source of uncertainty. An expanded network of Scots pine field trials throughout Europe, facilitated by data collection and international research collaboration, would limit the need for uncertain predictions based on extrapolation.

Keywords: adaptation, tree height, mixed-effect models, climate change, Spain, Nordic countries of Europe, provenance, *Pinus sylvestris* (L.)

INTRODUCTION

Climate change is reshaping species distributions at an unprecedented pace. Evidence of range contraction has been observed in European forests, for example, caused by the increase in drought-related tree mortality rates in climatically marginal populations (Archambeau et al., 2020; Changenet et al., 2021), as well as the maladaptation of climatically marginal populations to current climate conditions observed in North American and European forests (Pedlar and McKenney, 2017; Fréjaville et al., 2020). To survive under new climates, climatically marginal populations can persist *in situ* through genetic adaptation or phenotypic plasticity (Valladares et al., 2014; Aitken and Bemmels, 2016). However, these two evolutionary processes have different implications for long-lived species such as trees. Plasticity imparts a rapid response to new environments without changes in the genetic structure (Nicotra et al., 2010) and can help some marginal populations to survive under climate change (Gárate Escamilla et al., 2019), whereas genetic adaptation occurs over generations, implying that trees may not be able to adapt to rapid environmental changes but rather carry the burden of maladaptation (Pedlar and McKenney, 2017; Fréjaville et al., 2020). Generally, conifers present higher adaptation rates for tree growth than broadleaf species (Benito Garzón et al., 2019), and that broadleaves tend to express high plasticity (Sáenz-Romero et al., 2017; Gárate Escamilla et al., 2019). Whether this characteristic would confer an advantage to broadleaf species over conifers to survive under fast climate change is still unclear because phenotypic plasticity may delay adaptation processes in the long term (Chevin et al., 2010). Furthermore, the drivers triggering adaptation may change across species ranges as a consequence of different climatic pressures, at least in trees covering large distribution areas. This can present different odds for a population to survive under future climates (Atkins and Travis, 2010). Therefore, understanding the climatic drivers of adaptation in the leading and trailing edges of species ranges is key to assessing the vulnerability of marginal and peripheral forest populations to climate change.

Genetic field trials (also called provenance tests) are controlled experiments where seed from natural populations is planted across large geographical gradients. Although field trials were originally planted for breeding purposes, they have proved to be a useful resource to understand the likelihood of survival under climate change (Mátyás, 1994) providing accurate indicators of plasticity and local adaptation of fitness-related traits among provenances. As such, field trials have been extensively used to improve breeding programs (Gray et al., 2016), quantify phenotypic plasticity (Matesanz and Ramírez-Valiente, 2019; Vizcaíno-Palomar et al., 2020), perform species range predictions accounting for local adaptation and phenotypic plasticity (Benito Garzón et al., 2019), and design assisted migration programs (Isaac-Renton et al., 2014).

One of the species most widely planted in genetic field trials is Scots pine (*Pinus sylvestris* L.), an economically and ecologically important species with the largest distribution among tree species in Europe. Its distribution range covers a wide climatic niche (Benito Garzón and Vizcaíno-Palomar, 2021) from southernmost Spain to Scandinavia (Caudullo et al., 2017). In spite of the large network of field trials, modeling approaches covering the entire distribution range of the species are scarce (Reich and Oleksyn, 2008), probably owing to the different drivers triggering adaptation of the population across its range (Torssonen et al., 2015; Berlin et al., 2016; Vizcaíno-Palomar et al., 2019; Rubio-Cuadrado et al., 2020) but also because of a lack of access to relevant range-wide comprehensive data. As such, many regional modeling approaches targeting Scots pine adaptation have been developed over the years. Studies of marginal populations suggest that Scots pine has adapted to different environments over time. For instance, populations at the northernmost part of the species range are mostly adapted to photoperiod and temperature (Rehfeldt et al., 2002; Berlin et al., 2016), whereas those at the southernmost part of Scots pine range show adaptation to drought (Matías and Jump, 2014; Vizcaíno-Palomar et al., 2019). Yet, to what extent these drivers triggering population adaptation across the range can confer an advantage of survival and growth, to this long lived tree species under climate change, is still not clear because of the uncertainty of the future climate.

The IPCC 5th Assessment Report (IPCC, 2014) synthesized knowledge regarding current climate change science and classified four scenarios of greenhouse gas (GHG) emissions leading to increased radiative forcing, causing a warming of the atmosphere by 2100. These Representative Concentration Pathways (RCPs) include: RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5. Many General Atmospheric-Ocean Circulation Models (GCMs) have been parameterised to link scenarios of population growth and socio-economic futures to the range of RCPs; these are termed Shared Socio-economic Pathways (SSPs). The link between SSPs and RCPs allows future global socio-economic scenarios to be assessed in terms of the spatial variation in changing temperatures. There is uncertainty about which SSP trajectory the global system will follow. The RCP 2.6 represents an increase in global temperatures below 2°C, whereas the intermediate RCP 4.5 is projected to cause temperatures to rise until 2040-50 after which reductions in GHG emissions forcing will occur. For RCP 6.0 emissions will peak in 2080 and then decline. For RCP 8.5 GHG emissions continue to rise throughout the 21st century leading to global warming of up to 4.8°C by 2080. However, some recent research suggests that the RCP 8.5 scenario is unlikely due to the recent technological development of renewable energy sources (see e.g., Hausfather and Peters, 2020). Additional uncertainty occurs among the GCMs as each differs slightly in model parameters. This is shown in the range of temperature increase in each of the RCP categories (IPCC, 2014).

Scots pine has a large natural distribution range from Finland and Sweden (hereafter Nordic countries) to Spain and it is locally adapted to a wide variety of environments. Uncertainty inherent in future climate projections hinders the assessment of the species and the vulnerability of the populations to global climate change. Our main goal is to assess this uncertainty in tree height growth linked to the genetic adaptation of Scots pine populations driven by different climatic drivers across its distribution range. Here we (i) review the main climatic drivers of adaptation of Scots pine range-wide; (ii) re-analyze tree height growth at the two extremes of the thermal gradient of its climatic niche: Spain and

Nordic countries, where populations show adaptation to drought and cold conditions, respectively; and (iii) estimate uncertainty in population tree height growth spatial predictions linked to the main drivers of local adaptation that may change among future scenarios (RCP 2.6, RCP 4.5, RCP 6, and RCP 8.5) differently in the Nordic countries and Spain.

MATERIALS AND METHODS

Tree Height Measurements and Field Trials

We used tree height data of Scots pine (*Pinus sylvestris* L.) compiled in the Nordic countries and Spain. For the Nordic experiments, tree height data were collected from 378 different field trials (**Figure 1**) established from 1951 to 1996 and measured at ages ranging from 8 to 35 years-old. Several of the trials were measured repeatedly but only one measurement per tree was used for further analysis. Among these field trials, a total of 276 seed-lots sampled from wild Scots pine provenances (populations) were distributed. This was not a complete reciprocal-transplant experiment because field trials were established according to slightly different objectives and using different materials. Since the Nordic tree height dataset had a heterogeneous planting design, data from single trees were not used for analysis. Instead, least-square means (LS-means) for each provenance/field trial combination were estimated in preparatory site-wise analyses. For these analyses GLM and MIXED procedures in the SAS STAT package were used (SAS Institute Inc., 2011; see Berlin et al., 2016 for details). LS-means were transformed by the

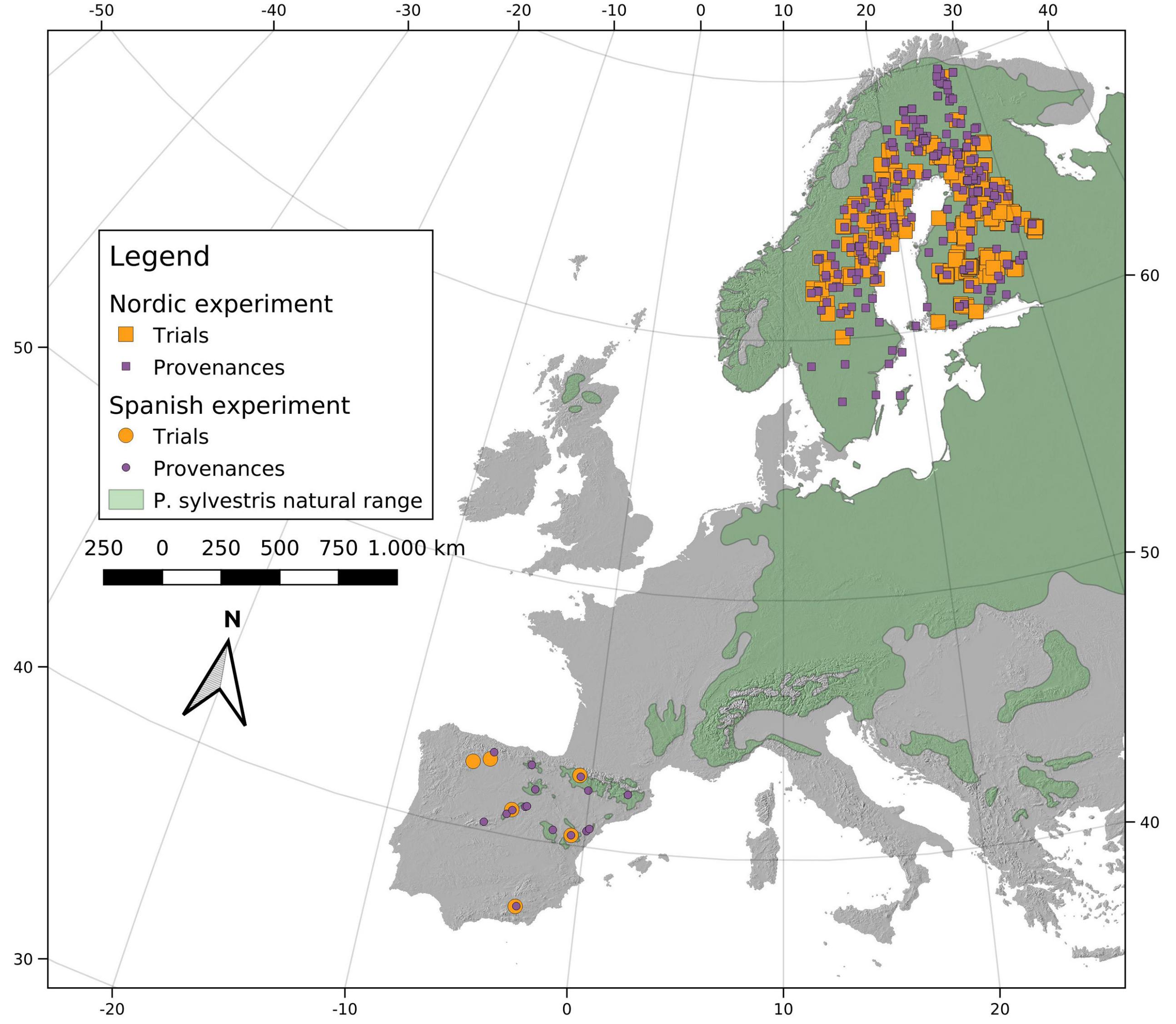

FIGURE 1 | Field trials and provenances planted in Sweden, Finland and Spain. The background area colored in green corresponds to the Scots pine native range (Caudullo et al., 2017).

natural logarithm prior to further analysis to assure normality and homogeneity of the data.

For the Spanish experiment, at the southern range of the species, tree height of individuals after 14 and 15 years of growth was measured at six field trials (**Figure 1**). Sixteen genetically distinct Spanish populations (Alía et al., 2001; Prus-Glowacki et al., 2003; Robledo-Arnuncio et al., 2005) covering the species distribution in Spain were planted in each of the six field trials. During the years 1988 and 1989, seeds were collected to form provenance (population) seed-lots (Agúndez et al., 1992; Alía et al., 2001). A seed-lot was created by mixing the clumped seeds collected in natural populations from at least 25 mother trees, with a 50 m separation distance between each individual to avoid interbreeding (González-Martínez et al., 2006). Between 1990 and 1991, 2-year-old plantlets originating from the seed-lots were planted in each field trial, following a randomized complete block design, with four blocks and a 16-tree square plot for each population, planted at a 2.5 m × 2.5 m spacing.

Climatic and Environmental Data

We combined several databases to characterize the climate at the origin of provenances and the climate at the field trials. This was achieved by downscaling the CRU-TS dataset (Harris et al., 2020) from ∼50 to ∼1 km (30-arc s) using WorldClim v1.4 (Hijmans et al., 2005) with the 1961–1990 climatic normal period as baseline. Our downscaling technique used the delta method (Ramirez-Villegas and Jarvis, 2010), a technique that accounts for topographic variation and improving the reliability and spatial resolution of coarser spatial datasets (Moreno and Hasenauer, 2016; Fréjaville and Benito Garzón, 2018). To characterize the climate of the future (period of years: 2056–2085 and called 2070s), we used five GCMs for each RCP generated from CMIP5 (see **Supplementary Material 1** for further details).

For the Nordic experiment, the annual accumulated growing day-degree temperature sum above a 5°C threshold (GDD5) was used as a climate variable for field trials (**Table 1**) as had been determined by previous modeling efforts (Persson and Ståhl, 1993; Persson, 1994; Berlin et al., 2016). For this variable, we used an average across all annual GDD5 values from the field trial establishment to the time of phenotypic measurements. In the Nordic experiment, however, the time periods varied substantially *per se*. The year of establishment ranged from 1951 to 1996 and year of height measurement varied from 1963 to 2011. With respect to conditions at the origin location of Nordic provenances, latitude was used as a proxy for photoperiod in the model, and was constant over time. For the Spanish experiment, we used the summer heat moisture index (SHM), spring precipitation (SPR) and temperature differential (TD–as a measure of continentality); these variables were selected previously in Vizcaíno-Palomar et al. (2019) (**Table 1**). Climate variables for the provenances consisted of averages calculated from 1901 to 1950, whereas the climate variables for field trials were obtained by calculating averages from the time the trial was planted to the time phenotypic measurements were taken (as in the Nordic experiment). As the Spanish field trials were established and measured in concert, this implies a time-period from 1990 or 1991 to 2005.

TABLE 1 | Environmental and climatic indexes used in the models.

Variable/Model	Description	Unit	Model	Use
Growing Day Degree (GDD5)	Accumulated annual sum of daily mean temperatures above 5°C termed growing day-degrees	day°C	Nordic	Field trial variable
Latitude (LAT)	Latitude of the provenances and field trials	°	Nordic	Transfer distance
Summer Heat Moisture Index (SHM)	Ratio of the mean temperature in the warmest month to meters of summer (june-august) precipitation	°C/m	Spanish	Transfer distance
Temperature differential (TD)	Difference between the mean temperature of the warmest month and the mean temperature of the coldest month	°C	Spanish	Field trial variable
Spring Precipitation (SPR)	Amount of rainfall in March, April and May	mm	Spanish	Field trial variable

Linear Mixed-Effect Models

We calibrated two independent models to assess how tree height (H) for different Scots pine populations respond to environmental variation. The Nordic model fitted field trial/provenance- wise means of tree height obtained from Nordic field trials and the Spanish model fitted individual tree height data measured in Spanish field trials. In both models, we used the environmental transfer distance, Δenv, calculated as the difference between the environment at the provenance origin and the environment of the field trial. This Δenv term allows us to assess variation in tree height due to shifts across environmental gradient. This variation occurs when $\Delta\text{env} < 0$, meaning that the provenance is transferred to sites with a greater environmental value than its origin, or transferred to sites with smaller environmental values than its origin when $\Delta\text{env}>0$. $\Delta\text{env} = 0$ means that the provenance is growing under local environmental conditions. Environmental variables relevant for the study of climate change and prediction uncertainty are listed in **Table 1**. For both Nordic and Spanish models, fixed effects were tested using the maximum likelihood (ML), and random effects were tested using the restricted maximum-likelihood method (REML).

Nordic Model

A linear mixed-effects model was used to predict tree height as a function of the transfer distance in latitude ($\Delta\text{env} = \Delta\text{LAT}$) being a proxy primarily for photoperiod. In addition, the GDD5 was used to describe the climate of the field trial and was used in interaction terms with the latitudinal transfer distance. These variables were included as fixed effects and the field trial site as a random effect, to account for unexplained environmental variation. This model was established by a hypothesis-driven process (see **Supplementary Material 2** for more details), building on the work of previous regional modeling (Persson and Ståhl, 1993; Persson, 1994; Eriksson, 2008; Berlin et al., 2016). Logarithm-transformed LS-means of tree height estimated for each provenance-field trial combination [ln(H_{jk})] were fitted as follows:

$$\begin{aligned}\ln\left(H_{jk}\right) \; = \; & \alpha_0 + \alpha_1 \ln\left(AGE_k\right) + \alpha_2 \ln\left(EST_k - 1945\right) \\ & + \alpha_3 \ln\left(GDD5\_s_k\right) + \alpha_4 \triangle LAT_{jk} + \alpha_5 \triangle LAT_{jk}^2 \\ & + \alpha_6 GDD5\_s_k \times \triangle LAT_{jk} + \alpha_7 GDD5\_s_k \times \\ & \triangle LAT_{jk}^2 + \beta\left(Trial\right) + \varepsilon_{jk}\end{aligned}$$

where AGE_k is the tree age for the kth field trial at measurement, EST_k is the establishment year of the kth field trial and $GDD5\_s_k$ is the kth field trial averaged from the year of planting to the year of height measurement. In addition, ΔLAT_{jk} is the latitudinal transfer distance between the kth field trial and the jth provenance present at the kth field trial. Finally, β is the random field trial effect and ε_{ijk} is the residual distribution of the jth provenance at the kth field trial following a Gaussian distribution.

Spanish Model

Also here we used a linear mixed-effects model to predict tree height as a function of the environmental transfer distance of the Summer Heat Moisture index (Δenv = ΔSHM), the SPRing precipitation climate at the field trial site (SPR_s) and the Temperature Differential (TD_s) following previous models of the species in Spain (Benito Garzón et al., 2011; Valladares et al., 2014; Vizcaíno-Palomar et al., 2019). In this model, climatic variables were included as fixed effects and specifically we modeled the linear, quadratic and linear interaction terms of ΔSHM and SPR_s, and the linear term for the covariate TD_s. In the random part of the model we included provenance for unaccounted environmental variation among populations (β). The final model was built based upon a hierarchical backward selection procedure from the most complex model and the procedure is further detailed in **Supplementary Material 2**. The final Spanish model for individual tree height, H_{ijk}, was fitted as follows:

$$\begin{aligned}H_{ijk} \; = \; & \alpha_0 + \alpha_1 TD\_s_{ik} + \alpha_2 SPR\_s_{ik} + \alpha_3 SPR\_s_{ik}^2 + \alpha_4 \triangle SHM_{ijk} \\ & + \alpha_5 \triangle SHM_{ijk}^2 + \alpha_6 SPR\_s_{ik} \times \triangle SHM_{ijk} + \\ & \beta\left(Provenance\right) + \varepsilon_{ijk}\end{aligned}$$

where H_{ijk} is tree height of the ith individual of the jth provenance in the kth field trial and α_s is the set of *n* parameters associated with the fixed effects of the model. Finally ε_{ijk} is the residual distribution of the ith individual of the jth provenance at the kth field trial following a Gaussian distribution.

Drivers of Adaptation

We performed a literature compilation of the different drivers triggering Scots pine adaptation across its distribution range. The review was done by searches on relevant phrases such as *adaptation, Scots pine, Pinus sylvestris* and *climate change* in Google scholar and by inspecting their reference lists in turn.

Uncertainty Analysis of Tree Height Predictions

Our uncertainty analysis used spatial predictions of tree height in Nordic countries and Spain performed on a synthetic mean provenance for each region, reflecting an average among the provenances used to develop the models. The predictions were performed only within the species distribution range taken from Caudullo et al. (2017). For the Nordic region the mean provenance had a latitudinal origin at 64.87°N, whereas for Spain, the mean provenance had an SHM value of 90.55°C/m. In addition, for model predictions across the Nordic region, the tree age (AGE) was set at 15 years in order to correspond with the Spanish model. For the Nordic model predictions, the year of establishment (EST) was set at 1980 as height predictions, plotted across the range of EST-values, suggested that no appreciable silvicultural improvements had been achieved since that time. We predicted tree height for the Nordic region and Spain using the respective models. Predictions were performed for all four RCPs scenarios combined with the five GCM variants resulting in a total of 20 scenario-variant predictions. In addition, we also calculated mean predictions for each RCP across all five GCMs by using the respective climate ensemble mean of that RCP. All analyses were undertaken in R (R Core Team, 2020) with the raster (Hijmans, 2020) and tidyverse (Wickham et al., 2019) packages.

Assessing Spatial Agreement Between General Circulation Models

For each scenario-variant combination described above, we calculated the difference in tree height between a prediction made for the future climate period (2070s) and the reference height corresponding to the climate normal period (1961–1990). Such prediction calculations (future height–reference height) were performed for each 1 km × 1 km location and a record was made where predicted future height was greater than the reference height. We grouped these records by RCP, and for every 1 km × 1 km location summed the number of GCMs which "agreed" that future height was greater than the reference height. We then subtracted from the sum, the number of GCMs which "disagreed" that future height was greater than the reference height. This assessment resulted in a score which ranged from +5 (maximum agreement among GCMs that future height will exceed reference height) to −5 (maximum agreement among GCMs that future height will be lower than the reference height). Areas where three or two GCMs either agreed or disagreed (scores +1 and −1) thus highlight areas of greater prediction uncertainty.

Model Predictability Limits

We defined model predictability based on the ecophysiological limits of the species recorded from our trials to account for areas where predictions were generated by extrapolation outside the environmental ranges of our data used for model development. For Nordic predictions, these limits were recorded for locations where environmental data points exceeded: (a) GDD5 below 527 day°C or above 1,349 day°C which, according to our climate data, was the smallest and greatest GDD5 experienced in the Nordic field trials included in the model, and; (b) a latitude greater than 5 degrees above or below the latitude of the mean provenance because provenance transfers of that magnitude were the greatest undertaken within the data used to calibrate the models. For the Nordic mean provenance these latitudinal limits were thus set at < 59.87°N and > 69.87°N. Following the same principles we established the ecophysiological limits of the species from recorded locations for Spanish predictions where climatic conditions exceeded: (a) TD below 13.65°C or above 17.25°C; (b) SPR below 177.75 mm or above 269.97 mm and; (c) where the location SHM differed below −213°C/m or above +115°C/m that of the mean provenance SHM.

Consequently, in order to visualize the model predictability limits, we carried out the same type of assessment based on GCM-agreement on increased tree height in a future climate, and where agreement was determined by whether model predictability limits were exceeded or not. We chose to only show where limits were exceeded by three or more GCMs, as we considered this to be "more likely than not."

Using Coefficient of Variation as an Uncertainty Metric

We used the Coefficient of Variation (CoV) as an indicator of variability between future predictions of tree height. This statistic presents a ratio of the standard deviation to the mean, with higher values indicating greater variation between predictions and therefore higher uncertainty in terms of the most likely outcome. CoV values were estimated for two different aspects of variation/uncertainty.

The first important aspect of prediction uncertainty is connected to the spatial variation of tree height predictions over the geographic study area for a specific climate scenario. In order to cover spatial prediction variation and uncertainty we calculated CoV for the ensemble mean predictions for each RCP across the studied regions (Nordic countries and Spain) and related the standard deviations to the average tree height prediction for the reference period. The nature of such geographic predictions means they have a very large number of data points, especially at higher resolutions, and this can affect statistical analysis. To reduce this spatial autocorrelation effect, we took 100 random samples of 1,000 data points from each set of predictions. We calculated the standard deviation of each RCP-prediction from the reference period mean height. CoV was then calculated as a percentage of the reference period mean height. This calculation was carried out for (a) a complete random sample, and (b) a random sample with data points removed where model predictability limits were exceeded.

The second quantitative measure of tree height prediction uncertainty is the variation in predictions at each location among different GCMs and RCPs. This uncertainty can also be quantified by estimating CoV under a future climate in relation to the predicted tree height during the reference period. We calculated CoV across GCMs within each RCP for each 1 × 1km location. For each location, we calculated an RCP mean prediction using all five GCMs, and the standard deviation of each individual GCM prediction from this overall RCP mean. CoV was calculated as follows, where σ is the RCP standard deviation and μ is the RCP mean:

$$CoV = \frac{\sigma}{\mu}$$

RESULTS

Drivers of Adaptation as Identified by the Literature and Models

A literature search for important climatic drivers of Scots pine growth across Europe indicated that drivers differed across the range; with temperature and photoperiod often found as the main drivers at high latitudes, while drought was found to dominate as a driver in central and southern Europe (**Table 2**).

Given the down-scaled CRU-TS dataset, GDD5 was confirmed to be a highly significant predictor ($p < 0.001$) for tree height at a given field trial in the Nordic region (**Table 3A**). Photoperiod, described as latitudinal transfer, was confirmed as a highly influential driver of adaptation. In the Spanish model, the final best model included SHM as the main driver of adaptation while TD and SPR were retained as significant site predictors of tree height (**Table 3B**). When accounting only for fixed effects, the height growth model in the Nordic region explained 77% of the total variance while the corresponding model in Spain explained 39% of the total variance.

Tree Height Predictions and Transfer Distances

Using our linear mixed models, we predicted tree height over a range of environmental transfer distances, i.e., across a range of values of the Δenv for a sample of field trials in the Nordic experiment and for all six available planting sites in the Spanish experiment (**Figure 2**). In general, we found that tree height curves were either almost flat (Nordic experiment) or slightly concave (Spanish experiment). This implies that optimal tree height was predicted over a broad range of values of ΔLAT using the Nordic model, or over a narrower range of values of ΔSHM using the Spanish model. From a practical point of view, this means that there are provenances of nearby origins that all would perform reasonably well at a given planting site both in Nordic and Spanish regions.

For the Nordic experiment, we usually observed that transfers of more southern provenances ($\Delta LAT < 0$) would result in higher predicted tree height in comparison to that of a local provenance, that is $\Delta LAT = 0$ (**Figure 2A**). However, the temperature climate at the field trial location (GDD5, **Table 4A**) interacted with this trend suggesting that the optimal transfer lengths would be longer for the trials with a mild climate (high GDD5) whereas, at the other extreme, the local provenance would be the best adapted given the coldest climate (low GDD5). For the Spanish experiment, in five out the six planting sites, we observed that transfers of provenances from colder or wetter summers, $\Delta SHM < 0$, than that of the local provenance, $\Delta SHM = 0$, would result in a slight improvement in tree height that is (**Figure 2B**, except the uppermost curve). For the uppermost curve (Aragüés) however, the finding was the reverse

TABLE 2 | Literature search for environmental adaptive drivers (All drivers of Adaptation and Main driver) of Scots pine phenotypic traits (Trait) and the geographic regions (Region) where these were found to be relevant.

Main driver	Region	Trait	All drivers of adaptation	Method	References
Photoperiod	Sweden, Finland	Tree height and survival	Growing day-degrees and latitude	Linear mixed-effects model analysis of 378 field trials	Berlin et al., 2016
Multiple	Sweden	Biomass production	Growing day-degrees, photoperiod, CO_2-concentration, soil moisture, nitrogen availability	Tree growth simulation models	Bergh et al., 2010
Maximum temperature	Iberian Peninsula	Tree height and survival	Maximum temperature of the warmest month	Random forest analysis of height growth and mortality–12 provenances grown at 4 sites	Benito Garzón et al., 2011; Valladares et al., 2014
Growing day-degrees	European and Asian countries of the former USSR	Tree height	Growing day-degrees, temperature differential (summer-winter), moisture index	Quadratic regression model analysis of 47 field trials	Rehfeldt et al., 2002
Growing day-degrees	Finland	Volume growth	Growing day-degrees, soil moisture, nitrogen availability and within-stand light	Forest ecosystem simulation models	Torssonen et al., 2015
Growing day-degrees	Finland	Radial growth	Growing day-degrees, soil moisture, precipitation and nitrogen availability	Forest ecosystem simulation models	Kellomäki et al., 2018
Temperature	Europe wide (west of 40.2 degrees E)	Radial growth	Mean annual temp, mean diurnal range, temp seasonality, mean temp of wettest quarter, mean temp of driest quarter, precipitation seasonality, precipitation of warmest quarter, precipitation of driest quarter	Analysis of tree ring database and ecological niche modeling	Bombi et al., 2017
Drought	Spain	Tree height	Spring precipitation of planting site and summer heat moisture index of population origin	Linear mixed-effects model analysis of tree height growth–16 Scots pine provenances at 6 common gardens	Vizcaíno-Palomar et al., 2019
Drought	Southern Spain–Northern Germany	Radial growth	Drought indices such as standardized evapotranspiration index (SPEI)	Analysis of tree ring network along approx. 2,800 km gradient	Bose et al., 2020
Drought	Spain	Radial growth	Tree size (DBH), temperature of the previous winter and current spring, SPEI (drought), altitude	Field samples from 2 sites, measurement of height, DBH, tree ring cores. Linear mixed-effects model of growth.	Rubio-Cuadrado et al., 2020
Drought	Scotland	Yield class	Temperature sum and moisture deficit	Ecological Site Classification (ESC) model, UKCP09 climate projections	Petr et al., 2014
Spring temperature	Russia, Central Siberia	Latewood formation	Euclidean distances between trial and provenance origin. Climate data from weather stations close to experiments.	Correlations, coefficient of synchronicity	Savva and Vaganov, 2003
Mean temperature	Europe, Russia, North America	Tree height and survival	Mean annual temperature (MAT), Delta MAT, latitude	Correlation and multiple regression	Reich and Oleksyn, 2008
Photoperiod and temperature	Eastern Europe, European Russia	Tree height	Temperature and photoperiod	Correlation and multiple regression	Oleksyn et al., 1998

and that transfer of provenances from hotter or drier summers, $\Delta\text{SHM} > 0$, than that of the local provenance would perform better (**Table 4B**).

Uncertainty in Predicted Increase/Decrease of Tree Height Under Alternative Representative Concentration Pathways

For the Nordic countries, model predictions for tree height at age 15 years showed an increase under various future climate scenarios (**Figure 3**). Predictions of increased height were consistently certain (predicted by all five GCMs) under all RCPs and at all locations. Predictions made using RCP ensemble means (**Supplementary Figure 1**) showed that the increase in height growth largely followed the greater increases in GDD5 shown for higher RCPs (up to 81%) in comparison to lower RCPs (39% at the lowest). The magnitudes of predicted increases were often substantial (by 300 cm or more). However, even if these results at first glance present a very clear view on future tree height in the Nordic region, it should be noted that for considerable areas predictions were also shown to be the result of extrapolation (**Figure 3**). Firstly, it was easy to identify the areas where latitudinal transfers of the mean provenance exceeded the coverage of the underlying model data (LAT < 59.87°N and LAT > 69.87°N). Secondly, increasing GDD5 (by 3–1,117 day°C, **Supplementary Figure 2**) also caused the areas within model thresholds to shift northwards, toward the interior of the Nordic landmass and toward the higher altitude Scandian mountain ranges (**Figure 3**). This trend was more pronounced for high emission RCPs (6.0 or 8.5) than for low emission RCPs (2.6 and 4.5).

TABLE 3 | Regression coefficients (estimate and standard errors), significance tests, variance component estimates [Var(*x*)] plus marginal and conditional coefficients of determination (R^2) for both Nordic (A) and Spanish (B) mixed-effect models.

Term	Estimate	Std. err.	df	*t*-value	*p*-value
(A). Tree height for Nordic countries, ln(*H*)					
α_0 (intercept)	−4.0215	0.3937	373	−10.21	$9.47 \cdot 10^{-22}$
$\alpha_1 \cdot \ln(AGE)$	1.5384	0.0408	369	37.68	$1.53 \cdot 10^{-128}$
$\alpha_2 \cdot \ln(EST\text{-}1945)$	0.0722	0.0332	364	2.17	0.0303
$\alpha_3 \cdot \ln(GDD5\_s)$	0.7898	0.0573	374	13.79	$3.04 \cdot 10^{-35}$
$\alpha_4 \cdot \Delta LAT$	0.0217	0.0045	2,472	4.77	$1.95 \cdot 10^{-6}$
$\alpha_5 \cdot \Delta LAT^2$	−0.0151	0.0016	2,466	−9.30	$2.97 \cdot 10^{-20}$
$\alpha_6 \cdot GDD5\_s \times \Delta LAT$	$-4.27 \cdot 10^{-5}$	$4.90 \cdot 10^{-6}$	2,473	−8.72	$5.23 \cdot 10^{-6}$
$\alpha_7 \cdot GDD5\_s \times \Delta LAT^2$	$9.34 \cdot 10^{-6}$	$1.73 \cdot 10^{-6}$	2,466	5.39	$4.90 \cdot 10^{-6}$
Var(β) (field trial)	0.0436				
Var(ε) (residual)	0.0331				
$R^2_{marginal}$	0.7733				
$R^2_{conditional}$	0.9021				
(B). Tree height for Spain, *H*					
α_0 (intercept)	298.49	8.16	21	36.59	$8.48 \cdot 10^{-20}$
$\alpha_1 \cdot TD\_s$	36.04	3.79	2,060	9.52	$4.70 \cdot 10^{-21}$
$\alpha_2 \cdot SPR\_s$	11.79	5.03	1,570	2.34	0.0192
$\alpha_3 \cdot SPR\_s^2$	57.04	3.53	4,366	16.14	$5.60 \cdot 10^{-57}$
$\alpha_4 \cdot \Delta SHM$	13.14	6.13	493	2.14	0.0327
$\alpha_5 \cdot \Delta SHM^2$	−42.68	2.91	4,280	−14.65	$1.84 \cdot 10^{-47}$
$\alpha_6 \cdot SPR\_s \times \Delta SHM$	30.33	5.52	4,229	5.50	$4.11 \cdot 10^{-8}$
Var(β) (provenance)	809.5				
Var(ε) (residual)	13,173.5				
$R^2_{marginal}$	0.3946				
$R^2_{conditional}$	0.4297				

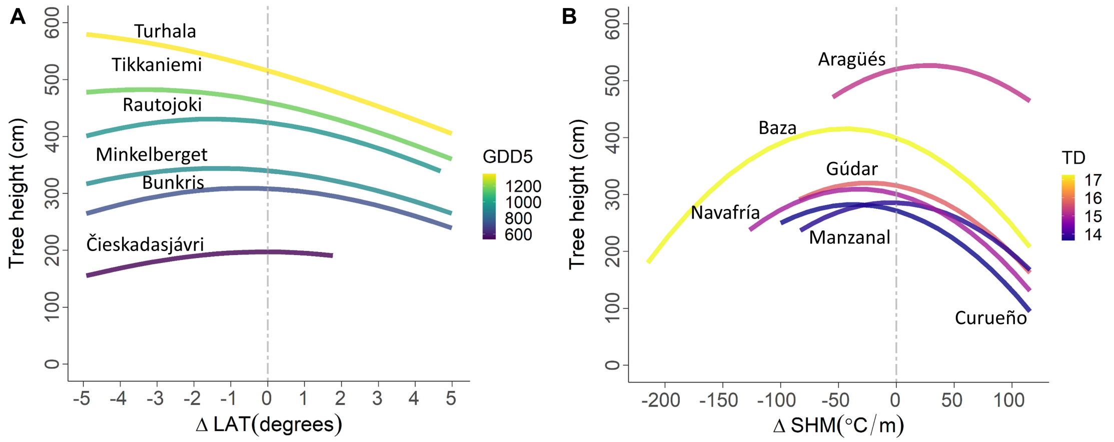

FIGURE 2 | Scots pine tree height predictions as a function of the environmental transfer distances for a sample of six field trials in the Nordic region **(A)** and for all six field trials in Spain **(B)** under the average climate during the growth of the trees (see **Table 4** for details). The plotting of biologically unreasonable transfer distances such as Nordic provenances originating north of Nordkapp (71.19°N) or Spanish provenances with negative SHM values were omitted.

In contrast to the Nordic region, the model results for Scots pine in Spain showed more uncertainty in the likelihood of increased tree height in 2070 (**Figure 4**). In the southwestern and northeastern part of the Pyrenees, and in the western part of central Spain tree height was predicted to increase under future RCPs in comparison to the reference period. Simultaneously, the magnitudes of tree height difference between climate scenarios and the reference period (**Supplementary Figure 3**) were small as they usually ranged from a 100 cm height loss to a 100 cm gain in height and there were no clear trends by increasing RCP. RCP ensemble means averaged across Spain ranged only from a 1% decrease to a 0.2% increase. The only exceptions to this lack of trend were the predictions for the southern refugium area in Andalusia which showed a consistent decrease

TABLE 4 | Environmental, climatic and age characterization of six field trials representing a sample of the 378 field trials used in the Nordic model (A) and the six field trials used in the Spanish model (B).

(A) Sample of field trials used for the Nordic model

Field trial	Lat	Long	Altitude	GDD5	Age	Class
Čieskadasjávri	69.4215	27.2626	258	534	14	North Cold
Rautojoki	66.5003	25.2167	115	950	17	North Mild
Minkelberget	63.1140	16.9873	152	920	15	Mid Cold
Tikkaniemi	63.2506	25.5166	144	1167	16	Mid Mild
Bunkris	61.4254	13.4763	584	729	17	South Cold
Turhala	61.6498	28.7170	99	1349	16	South Mild
Mean Provenance	64.8670			897	15	

(B) Field trials used for the Spanish model*

Site	Lat	Long	Altitude	SHM	SPR	TD
Aragüés	42.7452	−0.6304	1,370	54.99	269.97	15.23
Baza	37.3596	−2.9074	1,850	250.24	177.75	17.25
Curueño	42.7756	−5.3844	1,150	100.16	187.99	13.65
Gúdar	40.4076	−0.6810	1,700	84.46	204.00	15.75
Manzanal	42.5486	−6.2383	1,350	83.23	228.03	13.77
Navafría	41.0181	−3.8341	1,600	126.99	192.66	14.93
Mean Provenance				90.55	219.49	14.63

**Spanish field trial predictions are always shown for a tree age of 15 years.*

Latitude (Lat) and longitude (Long) are given in decimal degrees; SHM, summer heat moisture index (°C/m); SPR, spring precipitation (mm); TD, temperature differential (°C); GDD5, growing day-degrees above 5°C (day°C); Age, tree age at the time of height measurement (years).

For Nordic and Spanish models, environmental and climate characteristics of their respective mean provenances are added for comparison and for the Nordic field trials, the site class is described by Class.

(<−100 cm) in tree height for high emission RCP scenarios. When taking into account model predictability thresholds, southern and central areas plus the central Pyrenees consistently fell outside of the model predictability range thereby increasing uncertainty in results from the model. The area within the model predictability range was predicted to decrease along with RCPs emission scenarios (**Figure 4**). Cross-examination with predictions of climate variables for Spain in 2070 indicated that increased future temperature differential (TD) was the most likely driving factor behind the shrinking areas of model predictability (**Supplementary Figure 4**) because the increase in TD was substantial (by 0.5 to 5.3°C) and became stronger with increasing RCP. For the Andalusian area, a considerable increase observed for SHM (by 11.5–309.7°C/m) may exacerbate the reliance on extrapolation (**Supplementary Figure 5**).

Spatial Variation in Tree Height Predictions for Each Representative Concentration Pathway

When considering all data, spatial CoV-estimates were in the range 12–18% in the Nordic area (**Figure 5**), with the range of CoV increasing under higher emission RCPs. In contrast, spatial CoV-estimates for Spain were lower (5–6%) and showed no discernable trend with respect to RCP. It was also notable that spatial CoV-estimates were considerably lower if the study areas were restricted to those within model predictability limits (4–5% for the Nordic region and < 2% for Spain). If only areas within model predictability limits were considered there was no longer any relationship between CoV-magnitude and RCP either in the Nordic or Spanish regions. This suggests that the considerable spatial CoV estimates using all data were associated with model extrapolation, in particular for the higher emission RCPs.

Coefficient of Variation Estimates Among General Atmospheric-Ocean Circulation Models Over the Study Areas

With respect to CoV among GCM for each potential planting site in the Nordic region we observed a substantial variation (0–27%, **Figure 6**) even when only considering areas within model predictability limits. CoV-estimates were also systematically greater and more widespread for more extreme RCPs. Regarding geographical trends, CoV-estimates were notably high (1034%) in the southernmost (LAT < 57°N, Denmark and Lithuania) and northernmost (LAT > 71°N, Nordkapp) margins of the studied region (11–61%). However, these regions were also consistently outside the model predictability (too long transfer distance) thus relying on extrapolation. There were also other specific alpine areas along the Scandian mountain range where CoV estimates were large (5% to a max of 187%). For low RCPs these areas were still largely outside model predictability limits as GDD5-levels were too low (**Figures 6A,B**), but for higher RCPs considerable portions of largely alpine locations were increasingly included within the area suitable for the model. For the parts of the mountain ranges, the high CoV-estimates in tree height are not ascribed to extrapolation.

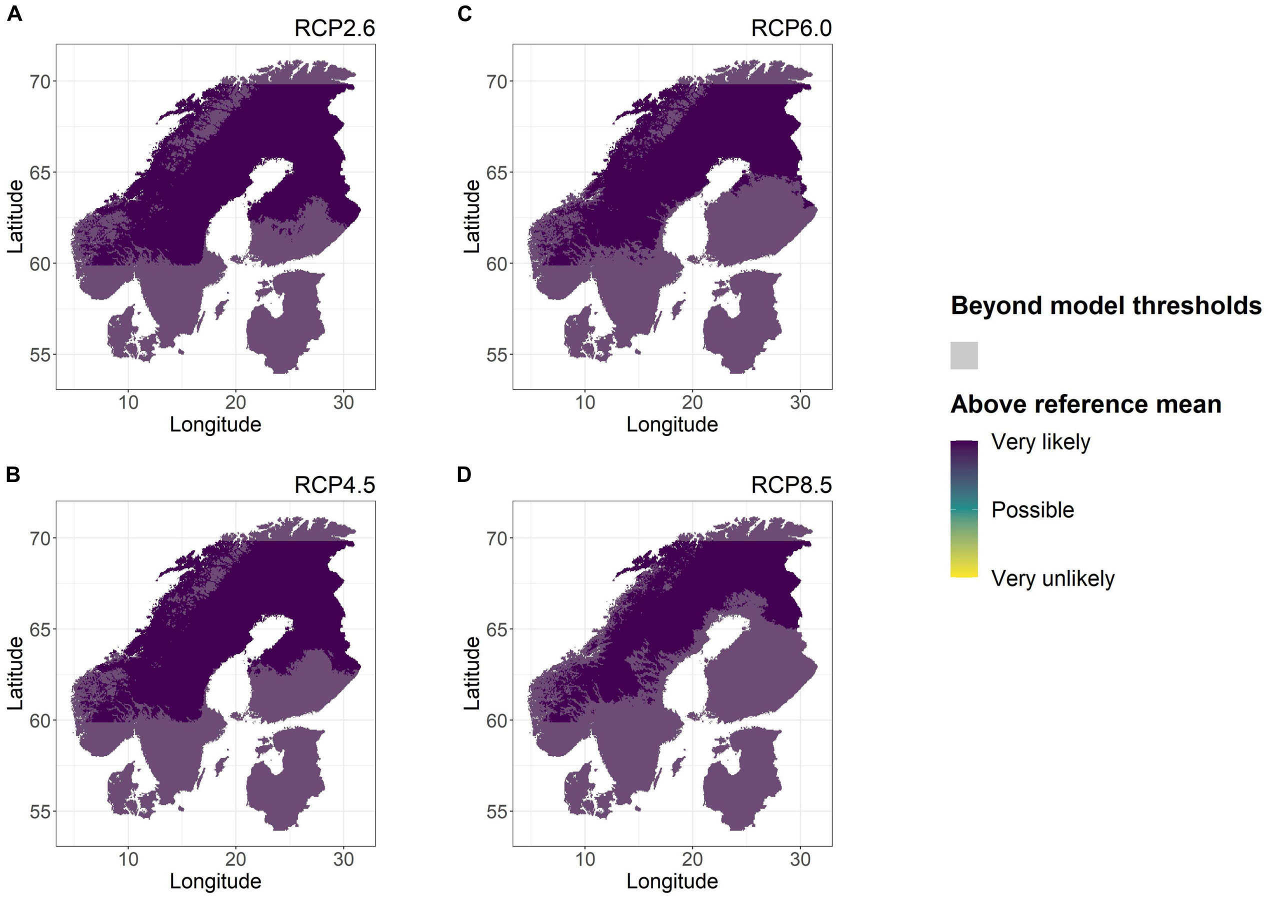

FIGURE 3 | Likelihood of tree height increase for Scots pine in the Nordic region under four future climate scenarios (RCP) in comparison to that of the reference period (1961–1990). The probability was assessed as the agreement among five GCMs within each RCP on tree height increase based on model predictions for RCPs 2.6 **(A)**, 4.5 **(B)**, 6.0 **(C)**, and 8.5 **(D)**. All locations where environmental variables exceeded those of the model data range according to at least three GCMs have been dimmed in semi-transparent gray.

In contrast to the Nordic region, tree height CoV among GCMs for Scots pine in Spain, was consistently low (**Figure 7**) ranging only from (3–11%). Also tree height CoV did not depend on RCP or on whether the studied areas were within the model predictability thresholds (0–2%). This finding suggests that, in quantitative terms, the uncertainty of future tree height predictions in Spain is very limited.

DISCUSSION

The large variety of environments inhabited by Scots pine has promoted populations adapted to a multitude of range-wide environmental conditions. Identifying these conditions is essential to assess the vulnerability of different populations to future climates, which are themselves inherently uncertain. With a literature review and a modeling approach covering populations at the leading and trailing edge of Scots pine, we addressed the problem of how the uncertainty associated with future climate projections may differently affect populations' vulnerability at the leading and trailing edges of the species range.

Drivers of Adaptation: From Literature Review to Modeling Approaches at the Leading and Trailing Margins

In general, our literature review showed that photoperiod constrains the tree height growth of local provenances in northern countries (Berlin et al., 2016), but also that northern and continental populations have adapted to a lower temperature sum to complete phenophases (Mátyás et al., 2004). Likewise, the Nordic model highlighted that photoperiod triggered local adaptation at the leading edge of the species, and that the GDD5 is an influential site-climatic predictor for tree height. This particular model is not new (Berlin et al., 2016), but we found it was robust for the Nordic area as all model terms previously indicated as highly significant remained highly significant, even though a very different climate dataset was used for this study (**Supplementary Material 2**). As in previous studies, we found that predictions of latitudinal transfer distance suggest that northward transferred material would achieve a greater height than local provenances, given increased GDD5 at the planting site (Rehfeldt et al., 2002; Reich and Oleksyn,

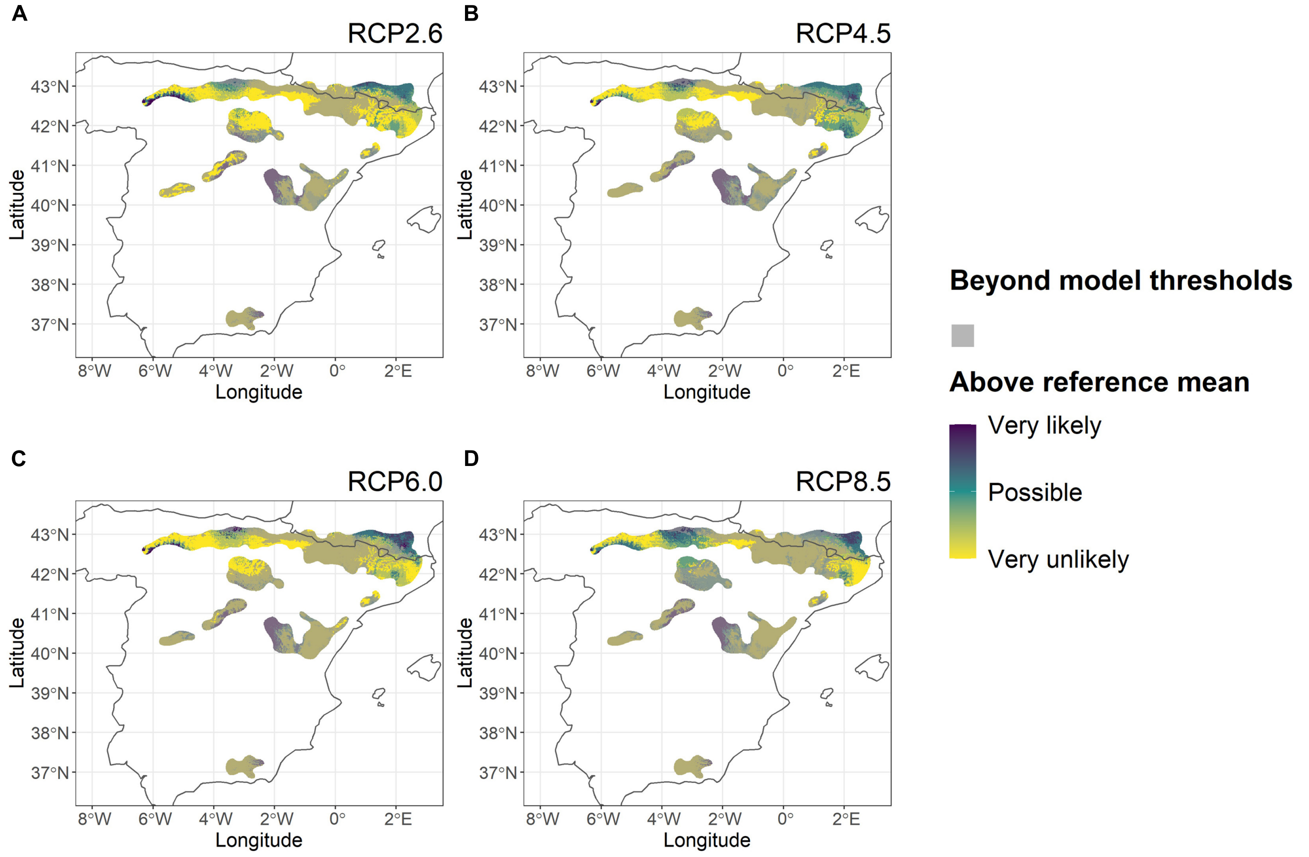

FIGURE 4 | Likelihood of tree height increase for Scots pine within its distribution range in Spain under future climate scenarios in comparison to that of the reference period (1961–1990). The probability was assessed as the agreement among five GCMs within each RCPs on tree height increase based on model predictions for RCPs 2.6 **(A)**, 4.5 **(B)**, 6.0 **(C)**, and 8.5 **(D)**. All locations where environmental variables exceeded those of the model data range according to at least three GCMs have been dimmed in semi-transparent gray.

2008; Berlin et al., 2016). However, at the extreme leading margin where temperatures are low, the model suggested that provenances with very small transfer-distances would be best adapted with respect to tree height. It should, however, be cautioned that transfer distance curves for the Nordic model had a very slight curvature suggesting that adaptational patterns were not sharply expressed and that, in many situations, a wide set of provenances would be likely to perform well at any given planting site.

The literature search showed that in southern and central areas of Europe, the effect of drought on Scots pine growth is not latitudinally driven, but depends on soil fertility, site topography and tree growth in the pre-drought period (Bose et al., 2020). Earlier assessments of future climate change suggest that drought could also become an important driver of Scots pine growth in lowland areas in north-western Europe (Petr et al., 2014). Recent work suggests that Spanish plantations show a great capacity to adapt to local climate conditions (Vizcaíno-Palomar et al., 2019), and that provenances from wetter sites in particular are expected to demonstrate resilience to drought and show increased growth under warmer conditions (Rubio-Cuadrado et al., 2020). Maximum temperature of the warmest month can also be an important driver in southern Europe, with populations able to cope with a wider range of maximum temperatures expected to be more likely to survive under climate warming (Valladares et al., 2014). Scots pine populations at the trailing edge of the range can adapt to drought, as was confirmed by our Spanish model, adapted from Vizcaíno-Palomar et al. (2019) to be comparable to the Nordic one. The main change was that the climate of the site and the provenance were independent drivers in Vizcaíno-Palomar et al. (2019), whereas the model presented here combined these in a transfer distance. In our Spanish model the peaks of the SHM-transfer distance curves were generally close to the SHM index experienced at the planting site, suggesting close-to-local adaptation by SHM. This suggests a certain resilience to future increased SHM-values associated with drier site types, and agrees with the results of some previous studies (Vizcaíno-Palomar et al., 2019; Rubio-Cuadrado et al., 2020).

The notable discrepancies in marginal and conditional R^2 between the Nordic and Spanish models are mostly due to the use of transfer distances that combine the climate of the provenance and the climate of field trial instead of using them separately in the model. As such, previous models based on the same data but

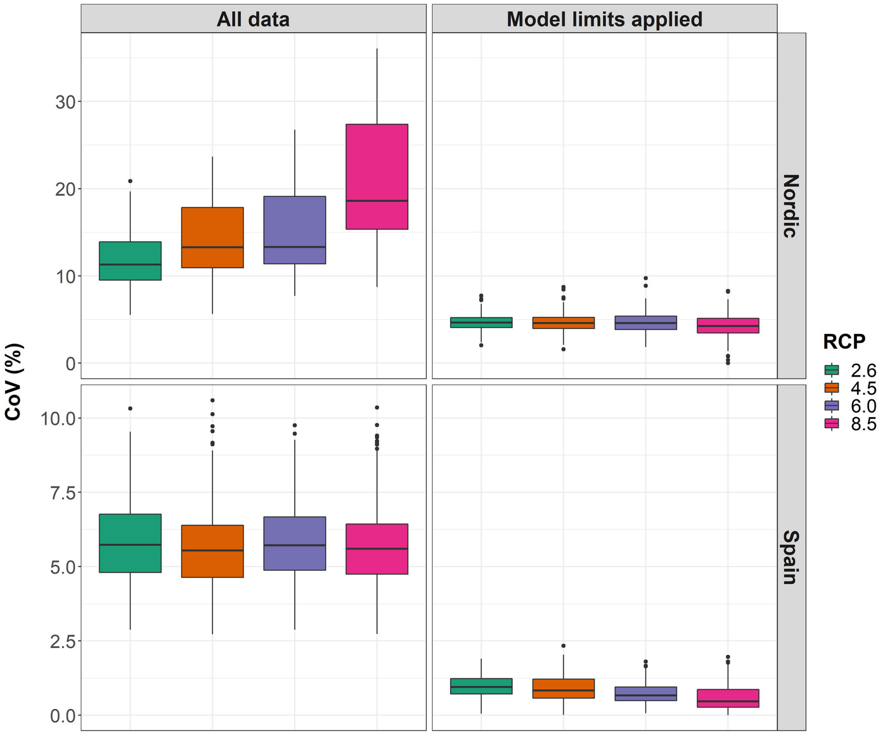

FIGURE 5 | Coefficients of Variation (CoV) calculated for Scots pine tree height predictions across the Nordic and Spain study areas respectively where the standard deviation of ensemble mean height predictions per RCP are given as a percentage of the 1961–1990 average height. On the left half of the figure CoV-calculations using all height prediction data is shown whereas for CoV-calculations made only from areas within the respective data ranges used for model development on the right half.

calibrated with the climate of the field trial and the provenance independently (i.e., without using the transfer distance), showed higher statistical performance (Vizcaíno-Palomar et al., 2019) than results presented here. Thus, this difference in statistical performance is likely due to the use of the transfer distance, a useful variable for estimating the odds of a population to survive in different environmental conditions, but difficult to interpret in biological terms as it merges the climate of the field trial (that we can attribute to the effect of phenotypic plasticity) and the climate of the provenances (that we can relate to the genetic effect of the provenance).

Prediction Uncertainty With Respect to Different Climate Change Projections

The most fundamental issue linked to adaptation and resilience to climate change is related to the question whether tree height at a predetermined age would increase or decrease at the northern and southern margin regions of the Scots pine distribution and whether this is subject to considerable uncertainty dependent on the variation in climate change projections. To address this question, we used a classification method based on climate projection data from five GCMs (within an RCP), agreeing or disagreeing with the notion that tree height will increase under a future climate. Varying classifications among GCMs constitute a useful measure of prediction uncertainty, whereas agreement among classifications suggests a greater likelihood of tree height increase. To our knowledge, such an approach has not been used to assess prediction certainty/uncertainty for tree species in boreal or temperate regions, although a similar method was used to determine the impact of climate extremes on a broad European range of environmental situations (Lung et al., 2013), and on climate change impact on a tropical rubber tree species (Hevea brasiliensis, Golbon et al., 2018). In addition to addressing such a dichotomous question as presence/absence or height increase/decrease, it is also important to evaluate a quantitative degree of uncertainty in the magnitude of tree height increase/decrease. For this purpose, we opted to use the percentage coefficient of variation in order to quantify the prediction uncertainty among GCMs.

In the Nordic region, the results of this study suggest that Scots pine tree height will increase in the 2070s as a result of warming temperatures (higher GDD5) in comparison to the reference climate period. This prediction was stable across the entire Nordic region and did not vary with RCP or GCM, thus giving an impression of great certainty at first glance. This observation agrees with a series of ecological model simulation studies separately performed for Sweden (Bergh et al., 2010) and for Finland (Torssonen et al., 2015; Kellomäki et al., 2018), where the growth of Scots pine was expected to increase regardless of climate change scenario or timespan based on increasing GDD5, along with site factors such as soil moisture,

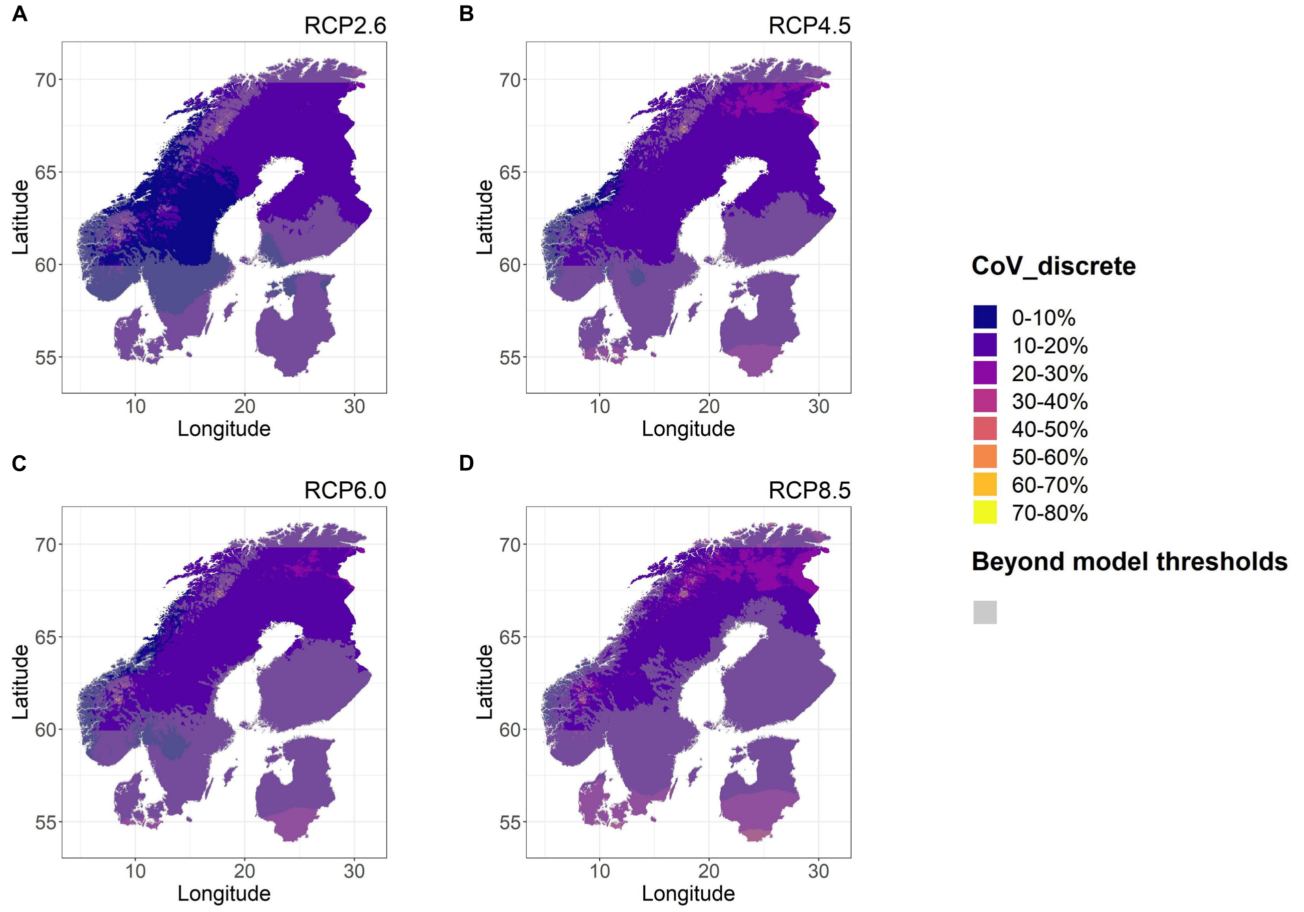

FIGURE 6 | Coefficients of variation (CoV) for Scots pine tree height among GCMs, calculated for each 1 km × 1 km prediction and for each RCPs 2.6 **(A)**, 4.5 **(B)**, 6.0 **(C)**, and 8.5 **(D)** in the Nordic region. All locations where environmental variables exceeded the model data range according to three GCMs or more have been dimmed in semi-transparent gray.

nitrogen availability and within-stand light. When considering the magnitudes of the predicted tree height increases, however, we observed substantial variation (i.e., uncertainty) both spatially across the Nordic region and connected to GCMs and RCPs. Given a situation where all predictions were considered, the uncertainty in magnitude also appeared to be greater for high emission RCPs (e.g., 8.5) than for low emission RCPs (2.6). From a quantitative perspective our results suggest considerable variation and uncertainty for the Nordic region with respect to the magnitude of tree height increase among differing climate scenarios. In summary, our results indicate that Scots pine height growth in the Nordic region will benefit from climate change. However, considerable uncertainty was revealed in the extent and magnitude of that potential climate change benefit.

For Spain, our model predictions indicated greater uncertainty with respect to whether future Scots pine tree height would increase or decrease as a result of climate change, compared to the Nordic model. Some areas in northern Spain showed increases in future tree height, and other areas in central and southern Spain showed tree height decreases. However, the observed patterns did not vary much across emission scenarios (RCP) and in quantitative terms prediction variation, and thereby uncertainty, was small both with respect to spatial predictions and across different GCMs. This agreement of predictions suggests that even though there is some uncertainty whether Scots pine provenances will remain adapted to their Spanish range under a future climate, the quantitative consequences of climate change will be limited. It should be cautioned that soil physical and chemical properties might interact with climatic factors, providing the detailed site conditions that maintain a site suitable for Scots pine resilience into the future (Mathys et al., 2014; Redmond et al., 2015). However, our study did not take account of local variation in site soil conditions. The cautious predictions reported for Spain in our study contrasts considerably with an Europe-wide analysis of radial growth which suggested that climate suitability for Scots pine will decline in central Europe (Bombi et al., 2017). In particular, this study observed that the most extreme climate GCMs included were coherent with observed trends from dendrochronological data. However, the use of Ecological Niche Modeling (ENM) which relies on static species distribution data means that these stark findings do not account for potential local adaptation or plasticity that are both included in our

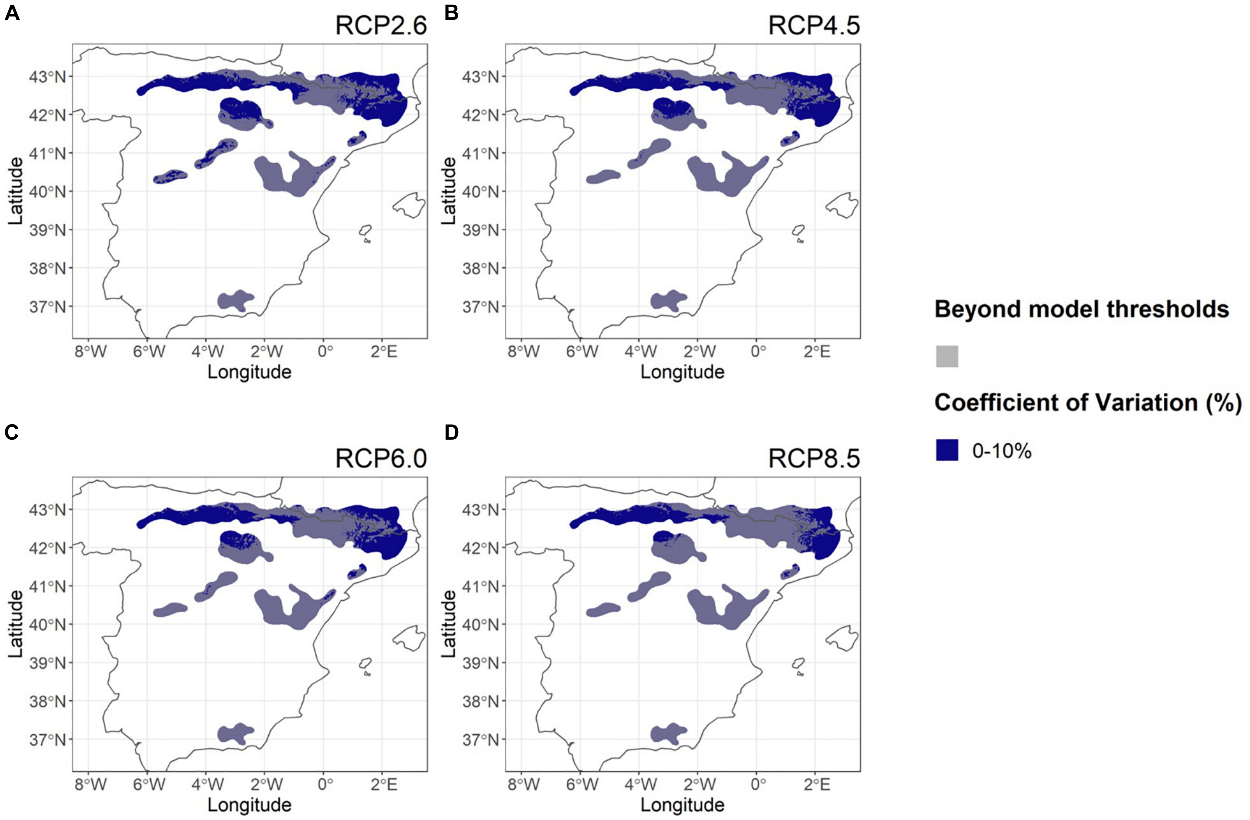

FIGURE 7 | Coefficients of variation (CoV) for Scots pine tree height among available GCMs, calculated for each 1 km × 1 km prediction and for each RCPs 2.6 **(A)**, 4.5 **(B)**, 6.0 **(C),** and 8.5 **(D)** with Scots pine distribution areas in Spain. All locations where environmental/climate variables exceeded the model data range according to three GCMs have been dimmed in semi-transparent gray.

models. Our results are nevertheless in agreement with another dendrochronological study that specifically covered the Spanish region and which also indicated some resilience of a central Spanish provenance to very dry conditions to which it was expected to be maladapted (Rubio-Cuadrado et al., 2020).

Prediction Uncertainties With Respect to Model Extrapolations

Apart from the uncertainty connected to the multitude of climate projection scenarios and their accuracy, the limitations of the applied linear mixed-effects models also have to be considered. A particular concern is that even predictions created by well developed and accurate models are subject to considerable error, and thereby uncertainty, if applied to climatic conditions outside the data range used for model development. Such problems of model limitation and extrapolation are relevant across several scientific fields that develop and utilize statistical models for prediction (see e.g., Miller et al., 2004; Stohlgren et al., 2011). Given the environmental conditions used for developing our adaptation transfer models, it is unlikely that extrapolation would be necessary because a wide variety of environmental conditions at field trial and provenance locations were studied. Nonetheless we observed that future climate change *per se* will create environmental conditions that necessitate extrapolated predictions provided that current height prediction models are used. We determined the extent of this issue and how its severity increased with increasing GHG emissions (i.e., RCP scenarios). For the Nordic region, we identified increasing GDD5 as the main reason for prediction extrapolation. For the areas where the majority of GCM predictions were made by extrapolation, there can be uncertainty about prediction quality even when GCM agreement is formally unanimous. For Spain, increasing temperature differentials, and to a limited degree increasing SHM, appeared to be the cause for extrapolated predictions. These increased temperature differentials may be linked to increased continentality as predicted for southern Europe (Szabó-Takács et al., 2015).

Given our findings it is reasonable to believe that the uncertainty and errors due to extrapolation in turn acts as a multiplier of the uncertainties connected to the variation in climate change scenarios previously discussed and may also result in systematic biases. In practical terms this presents a trade-off dilemma for foresters and tree ecologists because, on one hand, they need predictions of tree adaptation in order to assess the species resilience to climate change, while on the other hand, extrapolations which threaten model prediction accuracy and precision should always be avoided from a strictly conservative perspective. As a compromise, we present predictions that often are extrapolated, but we also explicitly highlight this type of uncertainty thereby making it possible to localize the issue. In the longer term, we instead emphasize increased provenance field testing throughout large environmental gradients including those outside the species range as a remedy. For the Nordic region, our results suggest that collection, collation, pre-analysis and modeling of additional data from field trials experiencing higher temperatures than what is currently included would result in improved models. For Nordic tree height models, it would also be possible to formally test climate variables that are currently employed in corresponding Spanish tree height models. For the Spanish model, our results also indicate that field trials located at sites experiencing greater temperature differentials would be useful in order to improve models and to reduce prediction uncertainty, although trees planted within very dry regions may not survive.

Other Uncertainties

For the purpose of this study, we used tree height as a proxy trait for tree fitness and using this trait we have illustrated climate associated prediction uncertainties. However, we are well aware that tree height growth only partially accounts for overall health, fitness and resilience of Scots pine. Seedling stage survival, phenology, water use efficiency, radial growth, fertility and resistance to pests and pathogens are additional and important aspects of fitness. Some of these traits are more or less important at the northern and southern margins, respectively. In the Nordic region, it is well known that early-life hardiness (i.e., seedling survival) is a crucial character in the face of a cold environment in general (Persson and Ståhl, 1993; Berlin et al., 2016), especially in the far North (LAT > 65°N) and at higher elevations (>400 m asl) where GDD5 historically is low (<800 day°C). In Spain, Scots pine survival analyzed from the same network of field trials and provenances was predicted to decrease in most parts of the species range, including the northern part of the range (Benito Garzón et al., 2011; Valladares et al., 2014), suggesting a likely trade-off between survival and growth in northern Spain that may lead to a less optimistic future than that shown here. This demographic compensation is a common phenomenon at the species margins (Doak and Morris, 2010; Benito Garzón et al., 2013; Peterson et al., 2018), where populations are expected to reach their tolerance limits and may present maladaptation (Fréjaville et al., 2020). If such additional measures of fitness are taken into account they may affect the assessment about the outlook of the species and the uncertainty of our predictions.

Another dimension of uncertainty is that the use of broad average-based and persistent climate variables based (e.g., temperature, precipitation, GDD5, SHM, etc.) overlooks the potential impact of extreme events and calamities that may occur sporadically but which may have a profound impact on Scots pine survival and health in general, and increases the uncertainty of predictions. For Scots pine, such extreme events could be storms, forest fires and attacks by various pests and pathogens (Lung et al., 2013; Allen et al., 2015; Seidl et al., 2017; Seidel et al., 2019). The prediction of stochastic extreme events is not as straightforward as the use of topographically downscaled climate data, based on averages of 30-year periods, which we used here. Extreme climatic events are more likely to be brief and could be extremely localized, thus requiring meteorological assessments made at an hour-by-hour resolution and which might have to target a different height above the ground than the classically used 2 m (e.g., Svystun et al., 2021). The impact of extreme events is also difficult to integrate into the classical adaptational model framework, but has been framed by Seidl et al. (2017).

Conclusion and Future Perspectives

In summary, the GCM-agreement results of our study suggests that Scots pine tree height will increase with great certainty in the Nordic region as an effect of climate change, while predictions of tree height in Spain under a future climate are more varied, and therefore uncertain with respect to increase or decrease. Coefficients of variation for tree height predictions in the Nordic region among climate scenarios were, however, considerably high, thereby suggesting uncertainty to the extent of predicted tree height increase and hence implying uncertainty in a quantitative sense. Conversely, coefficients of variation, spatial and among climate scenarios, for the Spanish region were consistently low thereby indicating limited prediction uncertainty. If taken at face value, prediction of future tree height in the Nordic region and in Spain appears to be subject to only low-to-moderate degrees of uncertainty if we only consider the variety of available climate change projections *per se*. For Scots pine in the Nordic region, climate change appears to have a predominantly positive influence and there were no obvious indications of threats against Scots pine adaptation and resilience. This was also the case in Spain except possibly for the southernmost Andalusian refugium. However, demographic compensation due to a likely decrease in population survival as a consequence of frost hardiness at the leading edge and drought at the trailing edge would reduce the odds of marginal populations to inhabit these regions in the near future.

Furthermore, our results showed that climate change will cause tree height model predictions to be increasingly based on extrapolation both in the Nordic and Spanish region. Our interpretation is that uncertainty due to extrapolation is the most important source of uncertainty with regards to future environmental conditions and this type of uncertainty is also more difficult to properly quantify. By using the method of GCM-agreement, we were nonetheless able to illustrate the geographical extent of uncertainty due to model extrapolation and thus assess the extent of the issue. However, in order to better account for model extrapolation uncertainty, we encourage more international collaboration to share datasets from larger networks of field trials throughout the Scots pine distribution range. Such model integration would then encompass data spanning a greater variety of environmental and climatological conditions thereby decreasing the need of extrapolated predictions. Nonetheless some extrapolation will still be unavoidable due to novel climates appearing.

Our attempt to review and model tree height with different adaptation drivers at the leading and trailing edge of Scots pine highlights the difficulty to apply range-wide models to a species with marked local adaptation to different conditions across its range. Furthermore, it suggests that new generation models accounting for Scots pine adaptation at large geographical scales under new climates would need to integrate fitness-related traits other than tree height, account for the risk and severity of extreme events and calamities induced by climate change and the odds of populations to adapt to them.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: Spanish field trial data is available upon request through www.genfored.es and Nordic field trial data is available upon request through www.skogforsk.se (henrik.hallingback@skogforsk.se). Climate data is available through the Climate Downscaling Tool (ClimateDT) at ibbr.cnr.it/climate-dt. The raw global files of the downloaded GCMs are available at https://worldclim.org/data/v1.4/cmip5_30s.html.

AUTHOR CONTRIBUTIONS

HH, MB, VB, MBG, NV-P, MM, ML, and DR conceived the study and its objectives. MM generated climate data for the reference period and for future climate scenarios. HH, NV-P, and MBG recalibrated and redeveloped the prediction models and generated the spatial tree height predictions. HH, VB, FT, NV-P, and MBG performed the downstream analyses on predictions and generated figures thereof. ML and VB performed the literature research on adaptive environmental drivers. HH and MBG organized and coordinated the manuscript writing and wrote the first draft. MB, MBG, and DR acted as quality checkers and contributed with the additional references. All authors read and commented on the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.724051/full#supplementary-material

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Limited Range-Filling Among Endemic Forest Herbs of Eastern North America and Its Implications for Conservation With Climate Change

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Biodiversity hotspots host a high diversity of narrowly distributed endemic species, which are increasingly threatened by climate change. In eastern North America, the highest concentration of plant diversity and endemism occurs in the Southern Appalachian Mountains (SAM). It has been hypothesized that this region served as a refugium during Pleistocene glacial cycles and that postglacial migration northward was dispersal limited. We tested this hypothesis using species distribution models for eight forest herb species. We also quantified the extent to which the geography of suitable habitat shifted away from the current range with climate change. We developed species distribution models for four forest herb species endemic to the SAM and four that co-occur in the same SAM habitats but have broader ranges. For widespread species, we built models using (1) all occurrences and (2) only those that overlap the SAM hotspot in order to evaluate the extent of Hutchinsonian shortfalls and the potential for models to predict suitable habitat beyond the SAM. We evaluated the extent to which predicted climatically suitable areas are projected to shift away from their current ranges under future climate change. We detected unoccupied but suitable habitat in regions up to 1,100 km north of the endemic species' ranges. Endemic ranges are disjunct from suitable northern areas due to a ∼100–150 km gap of unsuitable habitat. Under future climate change, models predicted severe reductions in suitable habitat within current endemic ranges. For non-endemic species, we found similar overall patterns and gap of unsuitability in the same geographic location. Our results suggest a history of dispersal limitation following the last glacial maximum along with an environmental barrier to northward migration. Conservation of endemic species would likely require intervention and assisted migration to suitable habitat in northern New England and Canada.

Keywords: assisted migration, biogeographical barriers, dispersal limitation, endemic species, forest herbs, geographic range limits, range expansion, species distribution models

INTRODUCTION

Understanding the abiotic, biotic, and historical factors that have shaped species' current geographic distributions is crucial for predicting how species might respond to modern climate change. If species' geographic distributions and range limits are determined largely by climatic factors (Woodward, 1987; Gaston, 2003), it is expected that ranges will need to shift substantial distances poleward in order to track favorable conditions as climate warms. There is growing evidence from empirical studies and predictive models that climate change is causing widespread shifts in the distribution and abundance of species (Chen et al., 2011; Bellard et al., 2012; Ehrlén and Morris, 2015; Dainese et al., 2017; Wang et al., 2018) and increasing extinction risk (Thomas et al., 2004; Keith et al., 2008). Similar range shifts are well-documented for past climate variation associated with glacial cycles (Betancourt et al., 1990; Jackson and Overpeck, 2000). However, it is unclear if all species share this capacity for rapid migration, especially given the more rapid pace of contemporary climate change (Svenning and Skov, 2004, 2005; Dullinger et al., 2012).

These range dynamics highlight a distinction between a species' realized distribution and the actual extent of its potential distribution. For well-dispersed species, the realized and potential distributions may overlap extensively at geographical scales, even during times of environmental change (i.e., ranges that are in "dynamic equilibrium" with the environment, Webb, 1986). For poorly dispersed species, or those facing geographical barriers to colonization of disjunct suitable habitat, the realized distribution might only partly fill the full extent of the species' potential distribution ("poor range-filling capacity," Svenning and Skov, 2004). Species tending toward the latter scenario represent a significant challenge for conservation in the face of modern climate change, as their distributions might already show long-term "disequilibrium" with the environment, and rapid and commensurate adjustments to further change might be unlikely.

Better documenting these range dynamics is particularly critical for protecting biodiversity hotspots, which often contain a concentration of narrow-ranged or endemic species: i.e., "hotspots" of endemism (e.g., Médail and Diadema, 2009). The locations of such hotspots appear to be linked to aspects of geography, physiography, and past climate change (Sandel et al., 2011). For example, Ohlemüller et al. (2008) showed that areas with high concentrations of narrow-ranged species have distinct climatic and physiographic characteristics compared to surrounding areas, often being cooler and higher in elevation. Similarly, it has been suggested that hotspots of endemism have formed in areas with reduced climate change "velocity" in the past, tracing to factors like elevational complexity, which can buffer species against rapid climate change (Loarie et al., 2009; Sandel et al., 2011; Scherrer and Körner, 2011).

In the North Temperate Zone, many endemic and small-ranged species tend to be concentrated around the locations of putative Pleistocene-era glacial refugia (Daubenmire, 1978; Estill and Cruzan, 2001). The long-term restriction of endemic species to these areas suggests a failure by some species to fill their expanding potential distributions as climate ameliorated during the Holocene (Jansson, 2003; Svenning and Skov, 2007). Consequently, there may already be substantial mismatches between some species' current realized distributions and their potential distributions owing to historical factors, such as dispersal limitation. In eastern North America, a major center of endemism for plants and animals of deciduous forests is the Southern Appalachian Mountains hotspot (hereafter SAM; Petranka, 1998; Estill and Cruzan, 2001). Of the 189 small-ranged endemic plant species reported from temperate deciduous forests in the eastern U.S., 119 overlap the SAM in their distributions and 18 are entirely restricted to this region (Bellemare and Moeller, 2014). The current concentration of endemic species in the SAM hotspot may trace to this area's history as a Pleistocene glacial refugium and to limited rates of postglacial dispersal (Stein et al., 2000). The observation that many of these range-restricted species can be grown in horticulture far to the north of their current native ranges, and sometimes even escape and naturalize, is consistent with the inferred role of dispersal limitation in these plants' distributions (Sax et al., 2013). However, a detailed analysis of these patterns, and possible mismatches between realized native vs. potential distributions, has not yet been undertaken.

In this study, we used species distribution models (SDMs; Franklin, 2010) to test the hypothesis that narrow endemic forest herbs of the SAM have limited range filling, such that there is substantial suitable habitat to the north of their current ranges. We developed SDMs using maxent and boosted regression trees for four well-known, endemic species: *Trillium vaseyi* (Melanthiaceae), *Shortia galacifolia* (Diapensiaceae), *Phacelia fimbriata* (Boraginaceae), and *Diphylleia cymosa* (Berberidaceae). By documenting mismatches between these species' realized vs. potential distributions, these models also allowed us to evaluate the role that historical factors, like dispersal limitation, might have played in forming their current ranges. Further, we used these models to predict the magnitude of projected changes in suitable habitat under climate change. As a point of comparison, we also developed SDMs for four more widespread forest herb species from the Appalachian Mountains that overlap in range with the SAM endemics but extend further north. We built these models using (1) occurrences from their entire range and (2) using just those from the SAM. These models provided two key insights. First, they determined whether models built with occurrences from only the SAM range had the capacity to accurately predict suitable habitat outside of the range. If the limited sampling of geographic space (Wallacean shortfall) results in sampling of a fraction of the realized niche (Hutchinsonian shortfall), SDMs may not predict the entirety of suitable habitat beyond the region where models were trained. Second, these models allowed us to quantify the extent to which geographic ranges might recede northwards with climate change and whether those projected changes are similar for endemic and widespread species. We addressed the following specific questions:

(1) For endemics, to what extent is apparently suitable habitat already present north of the species' ranges, and is that unoccupied habitat contiguous or disjunct from the

current range? How do these patterns differ from those of more widespread forest plants?

(2) What is the magnitude of loss of suitable habitat in the SAM under future climates? To what extent do projections of potential habitat under future climates overlap with current ranges, and are extrinsic dispersal barriers (environmental or physical) likely to influence the possibility of northward population expansion?

(3) What is the relative magnitude of projected northward range shifts under climate change for narrow endemics vs. more widespread forest herbs? In addition, to what extent do Wallacean shortfalls result in Hutchinsonian shortfalls and influence projections of suitable habitat beyond the SAM biodiversity hotspot?

MATERIALS AND METHODS

Study Species

We focused on eight species of herbaceous flowering plants whose ranges overlap in the forests of the Southern Appalachian Mountains (SAM: **Figure 1**). Four of these species are endemic to western North Carolina, eastern Tennessee, and adjacent regions (*Phacelia fimbriata* Michx., *Diphylleia cymosa* Michx., *Shortia galacifolia* Torr. & A. Gray., and *Trillium vaseyi* Harbison); two have widespread ranges across the eastern United States (*Maianthemum canadense* Desf., *Trillium undulatum* Willd.) and two have ranges that are intermediate to the others in size (*Prosartes lanuginosa* Michx., *Houstonia serpyllifolia* Michx.). The four more widespread species have similar habitat requirements to the four endemic species (Gleason and Cronquist, 1991 and personal observations), and in the southeastern United States their ranges are partially overlapping and restricted to the SAM.

Locality Data

We obtained occurrence records from the online database gbif (Global Biodiversity Information Facility[1], see **Supplementary Table 2.1** for DOIs), correspondence with other researchers, and our own field surveys for three of the four endemics: *D. cymosa*, *P. fimbriata*, and *T. vaseyi*. For the fourth endemic, *S. galacifolia,* we used pre-existing locality data, as it is a rare species that has been of considerable interest to botanists for centuries and its distribution is well-documented (e.g., Davies, 1955). Our field searches for the first three endemics occurred throughout sections of the Great Smoky Mountains National Park, Nantahala National Forest, and Cherokee National Forest during April, May and June of 2013 and 2014 when the species were flowering and most easily detected. The final set of occurrence data was filtered to remove duplicate or erroneous records, and eliminate those that lacked specific coordinates. Across all eight species, the total number of occurrences ranged from 20 to 1017 per species (**Supplementary Appendix 2** and **Supplementary Table 2.1**). For the two widespread non-endemics, *M. canadense* and *T. undulatum*, some portions of the species' range were far more heavily sampled than others. Therefore, we down-sampled occurrences across the range such that there was only one presence point per raster cell (0.1 degrees or 30 arc-seconds) using the R function "gridSample," in the package "dismo" (Hijmans et al., 2017; R Core Team, 2017).

Environmental Data

We obtained environmental data from the online database WorldClim (version 1.4[2], Hijmans et al., 2005). We used a grid cell resolution of 1 × 1 km (30 arc-seconds) for the eastern United States (30–60 degrees latitude; −90 to −60 degrees longitude; tile 13). For each species, we selected environmental variables from the full list of 67 (36 temperature, 12 precipitation, 19 bioclim). Bioclim variables include various interactions among temperature and precipitation variables, such as the temperature of the wettest quarter. For maxent models, we pared down the number of environmental predictors using a principal components analysis (PCA) on the environmental data for the background points plus occurrences. Based on the PCA loadings, we eliminated highly correlated environmental predictors. This resulted in set of 3–6 predictors for each species (see **Supplementary Appendix 2** and **Supplementary Table 2.2**). For boosted regression tree models, we conducted stepwise backward elimination until the deviance was minimized using the gbm.simplify function (Elith et al., 2008; **Supplementary Appendix 3** and **Supplementary Table 3.2**).

Niche Breadth and Overlap

To examine whether pairs of our eight species share similar climate niches, we calculated Schoener's D (using the R package dismo) for each pair of species using all Worldclim variables. Values of D may range from 0 (no niche overlap) to 1 (complete overlap).

We used the ecospat package in R to test for niche differentiation (Broennimann et al., 2012; Di Cola et al., 2017). For each non-endemic species, we used a principal components analysis (PCA-env) of the environmental variables incorporated into their respective SDMs (see below). We used Schoener's D to quantify niche overlap. We tested if the climate niches for the full range of each species niches are more similar to the climate niches of their range in the Southern Appalachian Mountains than expected by chance using a permutation test ($N = 999$ permutations).

Species Distribution Models

We used two methods separately to develop species distribution models, maxent and boosted regression trees (general boosted models), as they have been shown to perform well compared to alternative methods (Elith et al., 2006; Hijmans and Graham, 2006; Phillips et al., 2006). Maxent is a machine-learning, presence-only method (Phillips et al., 2004); boosted regression trees (brt) is an ensemble method that combines regression trees and boosting (Elith et al., 2008). For simplicity, and because the models have similar predictions and evaluation scores, we present only the maxent results hereafter. Details of the brt methods and results can be found in **Supplementary Appendix 3**.

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[1] www.gbif.org

[2] www.worldclim.org

FIGURE 1 | Species endemic to the Southern Appalachian Mountains biodiversity hotspot are shown in the top row. From left to right: *Phacelia fimbriata*, *Diphylleia cymosa*, *Trillium vaseyi*, and *Shortia galacifolia*. Non-endemic species with broader distributions are shown in the bottom row. From left to right: *Maianthemum canadense*, *Houstonia serpyllifolia*, *Trillium undulatum*, and *Prosartes lanuginosa*. Photo credits: *M. canadense*: By Halpaugh at English Wikipedia—Transferred from en.wikipedia to Commons., Public Domain. *H. serpyllifolia*: By Masebrock at English Wikipedia—Transferred from en.wikipedia to Commons., Public Domain. *P. fimbriata*, *P. lanuginosa*: Stephanie Erlandson. *D. cymosa*, *S. galacifolia*, *T. vaseyi*, *T. undulatum*: Jesse Bellemare.

For the four endemic species, we built one type of model, which involved using all of our occurrence points (Southern Appalachian models: SA models). For the four non-endemic species, we built two different kinds of models. First, we built models using all of the occurrences from across the range as would be standard practice for SDMs (Full Range models: FR models). Second, we used only the subset of occurrences from the SAM; i.e., those that overlapped in distribution with the endemic species (SA models). This second approach provides a means for evaluating how well SDMs predict suitable territory outside of the SAM using only data from that region. This additional approach is important because it is well known that SDMs may perform poorly beyond the region where the model was developed and fail to predict range expansion (e.g., Briscoe Runquist et al., 2019, 2021; Lake et al., 2020).

We built SDMs using maxent version 3.4.1 implemented in R (Phillips et al., 2017a,b). Ten thousand background points were generated for non-endemic species; slightly fewer (6,000–9,000) were generated for the endemics because they had fewer occurrences over a narrower geographic extent (see **Supplementary Table 2.3** for more details). To generate background points, we delineated a box encompassing the entire species' range. For SA models (both endemics and non-endemics) background points were generated over an area encompassing the SAM plus adjacent lowland areas (34–36.5 degrees latitude; −85 to −80 degrees longitude). This area included the entire ranges of the four endemics. For the FR models for non-endemics, the area over which background points were generated included the entire temperate deciduous forest biome of eastern North America (30–60 degrees latitude; −90 to −60 degrees longitude). We clipped environmental layers for each model to these boxes using ArcMap software (ESRI, 2016).

For all species, hinge and product features were turned off. We increased the regularization coefficient (betamultiplier) to produce smoother response curves and prevent overfitting of models, especially when projecting to new areas (**Supplementary Table 2.3**; Warren and Seifert, 2011). Because our focal endemics are easily detectable during the period of time in which searches occurred, we increased the value of τ, the default presence detectability for them (**Supplementary Table 2.3**). Last, we used multivariate environmental similarity surfaces (MESS; Elith et al., 2010) to determine the distribution of analogous environments and limited our inferences about the distribution of potential suitable habitat to those geographic areas. For each species (and combination of SA and FR models) we report the results of one run of the model. We ran each model multiple times, each time drawing new background points, and the projections were very stable across model runs.

More details of model generation and setting selection can be found in **Supplementary Appendix 2**.

Model Evaluation

For all species, we used AUC and TSS for model evaluation. AUC, the area under the (receiver operating characteristic) curve, assesses model performance relative to random chance and ranges from 0 to 1 (Phillips and Dudiík, 2008). The true skill statistic, TSS, is a threshold-dependent metric based on the sensitivity (true positive rate) + the specificity (true negative rate)−1 (Allouche et al., 2006). Values range from −1 to +1, with 0 indicating model performance no better than chance, 1 indicating perfect accuracy, and −1 indicating perfect inaccuracy. We evaluated TSS at a model-dependent threshold value, where the sum of the true positive rate and the true negative rate was maximized (Freeman and Moisen, 2008).

We evaluated all models using fivefold cross validation. We trained each model with 80% of the occurrence and background data, and then tested against the other 20% of occurrences (fivefold cross-validation). AUC and TSS values were averaged across the five runs. Second, we evaluated how well the SAM models predicted occurrences outside (to the north) of the SAM for the four more widespread species.

The environmental variables that most negatively affected the probability of occurrence for each raster cell were determined using the "limiting" function in the package "maxent" (Elith et al., 2010). We were particularly interested in which environmental factors limited suitability at and beyond the northern border of the endemic species' ranges.

Projections Under Climate Change

We projected future ranges of each species using two global circulation models (GCMs) and two emission scenarios: GCMs HadGEM2-ES and NorESMI-M from among the five recommended by Warszawski et al. (2013) and McSweeney and Jones (2016). These represent two potential extremes in temperature and precipitation variability in the eastern United States: the HadGEM2-ES model has high temperature variability and low precipitation variability, while NorESMI-M is the reverse. As the HadGEM2-ES model makes more extreme predictions as far as the severity of climate change compared to NorESMI-M, hereafter we focus on the more moderate and conservative NorESMI-M models (see **Supplementary Appendix 4** for HadGEM2-ES Figures). For each GCM, we made projections under the "worst-case" carbon emission scenarios (no change in emissions: rcp8.5). The resulting two types of climate change scenarios were then projected for years 2050 and 2070.

We also projected the distribution of suitable habitat at the last glacial maximum (∼21,000 years BP) using paleoclimate data from the PMIP2 database[3], accessed in WorldClim, and using the MIROC global circulation model. Results are shown in **Supplementary Appendix 6**.

RESULTS

Niche Breadth and Overlap

Endemics and non-endemics had a wide range of niche overlap within and between groups. For example, the endemic *P. fimbriata* had very high niche overlap with the endemic *D. cymosa* (0.96) and the non-endemic *H. serpyllifolia* (0.90) but low overlap with the endemic *S. galacifolia* (0.18). The mean niche overlap did not differ significantly when comparing pairs of endemics (mean $D = 0.56$), pairs of non-endemics (mean $D = 0.56$), and pairs including one endemic and one non-endemic (mean $D = 0.58$; $P = 0.983$). More information on the natural history of each species and pairwise *D*-values can be found in **Supplementary Appendix 1** (see **Supplementary Table 1.1**. for pairwise *D*-values).

As expected, climate niche breadth was greater for the full range (FR) of occurrences compared to the Southern Appalachian (SAM) occurrences for all four non-endemic species (**Supplementary Figure 1.1**). When comparing FR and SAM niches, Schoener's *D*-values were highest for *H. serpyllifolia* and *P. lanuginosa* (0.75 and 0.63, respectively) and there was significant niche overlap between the SAM and FR occurrences for each species ($P = 0.021$ and 0.014, respectively). By contrast, niche overlap was lower for *M. canadense* and *T. undulatum* (0.32 and 0.31, respectively) and niche overlap was not greater than expected by chance for each species ($P = 0.26$ and 0.33, respectively).

Endemic Species: Current Ranges and Species Distribution Model Predictions

Model evaluation showed high AUC scores for all endemic species (0.86–0.98), indicating good model fit, as well as moderate to high TSS values (0.63–0.95; **Table 1**). Below we focus our discussion of the distribution of suitable habitat to areas with suitability scores of 0.7 or greater. Predicted suitable habitat in all models for the SAM overlapped with the current ranges (i.e., realized distributions) of the endemic species (**Figures 2A,E,I,M**). Suitable habitat for *P. fimbriata* and *D. cymosa* spanned most of the SAM along the border of North Carolina (NC) and Tennessee (TN), while suitable territory for *T. vaseyi* and *S. galacifolia* was concentrated in the southern half of this region.

Beyond the SAM, the SDMs for *P. fimbriata* and *D. cymosa* also predicted highly suitable habitat (i.e., potential range) in some northern areas outside these species realized distributions or native ranges (**Figures 2C,O**). For *P. fimbriata*, predicted suitable habitat occurred in West Virginia (WV), Pennsylvania (PA), and portions of New York (NY) and New England (see **Supplementary Figure 2.1** for maps that show the entirety of the Appalachian range including New England). For *D. cymosa*, our model predicted parts of WV, upstate NY, and New England to be highly suitable. Notably, models for both species predicted

TABLE 1 | Evaluation metrics of SDM predictive performance based on fivefold cross validation where 80% of occurrences and background points were used for training and 20% of occurrences for testing.

Species	AUC	TSS
Endemics		
Diphylleia cymosa	0.98	0.95
Phacelia fimbriata	0.86	0.63
Shortia galacifolia	0.87	0.77
Trillium vaseyi	0.93	0.72
Non-endemics—Southern Appalachian models (SA)		
Houstonia serpyllifolia	0.94	0.80
Maianthemum canadense	0.96	0.89
Prosartes lanuginosa	0.96	0.80
Trillium undulatum	0.97	0.94
Non-endemics—Full Range models (FR)		
Houstonia serpyllifolia	0.91	0.72
Maianthemum canadense	0.71	0.35
Prosartes lanuginosa	0.78	0.50
Trillium undulatum	0.70	0.37

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[3] pmip2.lsce.ipsl.fr

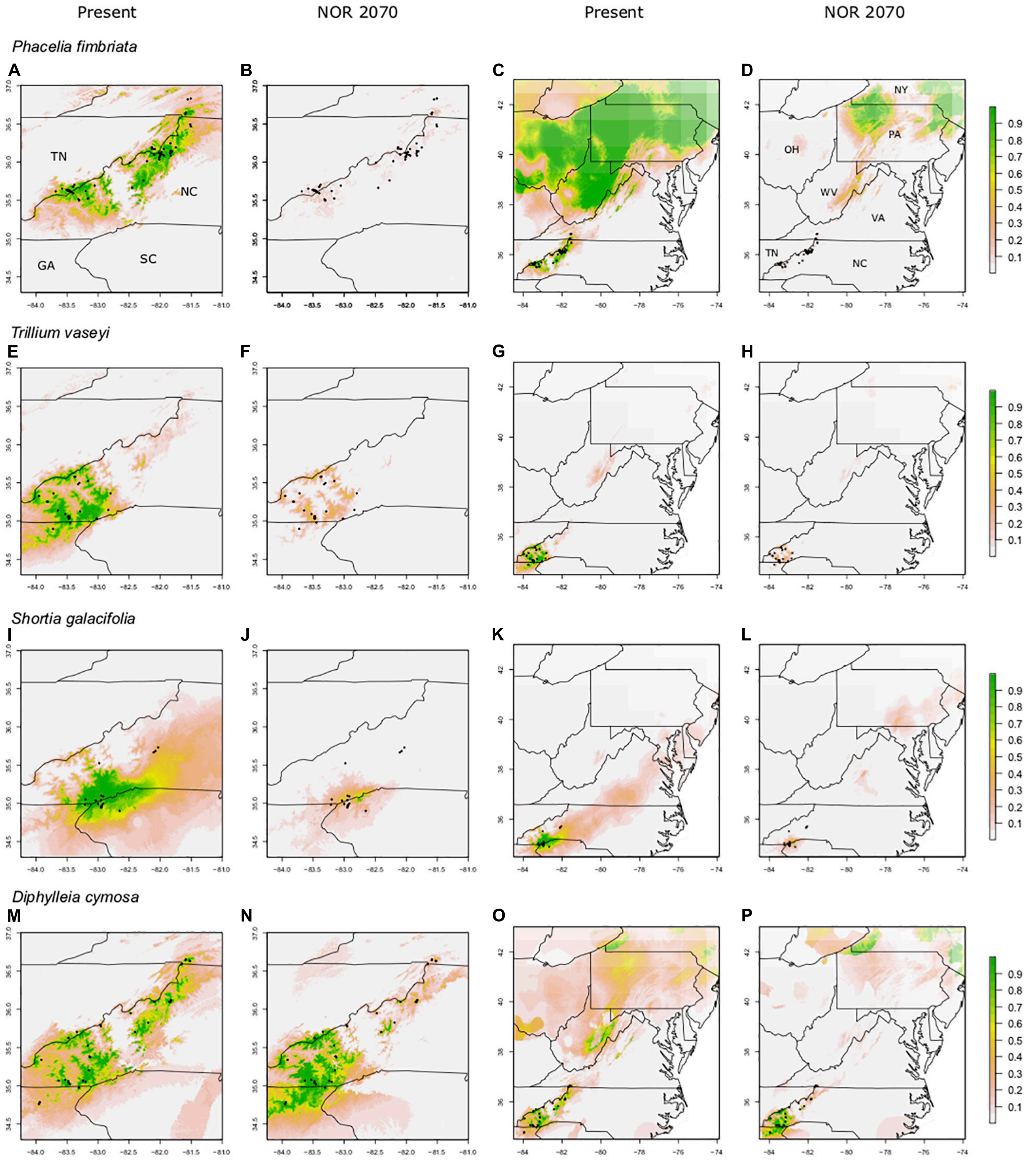

FIGURE 2 | Predicted suitable habitat of endemic species using the maxent modeling method. A portion of the eastern United States overlapping our focal area is shown; Tennessee (TN), North Carolina (NC), South Carolina (SC), and Georgia (GA). Other labeled states include New York (NY), Pennsylvania (PA), Virginia (VA), West Virginia (WV), and Ohio (OH). Both present and future climate scenarios are shown. Rows indicate species, columns indicate climate data used. Present and future climate data are taken from WorldClim version 1.4. "NOR" indicates the general circulation model NorESMI-M. Models are projected into the year 2070 using the climate emission scenario rcp8.5. A pseudo Plate Carree projection is used, which is the default in ArcMap. We refer the reader to particular plots in the text using the letter labels **(A–P)**.

a gap or break in suitable habitat in Virginia (VA), spanning west-to-east across the Appalachians in a region of lower elevation terrain. This gap in suitability (∼140 km wide along its south-to-north axis) across the mid-Appalachians results in a discontinuous distribution of predicted suitable habitat along the Appalachian Mountain corridor. For *T. vaseyi*, there is a small area of high suitability in the White Mountains of New Hampshire (**Supplementary Figure 4.4**). For *S. galacifolia*, SDMs predicted no highly suitable habitat outside the current range (**Figures 2K,G**). In **Figure 2**, we show a portion of the Appalachians up to southern New York so that details of the projections are easily visualized. In **Supplementary Figure 2.1**, we show projections for the entirety of Appalachian Mountain range including New England and southern Canada.

Endemic Species: Future Projections Under Climate Change

We limited our future projections to analogous environments, determined by MESS plots, in the eastern United States. To describe changes in the distribution of suitable habitat we used a threshold of 0.7 suitability. Most future climate projections showed moderate to severe reductions (range 86.5–100%) in suitable habitat within the endemics' current ranges, while one species (*D. cymosa*) showed both retention and gain of suitable habitat (31% gain). In most cases, species also showed losses of suitable habitat to the north of their current ranges. We focus on the results of future projections for one climate change scenario (NorESM1-M, rcp8.5, 2070; see **Supplementary Appendix 4** for HadGEM2-ES Figures). In this scenario, only *P. fimbriata* and *D. cymosa* retained substantial areas of highly suitable habitat (>70% suitability) to the north of their ranges (**Figures 2D,P** and **Supplementary Figure 2.1**). Descriptions of other climate change scenarios and future time points can be found in **Supplementary Appendix 4**.

Non-endemic Species: Current Ranges and Species Distribution Model Predictions

For the non-endemics, the Southern Appalachian (SA) models had high AUC (0.94–0.97) and TSS scores (0.80–0.94; **Table 1**). Full Range (FR) models had moderate to high AUC (0.71–0.91) and TSS scores (0.35–0.72; **Table 1**). FR model predictions overlapped strongly with the species' current ranges, with 78–91% of presence points falling in areas predicted by models to be suitable habitat (**Figures 3C,G,K,O**); this suggests substantial "filling" of climatically determined potential distributions. For all non-endemics, SDM predictions also captured the observed restriction of these species to the high elevation areas of the Southern Appalachian Mountains in the southeastern U.S., as well as their much broader east-west distribution north of PA.

The non-endemic SA models for *M. canadense*, *T. undulatum,* and *P. lanuginosa* had greater predictive performance than the FR models for both AUC and TSS (**Table 1**). Whereas, for *H. serpyllifolia*, performance metrics were very similar for the two types of models.

We also evaluated how well SA models predicted occurrences to the north of SAM that were not included in model building. Overall, SA models had fair to moderate predictive performance for *H. serpyllifolia* (AUC: 0.70; TSS: 0.41), *M. canadense* (AUC: 0.65; TSS: 0.23), *P. lanuginosa* (AUC: 0.55; TSS: 0.21), and *T. undulatum* (AUC: 0.62; TSS: 0.11).

Non-endemic Species: Future Projections

For most species, the FR models predicted significant reductions in suitable habitat within current ranges and often losses outside of ranges as well; however, those losses were not nearly as severe as in the SA models (61–95% losses for SA models; 23–66% losses for FR models; **Figures 3**, **4**). For example, SA models predicted that *M. canadense* would lose 95% of its predicted suitable habitat in North America (**Figure 4P**); whereas, FR models predicted a loss of less suitable territory in North America (66%) and a shift of 23% of its range to northern NY and New England (**Figure 3P**). SA models predicted *T. undulatum*'s range to recede (61% lost; 26% shifted north) primarily to parts of Ontario and Quebec (**Figure 4L**), whereas FR models were less severe in predicting recession (45% lost; 50% shifted north) to northern NY, New England, and parts of Canada (**Figure 3L**). Areas of suitable habitat for *P. lanuginosa* and *H. serpyllifolia* show no movement northwards, but simply retention or loss.

Environmental Predictors and Limiting Factors

Common environmental predictors emerged among models for different species, including temperature of the wettest quarter and of the driest quarter (**Supplementary Table 2.2**). Based on response curves to all common predictors, species prefer cool temperatures year-round, narrow annual temperature ranges, high precipitation, and low precipitation seasonality.

Three endemics had an area of predicted unsuitable habitat in VA, resulting in a discontinuous distribution along the Appalachians. For all endemics, low precipitation was a key limiting factor in this region (as well as in geographic regions to the north). Low precipitation of the warmest quarter most limited the range of *P. fimbriata* and *D. cymosa*, low precipitation of the coldest quarter for *T. vaseyi*, and low precipitation of the driest month for *S. galacifolia*.

DISCUSSION

In response to historical and recent climate change, the ranges of many plant species have shifted to higher elevations and to higher latitudes (Jackson and Overpeck, 2000; Kelly and Goulden, 2008; Chen et al., 2011). However, evidence is increasing that for other plant species, particularly small-ranged endemics, there might be large mismatches between species' realized and potential distributions (Svenning and Skov, 2004, 2007; Van der Veken et al., 2008; Sax et al., 2013). This phenomenon of "poor range-filling capacity" seems likely to trace to long-term dispersal limitation and the existence of biogeographical barriers or disjunctions between occupied vs. suitable-but-unoccupied regions. Our results for a set of four endemic forest herbs from the Southern Appalachian Mountains (SAM) of the eastern U.S. indicate that this dynamic may explain the restricted distributions of some endemic species, and could be important for gauging these species' capacities to respond to modern climate change.

Past work showed that the majority of narrow-ranged forest herbs overlap the SAM biodiversity hotspot in distribution

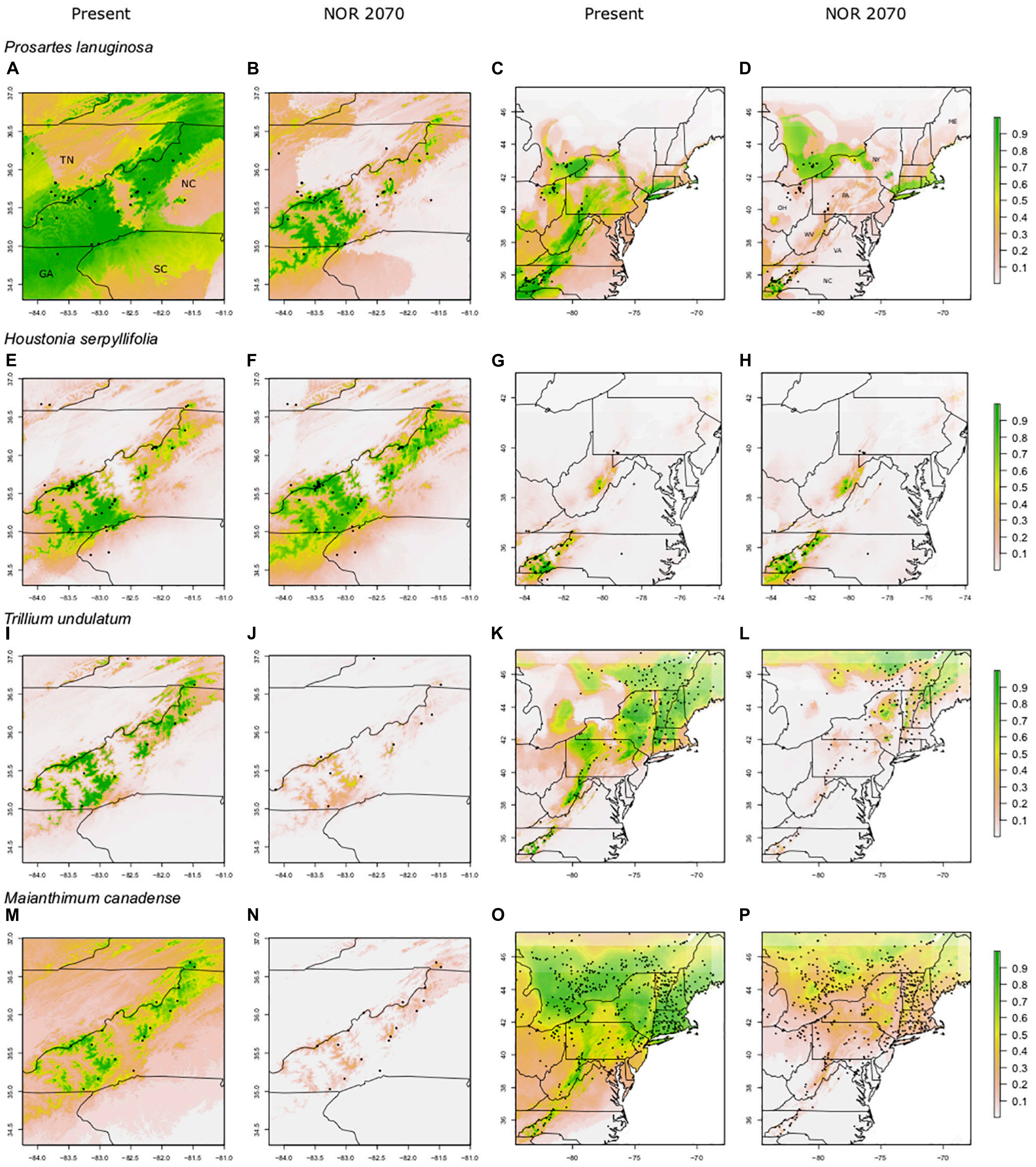

FIGURE 3 | Predicted suitable habitat of FR (full range) models for non-endemic species using the maxent modeling method. A portion of the eastern United States is shown; Tennessee (TN), North Carolina (NC), South Carolina (SC), and Georgia (GA). Other labeled states include New York (NY), Pennsylvania (PA), Virginia (VA), West Virginia (WV), Ohio (OH), and Maine (ME). FR (full range) models were constructed using presence points found within the entire range of the species. Rows indicate species, columns indicate climate data used. Both present and future climate scenarios are shown. Present and future climate data are taken from WorldClim version 1.4. "NOR" indicates the general circulation model NorESMI-M. Models are projected into the year 2070 using the climate emission scenario rcp8.5. A pseudo Plate Carree projection is used, which is the default in ArcMap. We refer the reader to particular plots in the text using the letter labels **(A–P)**.

(Bellemare and Moeller, 2014). However, it has been unclear as to whether that concentration of diversity reflects dispersal limitation following the last glacial maximum vs. specialization to the Southern Appalachian climate. Species distribution models (SDMs) revealed areas of high predicted habitat suitability up to 1140 km north of the endemic species' current ranges in the SAM.

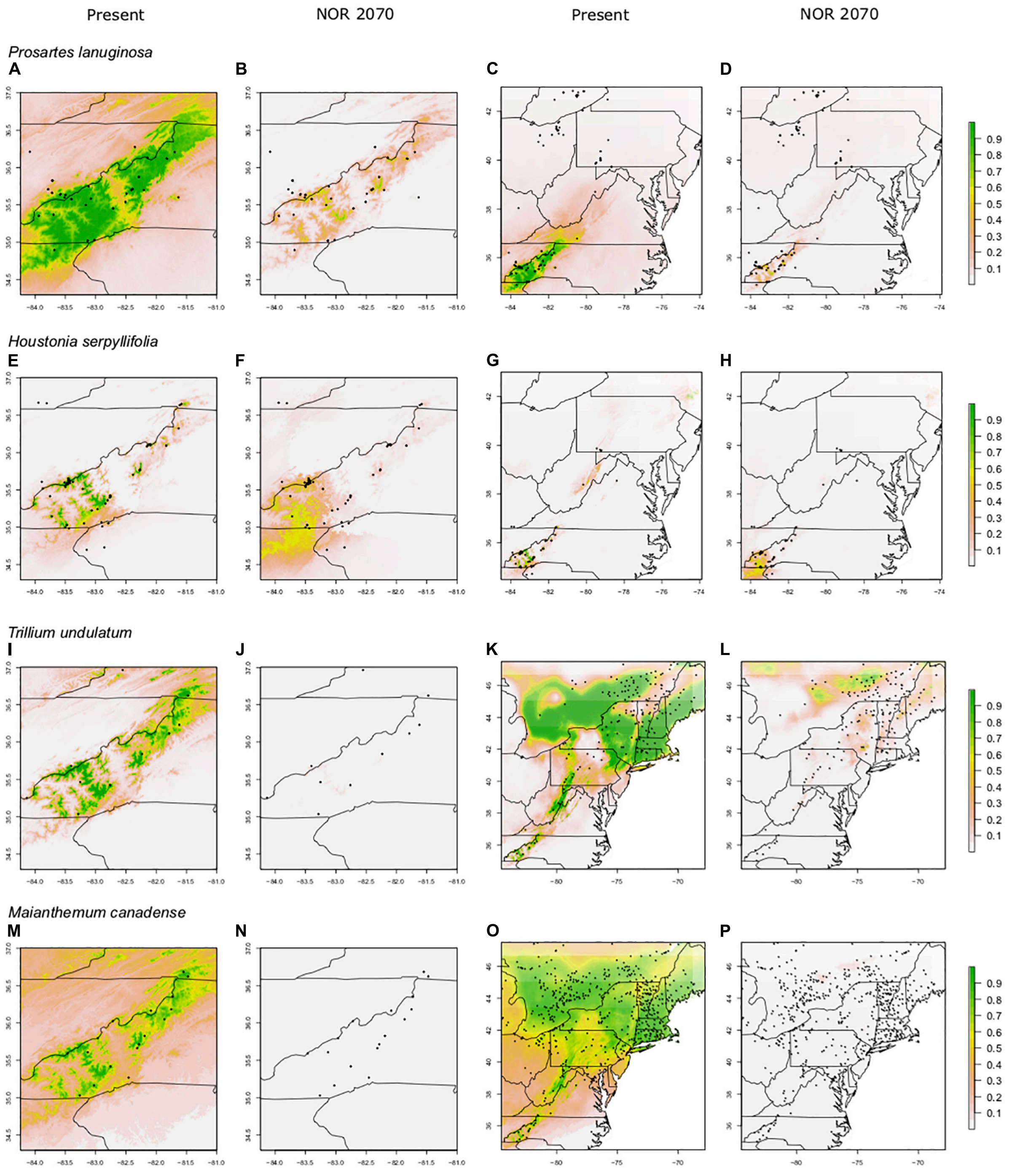

FIGURE 4 | Predicted suitable habitat of SA models for non-endemic species using the maxent modeling method. A portion of the eastern United States is shown; the maps in the first two columns are centered on the border between North Carolina and Tennessee. SA (Southern Appalachian) models were constructed using presence points found only within the Southern Appalachian Mountains. Rows indicate species, columns indicate climate data used. Both present and future climate scenarios are shown. Present and future climate data are taken from WorldClim version 1.4. "NOR" indicates the general circulation model NorESMI-M. Models are projected into the year 2070 using the climate emission scenario rcp8.5. A pseudo Plate Carrée projection is used, which is the default in ArcMap. We refer the reader to particular plots in the text using the letter labels **(A–P)**.

For example, with the endemics *P. fimbriata* and *D. cymosa,* large areas of currently suitable habitat were predicted in northern areas that are disjunct from their restricted native ranges in the southeastern United States. The largest area of predicted suitable habitat for both species, and the closest to the SAM, occurred in the Allegheny Mountains of West Virginia (WV).

This region was also identified as the most suitable region for the endemic *T. vaseyi* outside of its native range; however, the predicted level of suitability was lower. In addition, all three of these endemics had areas projected to be suitable in southern New England. For most SA non-endemic models, the Allegheny Mountains were also predicted to be suitable (with 60–100% suitability), indicating agreement among model predictions for a variety of Southern Appalachian Mountain forest herbs. The Allegheny Mountains region receives similar amounts of both annual precipitation and precipitation in the driest month as the SAM and hosts a high diversity of forest plant species, constituting a northern extension of a biodiversity hotspot for temperate forest herbs (Bellemare and Moeller, 2014). Overall, our models identify this region as most climatically similar to the Southern Appalachians and suggest that it might currently allow for the persistence of the endemics if colonized naturally or via "assisted migration."

Barriers to Northward Migration From the Southern Appalachian Mountains Hotspot

All eight of our SA models (both endemic and non-endemic) predicted highly *unsuitable* habitat in southwest VA, spanning across the east-west extent of the Appalachians Mountains (ca. 140 km wide from south-to-north). This gap lies just north of the SAM biodiversity hotspot, and just south of the Allegheny Mountains of WV. Without this distinct gap, suitable territory would be continuous along the north-south axis of the Appalachian Mountains for most species investigated. Therefore, this gap could have functioned as a significant barrier to dispersal, preventing northward migration of the endemics following the Pleistocene.

If this gap was important in limiting postglacial migration of the endemic plants investigated, what might explain the presence of ecologically similar non-endemics on both sides of this gap? Recent studies suggest at least two non-exclusive hypotheses for the wide disparity in ranges seen among temperate deciduous forest species. First, non-endemics may differ from endemics in their dispersal capacity, which may have enabled long-distance dispersal for some species across the lower-elevation gap inferred from our models. Based on our current knowledge and small sample size, there is no obvious relationship between dispersal mode and range size (endemics vs. non-endemics) in our pool of species (e.g., the endemic *D. cymosa* produces fleshy fruits seemingly attractive to birds). Second, the non-endemics might have persisted through the Last Glacial Maximum in northern microrefugia, rather than retreating exclusively to the SAM. Phylogeographic studies have suggested that a variety of taxa may have had northern refugia, closer to the LGM, that allowed for rapid recolonization of northern areas and formerly glaciated regions (McLachlan et al., 2005; Beatty and Provan, 2011; Li et al., 2013). Projections of our models for the LGM suggested that endemic species had highly suitable habitat only south of the Virginia gap; whereas, projections for one of the wider-ranged, non-endemic species (*M. canadense*) suggested that populations could have potentially persisted to the north of the gap (**Supplementary Figure 6.1**). Overall, widespread plants of this biome may have expanded their ranges following the last glacial maximum from multiple refugia. It is therefore possible that the endemic species' ranges may have simply contracted more severely during the late Pleistocene and become isolated and stranded on mountains south of the VA gap.

Predicting Poleward Range Expansion

We constructed SDMs for a set of more widespread forest herbs using (1) occurrences from across the full range (FR models) and (2) occurrences only in the Southern Appalachians (SA models). Specifically, we asked whether SA models (having a Wallacean shortfall) successfully predicted known occurrences to the north and the extent to which they differed from the FR models (i.e., to what extent do FR models exhibit a Hutchinsonian shortfall). Overall, predictive performance was fair to moderate when we tested whether SA models predicted occurrences to the north of the SAM. These results suggest that Hutchinsonian shortfalls likely compromised predictive capacity beyond the range. Such Hutchinsonian shortfalls are evident from the niche overlap analyses, which showed that SAM occurrences reflected a subset of the overall climate niche of each species. This discrepancy was more pronounced for *T. undulatum* and *M. canadense*. Nevertheless, for those two species, we found similar predictions of the geographic extent of suitable habitat outside of the SAM from the FR and SA models. Overall, our niche analyses and SDMs suggest that projections of suitable habitat to the north of current ranges can be challenging because the range where models were trained includes only a subset of environmental variation to the north. Although our models may not identify all of the potentially suitable areas beyond the range, they do predict a fraction of them, and those areas could be targeted for conservation efforts like assisted migration.

Climate Change and Implications for Conservation

Species with low dispersal and poor range-filling capacity may be especially threatened by modern climate change because they are unlikely to migrate quickly enough to keep pace with changing climate (Thomas, 2011). In some cases, their realized and potential distributions might shift apart entirely, exposing them to high risk of extinction (Sax et al., 2013). In this context, many endemics might be particularly susceptible, as their distributions often reflect past marginalization by climate change (e.g., Pleistocene glaciations), and their current distributions are often restricted to unusual habitats (high elevations, north slopes) in southern areas that are surrounded by warmer, unsuitable habitat (Ohlemüller et al., 2008). Conservation of such endemics may require assisted migration (McLachlan et al., 2007). However, in the case of endemic forest herbs of the SAM, it has been unclear whether suitable habitat already exists outside their native ranges.

Our models based on current climates predicted suitable habitat north of the range margins of three endemics, suggesting that assisted migration could be successful currently and that single, larger-scale translocations might be feasible, rather than "many small steps" moving incrementally northward over decades. It is important to note that SDMs are correlative and may not be effective at predicting suitable habitats in future environments or beyond the range. Moreover, predictors in SDMs may not have a causal relationship to the distribution of suitable habitat even in the calibration range. Important predictors in models could be correlated with one or more variables that were eliminated. Nevertheless, we found that similar areas of potentially suitable habitat north of the SAM were identified for different species whose models were built with different environmental variables.

By the year 2070, the native ranges of the endemics were predicted to become almost completely unsuitable, with the exception of *D. cymosa*, whose range receded to the southern half of its current distribution. In the southern half of its range, there is projected to be a large decrease in the temperature of the driest quarter; this variable remains unchanged in the northern half of its range. Additionally, in the northern half of its range, temperature of the wettest quarter is projected to increase, and this variable remains unchanged in the southern half of its range. Outside of native ranges, only *P. fimbriata* retained predicted suitable habitat in the more northern areas where we projected our models (upstate NY, northern New England, and Canada). Notably, *D. cymosa* and *S. galacifolia* are known to survive, reproduce, and recruit new adults in parts of New England where they have been transplanted decades ago, making these patterns plausible (J. Bellemare, pers. obs.). For non-endemics, the FR models predicted strong declines in suitable habitat within the SAM for both *T. undulatum* and *M. canadense*, but more modest changes for *P. lanuginosa* and *H. serpyllifolia*. Although species' responses are clearly individualistic, the underlying trend toward poleward movement of suitable habitat, and decline within current ranges, is generally consistent across species.

Species distribution models presume a close match between species' current native distributions and their fundamental climate tolerances. However, it is possible that rapid evolution could alter species' tolerances to novel climatic conditions in the future, allowing populations to persist *in situ* despite altered conditions. Rapid evolution in response to climate change, though well-documented in some plant species (Franks et al., 2007), appears insufficient to counter the rapid pace of modern climate change (Franks et al., 2018). Rapid evolution may be particularly unlikely for long-lived perennials with protracted generation times, like the forest plant endemics investigated in this study. Beyond rapid evolution, it is also conceivable that the fundamental niches of some plant species, especially small-ranged endemics, might already include tolerances for abiotic conditions beyond those inferred from their current native ranges (Sax et al., 2013). In the case of the endemics investigated here, our LGM projections suggest that they could have persisted near their present-day distributions in the SAM even during the colder climatic conditions of the Pleistocene (**Supplementary Figure 6.1**). This pattern is consistent with horticultural observations that narrow endemics of the SAM often survive and reproduce in gardens far to the north. However, this Pleistocene context might not suggest a similar likelihood for pre-existing tolerance to the significantly warmer conditions projected for the future given that they would be unprecedented in the recent geological past.

In the absence of rapid evolution or preexisting tolerances, poleward migration might be necessary for the long-term survival of the endemic species investigated here. However, natural dispersal to northern areas for endemic species may be particularly unlikely, given their apparent lack of substantial northward migration during the Holocene. Diffenbaugh and Field (2013) predicted that range shifts of several kilometers per year would be needed to shift in response to warming climate for species' whose range limits are closely matched to current climate. The endemic species in our study would need to be able to disperse at least 2.7 km per decade in order to reach predicted suitable habitat in eastern WV by 2070, if dispersal was diffuse. However, it is important to note that for *D. cymosa* and *P. fimbriata* suitable habitat in WV disappeared by 2070. This area may be a crucial stepping-stone in northward migration, but its future unsuitability could further minimize the probability of natural northward range shifts. Given the severity of reductions in suitable habitat within the range and the disjunct nature of suitable habitat outside the range, assisted migration may be an important strategy for long-term conservation (Hoegh-Guldberg et al., 2008). An important next step in evaluating these SDMs is to confront predictions of habitat suitability with estimates of fitness and population growth from transplant experiments. Our efforts in that area are ongoing.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

SKE collected field data, developed and evaluated models, and wrote an initial draft of the manuscript. JB assisted in providing field data and contributed to writing the manuscript. DAM assisted in project design, model development and evaluation, and contributed to writing the manuscript. All authors contributed to the article and approved the submitted version.

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Effects of Climate Change on the Distribution of *Akebia quinata*

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Akebia quinata, also known as chocolate vine, is a creeping woody vine which is used as Chinese herbal medicine, and found widely distributed in East Asia. At present, its wild resources are being constantly destroyed. This study aims to provide a theoretical basis for the resource protection of this plant species by analyzing the possible changes in its geographic distribution pattern and its response to climate factors. It is the first time maximum entropy modeling (MaxEnt) and ArcGIS software have been used to predict the distribution of *A. quinata* in the past, the present, and the future (four greenhouse gas emission scenarios, namely, SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5). Through the prediction results, the impact of climate change on the distribution of *A. quinata* and the response of *A. quinata* to climate factors were analyzed. The results showed that the most significant climatic factor affecting the distribution pattern of *A. quinata* was the annual precipitation. At present, the suitable distribution regions of *A. quinata* are mainly in the temperate zone, and a few suitable distribution regions are in the tropical zone. The medium and high suitable regions are mainly located in East Asia, accounting for 51.1 and 81.7% of the worldwide medium and high suitable regions, respectively. The migration of the geometric center of the distribution regions of *A. quinata* in East Asia is mainly affected by the change of distribution regions in China, and the average migration rate of the geometric center in each climate scenario is positively correlated with the level of greenhouse gas emission scenario.

Keywords: MaxEnt, suitable distribution, resource protection, geometric center of distribution regions, geographical distribution pattern

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INTRODUCTION

Akebia quinata, also known as chocolate vine, is a creeping woody vine widely distributed in East Asia (Wang et al., 2021). As a valuable Chinese herbal medicine, its fruit and stem have analgesic, diuretic, and anti-inflammatory effects (Park et al., 2018; Song et al., 2018). Over the years, the wild resources of this species have been destroyed due to increased cutting, and this species is facing more and more severe survival challenges. The protection of *A. quinata* is very urgent, and some reasonable and efficient protection schemes need to be implemented. This requires us to understand the suitable growth conditions of *A. quinata* and understand its geographical distribution and the impact of climate change upon it. At present, this species has only been reported in the fields of pharmacological activity (Sung et al., 2015; Lee et al., 2017), chemical composition (Jiang et al., 2006; Mimaki et al., 2007), and genome research (Li et al., 2016), but there are still gaps in knowledge around its geographical distribution and climate response.

The geographic distribution data of species are the basic information for studying their life process. In recent years, due to human activities and climate change, the habitat of many species has been destroyed and changed, and the survival of species has been threatened, or some even driven to extinction. Accurate simulation and prediction of species' distribution area is the key to their conservation. To achieve this goal, many factors need to be considered, especially climatic factors. On the one hand, climatic factors play a decisive role in the life process of species, and the accelerated prosperity or extinction of species can even depend on it (Lenoir et al., 2008; Acevedo et al., 2020). On the other hand, climate change also has a profound impact on the distribution pattern of species (Moraitis et al., 2019; Wang et al., 2019; Wilson et al., 2019) and will lead to a series of changes in the survival rate, dominance, community structure, and replacement rate of species (Yi et al., 2018). Therefore, it is more important to make clear the distribution of species and predict the change of their distribution in the future. Accurate distribution data can not only be used to predict the various possibilities of species distribution change but are also critical to assess the potential impact of changing ecosystems.

Climate is one of the main determinants delimiting the geographical distribution of plant species on large scale (Ferrarini et al., 2019). There is a considerable amount of research declaring that climate change leads to expansion or retraction in plant species' ranges (Thuiller et al., 2005; Ferrarini et al., 2018). To assess the vulnerability of plant species under a rapidly changing climate, we can use species distribution modeling (SDM) to predict species climate niches and project their potential future range shifts (Huntley et al., 1995; Pearson and Dawson, 2003; Thuiller et al., 2005; Alavi et al., 2019).

Maximum entropy modeling (MaxEnt) is a very powerful presence/pseudo-absence algorithm. Many authors have suggested that it is one of the most efficient approaches for predicting the potential distributions of species (Elith et al., 2006, 2011; Phillips et al., 2006a). The model can simulate and predict the potential geographical distribution of species by using the current distribution data and various environmental parameters (Phillips et al., 2006a; Phillips and Dudík, 2008). It has the advantages of small sample size, fast running speed, and stable operation (Phillips et al., 2006a; Estes et al., 2013; Li J. et al., 2020). Even in the case of insufficient species distribution information, it also has good accuracy and can test the accuracy of prediction results (Saatchi et al., 2008; Yi et al., 2017). Therefore, it is widely used in many aspects of species distribution analysis (Yang et al., 2013; Qin et al., 2017; Zhang et al., 2019).

In this study, the MaxEnt model was used to simulate and predict the distribution of *A. quinata* in different climatic scenarios. The purpose of this study was (1) to find the key climatic factors that restrict the distribution of *A. quinata*; (2) to predict the distribution pattern of *A. quinata* under different climate scenarios; (3) to evaluate the impact of climate change on the distribution pattern of *A. quinata*; and (4) to predict the concentrated distribution region of *A. quinata*, analyze the migration of its concentrated distribution region, and explore the migration reasons of its concentrated distribution region.

MATERIALS AND METHODS

Location Data Sources of *A. quinata*

The geographic data on *A. quinata* distribution were collected from two sources. Data were collected within China using a GPS device (GARMIN GPSMAP 63SC, Kansas City, KS, USA) from the field survey in 2017–2019, covering Northwest China, Central China, South China, and East China. Data from other parts of the world were collected from the website of the Global Biodiversity Information Facility (GBIF, https://www.gbif.org). Based on the above 1,024 effective records (**Figure 1**), the prediction model was established. The actual distribution of *A. quinata* was analyzed using ArcGIS (version 10.2, ESRI, Redlands, CA, USA) software. The geographic distribution map of richness ×1 was drawn using a geographic information system (GIS).

We used two methods to filter the data downloaded using GIBF. First, we deleted the data with missing longitude and latitude information and fuzzy geographic location information and, second, we deleted the data that did not conform to the geographic coordinate system (World Geodetic System 1984) used in this study.

Climate Data Sources

It is reported that 19 bioclimatic variables (**Table 1**) are the most typical and important variables to form the potential species distribution model (Molloy et al., 2013; Li J. et al., 2020). In this study, the current (1970–2000), past, and future climate scenarios were downloaded from WorldClim Version 2.1 (this version was released in January 2020) (www.worldclim.org) (Fick and Hijmans, 2017). These data include 19 climate variables. All variables were cast to USA Contiguous Albers Equal Area Conic (NAD 1983) and resampled using nearest-neighbor to a 30 arc-second resolution using ArcGIS. Using ArcGIS conversion tools, the environment variables were converted to ASCII format.

This study used the scenarios of the Last Interglacial, the Last Glacial Maximum, and the Mid-Holocene to predict the species distribution in the past. These three scenarios were provided by the Fourth Phase of Community Climate System Model (CCSM4) in the Fifth Phase of Coupled Model Intercomparison Project (CMIP5).

When simulating future species distribution, this study used the scenarios from shared socioeconomic pathway (SSP)-representative concentration pathway (RCP) (SSP1-1.9, SSP1-2.6, SSP4-3.4, SSP2-4.5, SSP4-6.0, SSP3-7.0, and SSP5-8.5) in the Sixth Phase of Coupled Model Intercomparison Project (CMIP6). These scenarios are a combination of SSPs and RCPs. Each scenario included a set of emissions and concentrations of chemically active gases, aerosols, and greenhouse gases. Among them, SSPs scenarios were the five basic scenarios (SSP1–SSP5) defined at the 2012 IPCC AR5 (Assessment Report 5 of the Intergovernmental Panel on Climate Change) special meeting, which are sustainable development path SSP1, intermediate path SSP2, regional competition path SSP3, unbalanced path SSP4, and traditional fossil fuel dominated path SSP5. RCPs scenario is from CMIP5, including a low emission scenario (RCP2.6), two medium emission scenarios (RCP4.5 and RCP6.0), and a high emission scenario (RCP8.5). CMIP6 inherits four

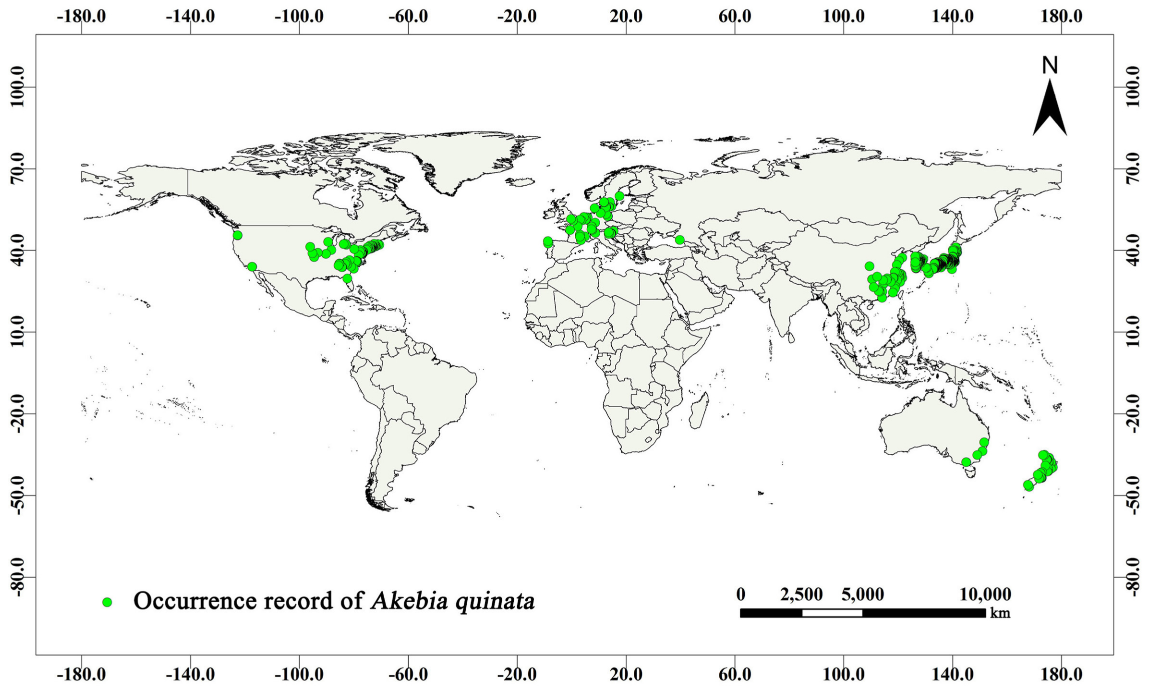

FIGURE 1 | Distribution of the occurrence record of *Akebia quinata* in the world.

TABLE 1 | List of climate variables.

Variables	Abbreviation	Unites
Annual Mean Temperature	bio1	°C
Mean Diurnal Range [Mean of monthly (max temp–min temp)]	bio2	°C
Isothermality (BIO2/BIO7) (× 100)	bio3	–
Temperature Seasonality (standard deviation × 100)	bio4	°C
Max Temperature of Warmest Month	bio5	°C
Min Temperature of Coldest Month	bio6	°C
Temperature Annual Range (BIO5-BIO6)	bio7	°C
Mean Temperature of Wettest Quarter	bio8	°C
Mean Temperature of Driest Quarter	bio9	°C
Mean Temperature of Warmest Quarter	bio10	°C
Mean Temperature of Coldest Quarter	bio11	°C
Annual Precipitation	bio12	mm
Precipitation of Wettest Month	bio13	mm
Precipitation of Driest Month	bio14	mm
Precipitation Seasonality (Coefficient of Variation)	bio15	–
Precipitation of Wettest Quarter	bio16	mm
Precipitation of Driest Quarter	bio17	mm
Precipitation of Warmest Quarter	bio18	mm
Precipitation of Coldest Quarter	bio19	mm

RCPs scenarios in CMIP5 (RCP2.6, RCP4.5, RCP6.0, and RCP8.5) and adds three discharge paths (RCP1.9, RCP3.4, and RCP7.0). According to the CO_2 emission of different scenarios (www.carbonbrief.org), we selected four emission scenarios with obvious classification for the simulation and prediction of this study, which are low emission scenario (SSP1-2.6), medium emission scenario (SSP2-4.5), medium-high emission scenario (SSP3-7.0), and high emission scenario (SSP5-8.5). The time span is 2021–2081.

Methods

Prediction Using the MaxEnt Model

The occurrence data of *A. quinata* and climate data were input into the MaxEnt (MaxEnt 3.4.1) model (Phillips et al., 2006b). We randomly selected 25% of the point data as the test set and 75% of the point data as the training set. The model was run 10 times to evaluate the average results. The area under curve (AUC) of the receiver operating characteristic (ROC) curve was selected to evaluate the performance of the model. The ROC curve analysis is a method to verify the performance of the MaxEnt model. Its principle is to judge the prediction accuracy of the model by calculating the area enclosed by the curve and abscissa, that is, the AUC value. Generally, the model has five accuracy levels. When the AUC value is between 0.50 and 0.60, the prediction fails. The prediction accuracy between 0.60 and 0.70 is poor, the prediction effect between 0.70 and 0.80 is average, the prediction effect between 0.80 and 0.90 is good, and the prediction accuracy between 0.90 and 1.00 is excellent (Li Y. et al., 2020). The response curve of climate variables generated by the model reflects the relationship between the value of climate variables and the existence probability of *A. quinata*. A jackknife test and statistical table of contribution rate of climate variables were used to screen the climate variables with high importance.

Too many climate variables will reduce the computational efficiency of the MaxEnt model in predicting the distribution of species on a large regional scale, and the climate variables with obvious collinearity will affect the prediction accuracy (Li Y. et al., 2020; Sillero and Barbosa, 2020). Therefore, after running the MaxEnt model with 19 climate variables, this study screened climate variables and compiled the model again for prediction. The screening process was as follows:

(1) The Pearson correlation coefficient in SPSS (Statistical Product and Service Solutions, version 26.0, Armonk, NY, USA) software was used to calculate the correlation between climate variables.

(2) We removed all variables (variables whose percent contribution is <1%) whose percent contribution in the model prediction is lower than the contribution threshold setting. Next, among the variables with high correlation (the absolute value of the correlation coefficient is greater than or equal to 0.8), the variable with the highest contribution rate was retained, and other variables were removed.

Suitability Division of the Distribution Regions

By using the To Raster tool in ArcGIS, the American Standard Code for Information Interchange (ASCII) file exported using the MaxEnt model converted the raster into a grid layer, and the suitable distribution regions of species were obtained. In the predicted suitable distribution regions, the existence probability of species was between 0 and 1. According to the actual distribution and field survey results, using the Reclassify tool of ArcGIS and artificial classification method, the prediction results were divided into four grades: high suitability (>0.66), medium suitability (0.33–0.66), low suitability (0.15–0.33), and no suitability (<0.15).

This study used the world climate data to run the MaxEnt model. The map data and results of specific regions in this study were extracted from the global prediction results.

Geometric Center Analysis of the Distribution Regions

Raster Calculator tool in ArcGIS was used to separate the grid layer of species distribution, and the suitable distribution regions were separated. Next, the Raster Domain tool was used to convert the grid layer of the suitable distribution regions into a face, and then the Mean Center tool was used to find out the geometric center of the suitable distribution regions.

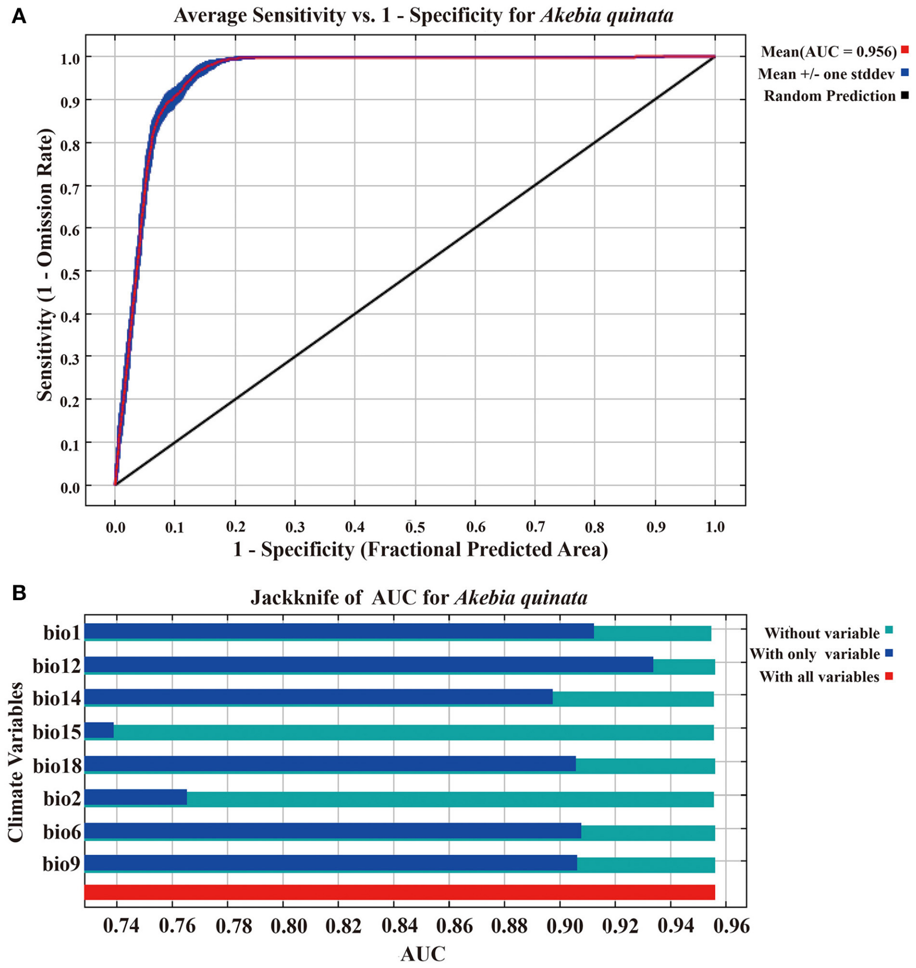

FIGURE 2 | The ROC curve analysis and Jackknife test of the MaxEnt model. **(A)** The ROC curve of the MaxEnt model (10 runs). **(B)** The Jackknife test of the MaxEnt model.

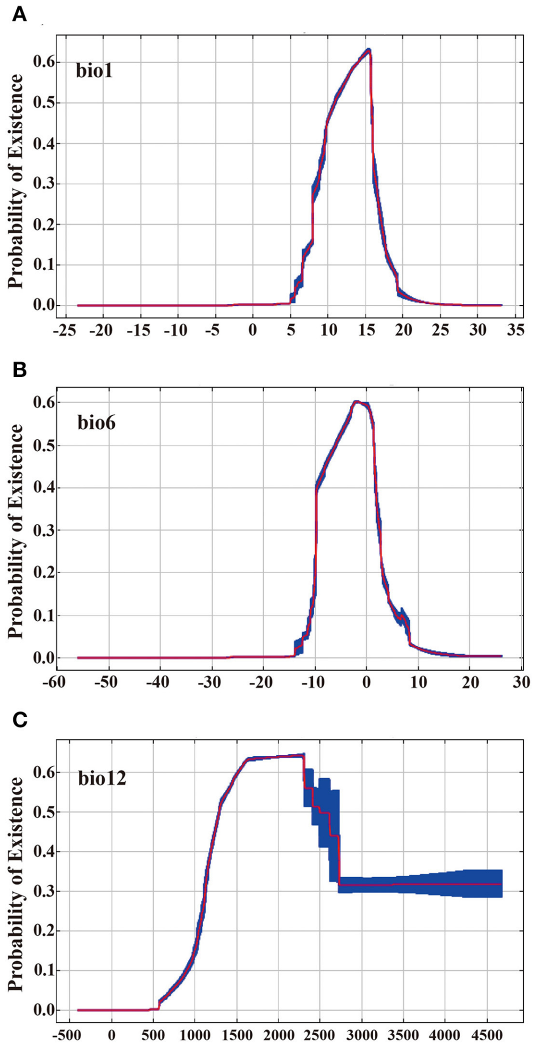

FIGURE 3 | Response curves between the probability of presence and climate variables (10 runs). **(A)** response curves between the probability of presence and bio1. **(B)** response curves between the probability of presence and bio6. **(C)** response curves between the probability of presence and bio12. Red: mean. Blue: mean ± 1 standard deviation.

RESULTS

Model Accuracy Evaluation

In this study, the average AUC of the MaxEnt model is 0.956 (**Figure 2A**), which indicates that the prediction accuracy is excellent, and the results can be used.

Important Climate Variables

Supplementary Table S1 shows the contribution rates of climate variables in the MaxEnt model. **Supplementary Table S2** shows the correlation test between 19 climate variables. According to the screening principle, eight climate variables (bio1, bio2, bio6, bio9, bio12, bio14, bio15, and bio18) are retained for recompiling the MaxEnt model operation. **Figure 2B** shows the Jackknife test (using AUC on test data). When using a single variable, the climate variable with the highest gain is bio12 (annual precipitation), and its gain value is >0.93. In addition, bio1 (annual mean temperature) and bio6 (minimum temperature of the coldest month) are the two most gain variables after bio12. They are three important climatic variables that restrict the geographic distribution of *A. quinata*. **Figures 3A–C** shows the response curves between the above three climate variables and the probability of the existence of *A. quinata*.

The probability of the existence of *A. quinata* is close to 0 when the annual precipitation (the most significant variable, bio12) is <570 mm, then increases rapidly and reaches the maximum when bio12 is 2,300 mm. The probability of existence decreases when bio12 continues to increase, but when bio12 is more than 2,700 mm, the probability of existence does not continue to decrease and remains in the low suitability range (0.15–0.33). There is no clear upper limit but there exists a clear lower limit of annual precipitation for the suitable distribution regions of *A. quinata*. According to the division of suitability, to meet the minimum existence probability (>0.15) of *A. quinata*, at least bio12 should be >1,000 mm. To achieve medium suitable survival conditions for *A. quinata* (probability of existence >0.33), bio12 should be in the range of 1,160–2,700 mm. The performance of the temperature factor in the suitable distribution regions of *A. quinata* is different from precipitation, and the temperature factor has clear upper and lower limits. When the temperature of bio1 (annual mean temperature) is <5.0°C, the probability of existence is close to 0. Due to the continuous increase of bio1, the probability of existence increases rapidly. When the temperature of bio1 increases to 15.5°C, the probability of existence reaches the maximum and is close to 0.63, then decreases rapidly and finally decreases to 0. The response curve of bio6 (minimum temperature of coldest month) is similar to bio1, except that the temperature threshold of existence probability is different. The two thresholds of existence probability approaching 0 are −14.0 and 19.0°C, respectively, and −3.0 and 0.0°C is the temperature range with the highest probability of existence (probability of existence is close to 0.60).

Potential Distribution Regions of *A. quinata*

According to the prediction results of the MaxEnt model, the prediction of the current and the future distribution is relatively clear, but the distribution of *A. quinata* is not found in the past three periods (**Supplementary Figure S1**).

Current Potential Distribution

According to the current prediction results (**Figure 4A**), most of the suitable distribution regions of *A. quinata* were mainly in the temperate zone, and a small number of suitable distribution regions were in the tropical zone. The total suitable area was 592.87 × 10^4 km^2, the low suitable area was 447.35 × 10^4 km^2, the medium suitable area was 143.99 × 10^4 km^2, and the highly suitable area was 1.53 × 10^4 km^2. In East Asia, the occurrence data of *A. quinata* were the most intensive. The suitable distribution regions were also mainly located in East Asia (**Figure 4B**), and the areas of medium and high suitability were 73.55 × 10^4 and 1.25 × 10^4 km^2, respectively, accounting for

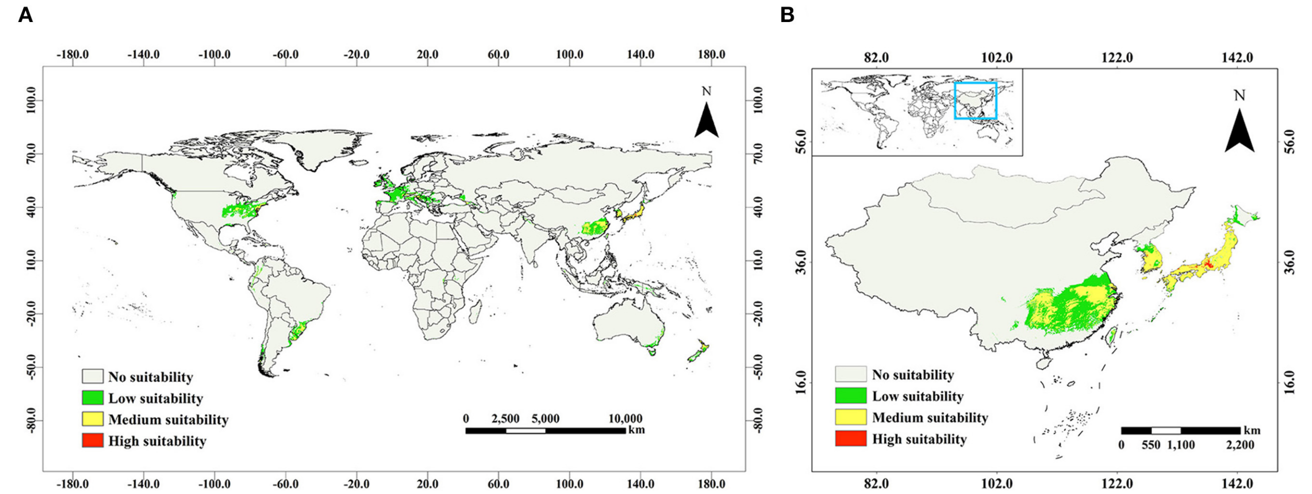

FIGURE 4 | Prediction of suitable distribution regions of *A. quinata* in the current climate scenario. **(A)** Distribution of *A. quinata* in the world. **(B)** Distribution of *A. quinata* in East Asia.

51.1 and 81.7% of the global medium and high suitable area, respectively. East Asia is the region with the most concentrated distribution of *A. quinata*, and so is a region worthy of attention in this study.

Potential Distribution in the Future

Supplementary Table S3 shows the suitable area of *A. quinata* in the world under different climate scenarios. **Figure 5A** shows the suitable area change of *A. quinata* in the form of a broken line diagram. Worldwide, regardless of the transition from the current scenario to any scenario in 2021, the suitable area of *A. quinata* shows an increasing trend. In the SSP1-2.6 scenario, the suitable area shows a downward trend after 2021 and an upward trend from 2041. In the SSP2-4.5 scenario, the suitable area shows an upward trend before 2041 and begins to decline after 2041. In the SSP3-7.0 and SSP5-8.5 scenarios, the suitable area increased significantly from 2041 to 2061 and then remained stable. In the first two scenarios, the suitable area remains relatively stable, while in the latter two scenarios, the suitable area shows a significantly increasing trend, especially in the SSP5-8.5 scenario. **Supplementary Figures S2–S5** shows the prediction picture of the suitable distribution regions of *A. quinata* in the world. A remarkable phenomenon is that from 2061 to 2081, with the upgrading of the greenhouse gas scenario, the suitable area for *A. quinata* in Europe will expand significantly, and there is a trend to expand to the northeast. With the upgrading of climate scenario, the suitable area of *A. quinata* in North America increases and tends to expand to the north, while the suitable area in South America shows a downward trend. In the rest of the regions except East Asia, the change in the suitable area of *A. quinata* is not obvious.

In East Asia, the suitable area of *A. quinata* shows a continuous decreasing trend under the SSP2-4.5, SSP3-7.0, and SSP5-8.5 scenarios, especially in SSP5-8.5 (**Figure 5B**). In the SSP1-2.6 scenario, the suitable area shows a downward trend before 2041, an upward trend in 2041 and 2061, and then continues to decline. *A. quinata* is mainly distributed in China, Korea, and Japan in East Asia. **Figures 6A–H** shows the suitable distribution regions of *A. quinata* in East Asia under the SSP1-2.6 and SSP5-8.5 scenarios. It is obvious that under the SSP5-8.5 scenario, the suitable distribution region of *A. quinata* in China shows a trend of continuous fragmentation from 2041 to 2081. Under the SSP1-2.6 scenario, the suitable distribution region in China can remain in a relatively stable state. From 2061 to 2081, under the SSP2-4.5 and SSP3-7.0 scenarios, the suitable distribution region in China also showed a fragmentation trend (**Supplementary Figure S6**). In Japan and South Korea, the suitable distribution regions of *A. quinata* remain stable in all scenarios. It can be seen from the line chart of suitable area that the suitable area of *A. quinata* in East Asia is closely related to that of China (**Figures 5B,C**). **Supplementary Tables S4, S5** show the specific suitable area values in East Asia and China, respectively.

Geometric Center of Suitable Distribution Regions and Its Migration

The overall change of the suitable area can be expressed by the shift of the geometric center of the suitable distribution regions of *A. quinata* in East Asia. Based on the predicted potential distribution, the geometric centers of the distribution regions under different climate scenarios are obtained (**Figure 7**). **Figure 7A** shows the geometric centers under the current climate scenario and the 16 different future scenarios. It can be seen intuitively that these geometric centers generally show a trend of migration to the northeast. The migration distance of the geometric center is different in four different climate situations. In the SSP1-2.6 scenario (**Figure 7B**), the migration distance of the geometric center is relatively small, in the SSP2-4.5 and SSP3-7.0 scenarios (**Figures 7C,D**), the migration distance of the geometric center is relatively medium, and in the SSP5-8.5

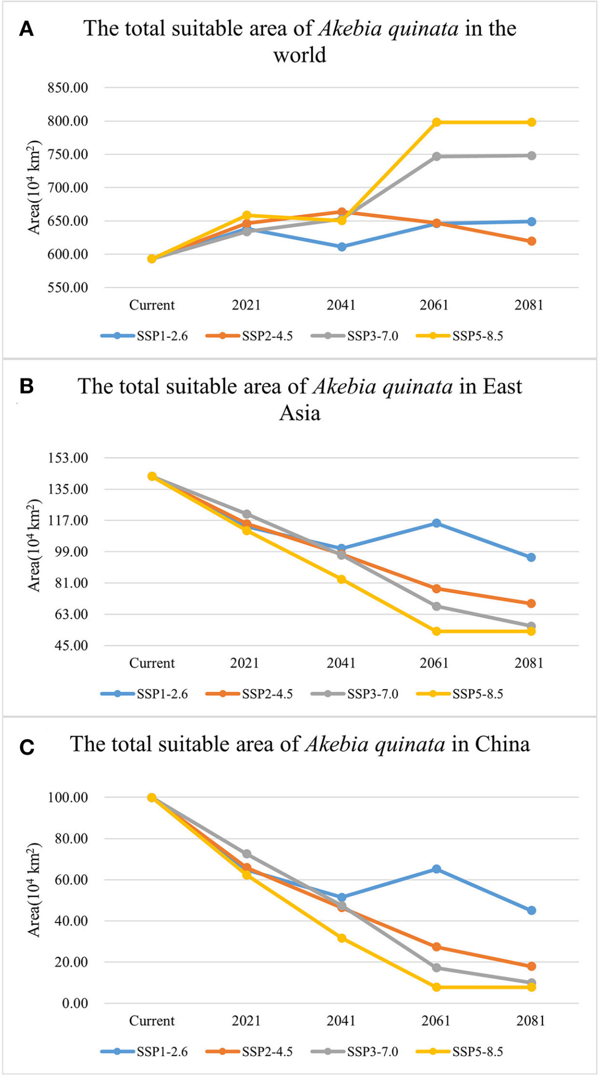

FIGURE 5 | Broken line chart of the total suitable area of *A. quinata* under four greenhouse climate scenarios. **(A)** The total suitable area of *A. quinata* in the world. **(B)** The total suitable area of *A. quinata* in East Asia. **(C)** The total suitable area of *A. quinata* in China.

scenario (**Figure 7E**), the migration distance of geometric center is relatively large.

To express them more clearly, the migration of the geometric center are quantified. Considering the geometric center under the current climate scenario as the origin, the migration rate of the geometric center farthest from the origin is expressed as 1. The ratio of the distance between other geometric centers and the origin to the farthest distance is the migration rate of these geometric centers (**Table 2**). The climate scenario with the largest migration rate is SSP5-8.5 in 2061 and 2081, and the migration rate is 1. The climate scenario with the lowest migration rate is SSP3-7.0 in 2021, and the migration rate is 0.17. The average migration rates of the four climate scenarios are 0.29 (SSP1-2.6), 0.49 (SSP2-4.5), 0.55 (SSP3-7.0), and 0.69 (SSP5-8.5), respectively.

In the SSP1-2.6 scenario, the migration rate of the geometric center increases slightly from 2021 to 2041, decreases in 2061 (the geometric center makes a return motion), and increases again in 2081, which is in a relatively stable dynamic equilibrium (the migration rate fluctuates between 0.22 and 0.37). It can be speculated that the distribution area of *A. quinata* may continue to maintain a relatively stable state in this scenario. In other scenarios, the geometric center does not make a return motion. And, with the continuous upgrading of the scene, the average migration rate of the geometric center also increases.

The decrease of the suitable area of *A. quinata* in East Asia is mainly affected by the change of the suitable area in China, while the suitable area of Japan and Korea has almost no change. Therefore, the weight of the suitable area of Japan and Korea in the total suitable area of East Asia has increased. The change of the suitable area weight causes the geometric center of the distribution area to move to the northeast, and the average mobility of geometric centers under different climate scenarios is positively correlated with the level of greenhouse gas emission scenarios.

DISCUSSION

The change of plant distribution patterns is different under climate warming. The related research on the prediction of *Cunninghamia lanceolata* distribution shows that an increase in greenhouse gas emissions may lead to the decrease of the suitable area of *C. lanceolata* (Li Y. et al., 2020). In the study of two species of peony (Zhang et al., 2018), the suitable areas of *Paeonia delavayi* and *Paeonia rockii* will increase under the low concentration greenhouse gas emission scenario (RCP2.6), but the suitable area of *P. rockii* will increase and the suitable area of *P. delavayi* will decrease under the high concentration greenhouse gas emission scenario (RCP8.5). According to the related research of *Coptis* herbs, the suitable areas of *Coptis chinensis* and *Coptis teeta* will decrease, and the suitable area of *Coptis deltoidea* will increase in the future RCP8.5 scenario (Li J. et al., 2020). The prediction in this study shows that the suitable area of *A. quinata* in different regions of the world changes differently. In East Asia, when transitioning from the current scenario to three greenhouse gas emission scenarios (SSP2-4.5, SSP3-7.0, and SSP5-8.5), the suitable area of *A. quinata* will be significantly reduced. Compared with other scenarios, in the low concentration greenhouse gas emission scenario (SSP1-2.6), the suitable area change of *A. quinata* in East Asia is more conservative.

Global climate change will not only cause temperature changes in different regions but also change the distribution pattern of precipitation, resulting in changes in the distribution of *A. quinata*. Generally, plants can adapt to the fluctuation of climate factors within a certain threshold range, but when the change of climate factors approaches or even exceeds the threshold range, it will lead to the migration of their distribution (Camille and Gary, 2003). Plants need enough water to grow,

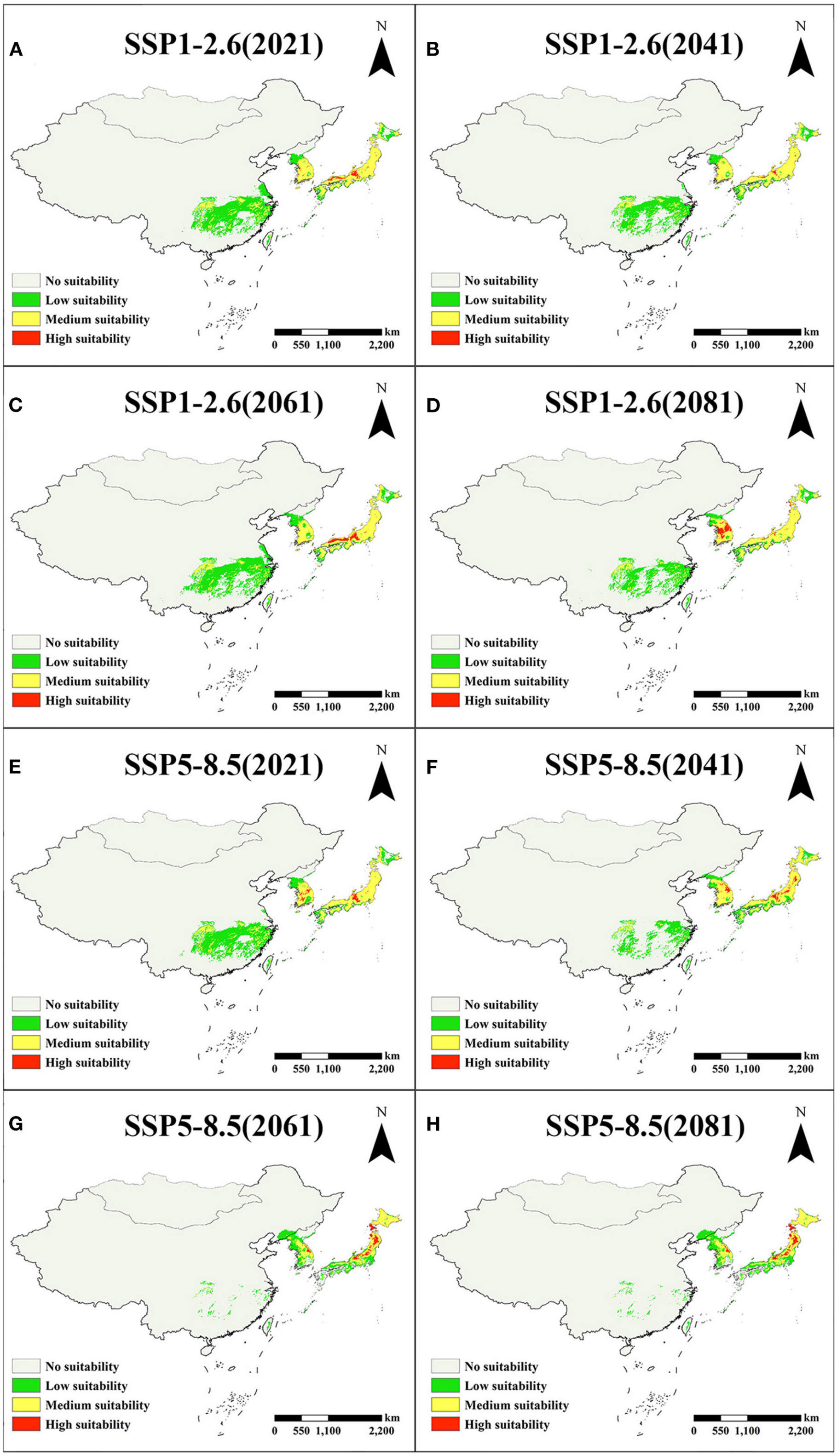

FIGURE 6 | Distribution of *A. quinata* in East Asia in the SSP1-2.6 and SSP5-8.5 scenarios. **(A–D)** Distribution under the SSP1-2.6 scenario. **(E–H)** Distribution under the SSP5-8.5 scenario.

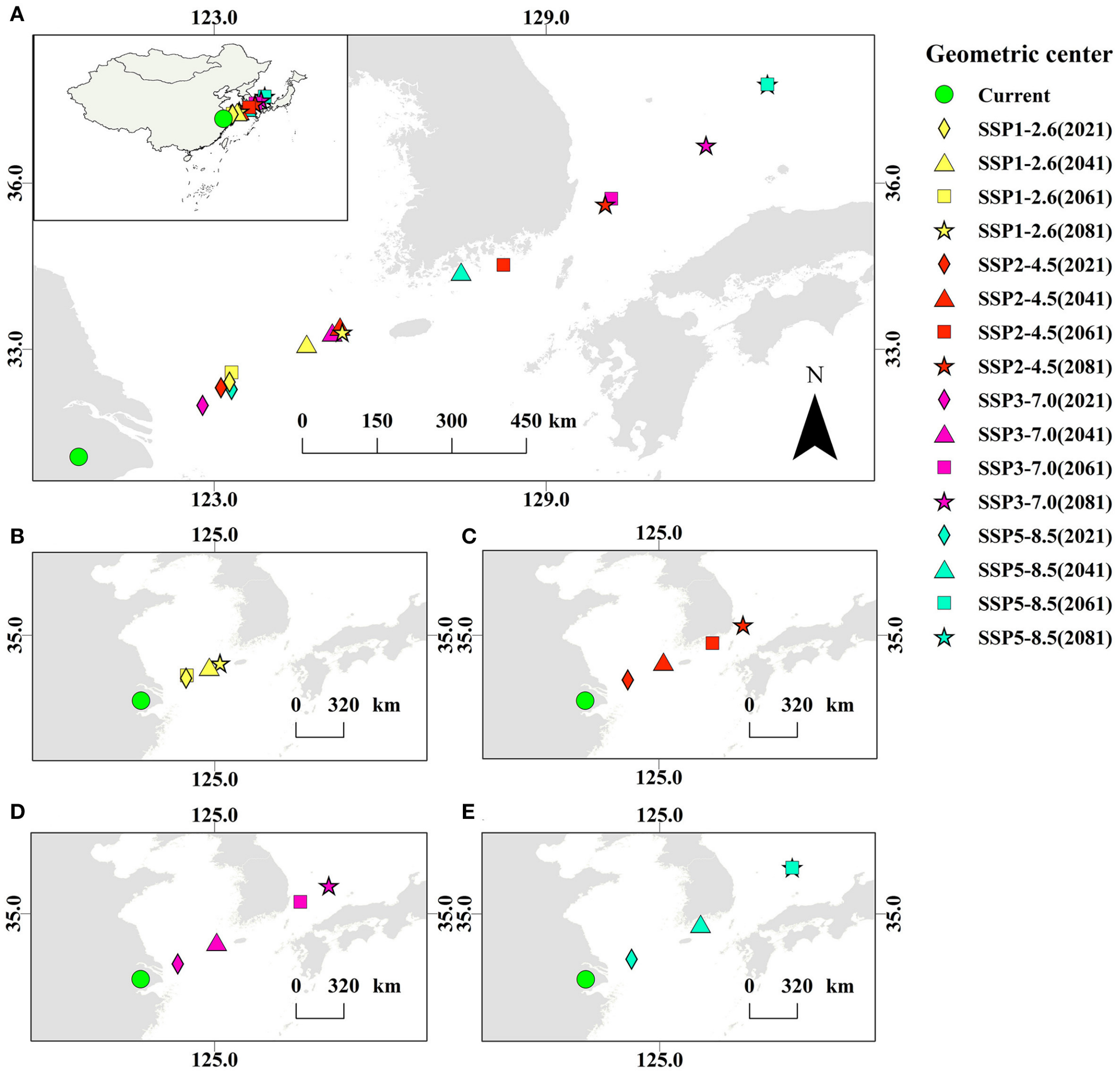

FIGURE 7 | Geometric centers of distribution regions of *A. quinata*. **(A)** Geometric centers in different climate scenarios. **(B)** Geometric centers in the SSP1-2.6 scenario. **(C)** Geometric centers in the SSP2-4.5 scenario. **(D)** Geometric centers in the SSP3-7.0 scenario. **(E)** Geometric centers in the SSP5-8.5 scenario.

but drought will limit their growth. When the precipitation in the driest month increases, it helps to prolong the growing season of the plants and promote their migration to more suitable habitats (Vaganov et al., 1999). In addition, extreme temperatures also significantly affect the growth of plants. If the minimum temperature of the coldest month drops, it will undoubtedly aggravate freezing and chilling injuries and cause plant death (Camille and Gary, 2003). The increase of maximum temperature in the warmest month may destroy the water balance in plants and hinder their metabolic function (Lemmens et al., 2006). The changes in these climate factors are directly reflected in the increase or decrease of suitable area. If the climate change is too large, it will cause more serious changes, that is, habitat fragmentation.

CONCLUSION

It is of great significance to predict the distribution pattern of *A. quinata* in different climatic conditions and analyze the response relationship between *A. quinata* and climatic factors for its protection and research. The results show that the concentrated distribution region of *A. quinata* is in East Asia. And, bio1 (annual mean temperature), bio6 (minimum temperature of the coldest month), and bio12 (annual precipitation) are the main climatic factors affecting the distribution pattern of *A. quinata*. In East Asia, when transitioningfrom the current scenario to three greenhouse gas emission scenarios (SSP2-4.5, SSP3-7.0, and SSP5-8.5), the suitable area of *A. quinata* will be significantly reduced. Compared with other scenarios, under

TABLE 2 | Migration rate of the geometric center of *Akebia quinata*'s distribution regions in East Asia.

Scenario	Year	Migration rate
Current		0
SSP1-2.6	2021	0.22
	2041	0.33
	2061	0.23
	2081	0.37
SSP2-4.5	2021	0.21
	2041	0.38
	2061	0.60
	2081	0.75
SSP3-7.0	2021	0.17
	2041	0.36
	2061	0.76
	2081	0.90
SSP5-8.5	2021	0.22
	2041	0.55
	2061	1
	2081	1

the low concentration greenhouse gas emission scenario (SSP1-2.6), the change in suitable area of *A. quinata* in East Asia is more conservative. The geometric center of the distribution area of *A. quinata* in East Asia will move to the Northeast under the climate warming, which is mainly due to the decrease of the distribution area of *A. quinata* in China. And, the average migration rate of the geometric center under each climate scenario is positively correlated with the level of greenhouse gas emission scenario.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

WW conceived and X-QX designed the study. J-MZ and WW processed the data, performed the analyses and analyzed the results, and wrote the manuscript. M-LS, Z-JL, X-YP, SS, and BL edited the manuscript. All authors read and approved the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.752682/full#supplementary-material

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Niche Shifts From Trees to Fecundity to Recruitment That Determine Species Response to Climate Change

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Anticipating the next generation of forests requires understanding of recruitment responses to habitat change. Tree distribution and abundance depend not only on climate, but also on habitat variables, such as soils and drainage, and on competition beneath a shaded canopy. Recent analyses show that North American tree species are migrating in response to climate change, which is exposing each population to novel climate-habitat interactions (CHI). Because CHI have not been estimated for either adult trees or regeneration (recruits per year per adult basal area), we cannot evaluate migration potential into the future. Using the Masting Inference and Forecasting (MASTIF) network of tree fecundity and new continent-wide observations of tree recruitment, we quantify impacts for redistribution across life stages from adults to fecundity to recruitment. We jointly modeled response of adult abundance and recruitment rate to climate/habitat conditions, combined with fecundity sensitivity, to evaluate if shifting CHI explain community reorganization. To compare climate effects with tree fecundity, which is estimated from trees and thus is "conditional" on tree presence, we demonstrate how to quantify this conditional status for regeneration. We found that fecundity was regulated by temperature to a greater degree than other stages, yet exhibited limited responses to moisture deficit. Recruitment rate expressed strong sensitivities to CHI, more like adults than fecundity, but still with substantial differences. Communities reorganized from adults to fecundity, but there was a re-coalescence of groups as seedling recruitment partially reverted to community structure similar to that of adults. Results provide the first estimates of continent-wide community sensitivity and their implications for reorganization across three life-history stages under climate change.

Keywords: climate change, regeneration niche, tree migration, life-history stages, seed production

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INTRODUCTION

Extensive climate changes in North America since forest stands established over the last few centuries may have changed where tree species can recruit in the aftermath of recent diebacks (Ibáñez et al., 2007; Woodall et al., 2009; Bell et al., 2014; Serra-Diaz et al., 2016; Davis et al., 2019). The notion of a *species' niche* (Hutchinson, 1957; Austin, 2002), typically quantified with models for adult distribution and abundance explained by climate and habitat variables, may represent past conditions, when current stands were established. The *regeneration niche* recognizes that conditions affecting fecundity and seedling establishment can differ from adults (Grubb, 1977; Clark et al., 1998; Ibanez et al., 2006; Engler et al., 2009; Swab et al., 2012). Accumulating climate changes can progressively distance the habitats where regeneration can occur from current distributions of mature trees (Sharma et al., 2021). If climate effects depend on soils, drainage, and biotic variables, then climate-habitat interactions (CHI) will complicate responses (Ibanez et al., 2009; Clark et al., 2016; Serra-Diaz et al., 2016). The emerging misalignment of adults and their recruits will be especially severe if recruitment stages are most sensitive to climate (Sharma et al., 2021). Related concepts like a species' *climate envelop* (Pearson and Dawson, 2003; Thomas et al., 2004) or *suitable habitat* (Freckleton and Watkinson, 2002; Iverson et al., 2008), quantified with adult trees and current conditions, may not align with the conditions for seed production and seedling recruitment (Ibanez et al., 2006; Clark et al., 2011). In this paper we show that the differences in niche requirements quantified from adult distributions can diverge from those for fecundity and seedling recruitment, with important implications for responses to contemporary climate change.

Contemporary forest composition is determined by seed availability and recruitment success in the past. Both fecundity and seedling success could be sensitive to climate-habitat interactions (CHI) in ways that are not apparent from studies on adult physiology. In North America, fecundity is highest in warm, moist climates of the south-central continent (Clark et al., 2021). Seedling recruitment is accelerated by temperature in early-successional environments (Fridley and Wright, 2018), and seedlings could be more sensitive to climate change than are adult survival and seed production (García-Camacho et al., 2010; Walck et al., 2011). Recruitment responses to temperature depend on water availability, which might limit upslope forest range expansion (Lenoir et al., 2010; Crimmins et al., 2011; Kueppers et al., 2017). Local moisture gradients controlled by drainage and soil type interact with moisture deficits (Ibáñez et al., 2007; Clark et al., 2014; Serra-Diaz et al., 2016), amplifying the effects of aridification (Seyednasrollah and Clark, 2020). With warming over much of North America and changes in precipitation, the recruitment that follows twenty-first-century diebacks may differ from that of the past.

Under slow climate change (Dawson et al., 2019), species composition is expected to integrate the fitness contributions of fecundity, seedling success, and adult survival, each of which might respond to CHI in its own way. Species with similar responses to climate and habitat that occur together in communities now, may respond differently to future environmental change. The similarities between species might typically be inferred from their tendencies to co-occur in the habitats where mature individuals are most abundant. However, the many ways in which species may differ in the responses at each life stage could result in novel communities as suggested by no-analog communities in the past (Williams and Jackson, 2007). If contemporary climate changes have effects that differ by recruitment stage, then biodiversity projections require an understanding of CHI not only on adult distributions, but also for fecundity and seedling recruitment. This study examines how climate and habitat variables differ in their effects on seed production and seedling establishment and survival.

Comparing the habitat relationships for adults, seed production, and recruits requires comparable methods. Models for the biogeographic distribution of seeds (Clark et al., 2021; Sharma et al., 2021) are necessarily *conditional* on the abundance of trees that produce those seeds; we cannot know how much seed would be produced by a species where it does not grow. An *unconditional* estimate would require wide availability of trees planted throughout climate/habitat space. We define *fecundity* to be the expected annual seed mass produced by a tree of a given species, size, crowding, and habitat.

Because recruitment can only be observed near adults, it too must be quantified *conditional* on adult presence. *Recruitment* ρ_i refers to seedlings expected to cross a size threshold per ha per year at location i. Estimates of habitat controls on recruitment unconditional on adults would require seed availability throughout climate/habitat space; in fact, the climate/habitat space for recruitment is constrained within that already occupied by adults. Like fecundity, recruitment depends on the abundance of adults and thus must be modeled conditionally. Unlike fecundity, recruitment rates obtained from ingrowth to forest inventory plots are not explicitly referenced to adults (they are numbers per area per year) (Sharma et al., 2021), but they implicitly depend on adult presence.

For comparison with fecundity, the conditional model for recruitment dependent both on adult abundance a and climate/habitat is given by $[\rho|a, \mathbf{x}]$, where the bracket notation indicates a distribution of recruitment rates ρ conditional on adults a and climate/habitat $\mathbf{x}$. To facilitate conditional analysis, these effects might be separable in a model, $[\rho|g(a) + h(\mathbf{x})]$, where $g(\cdot)$ and $h(\cdot)$ are functions. Unfortunately, adults cannot be used as predictors of recruitment, because both are random–they both depend on environment, and they are both encountered as random variables when inventory plots are sampled. Clearly, the comparison of fecundity and recruitment requires joint analysis of recruits and adults $[\boldsymbol{\rho}, \mathbf{a}|\mathbf{x}] = [\mathbf{y}|\mathbf{x}]$, where $\mathbf{y}$ is a vector holding recruitment and adult abundances of all species, followed by conditioning on adults and environment, $[\boldsymbol{\rho}|\mathbf{a}, \mathbf{x}]$.

Using conditional models that allow us to compare the communities represented by joint fecundity and recruitment responses we expose a reorganization across life stages that will contribute to the next generation of forests. Changing niche space is summarized by the ways in which species reorganize in their responses from adults to fecundity to recruitment and by the CHI that are responsible for those changes.

MATERIALS AND METHODS

Our goal is to jointly model recruits and adults of all species, thereby accommodating their mutual dependence structure, but then to isolate the effects of adults from direct CHI effects through conditioning. This conditional recruitment can then be compared with fecundity, which is necessarily conditional on the trees producing seeds. The fitted model provides a basis for defining communities in terms of the responses of each stage to CHI. The reorganization of these communities across life history stages is the basis for interpreting potential forest changes that account for recruitment responses.

Theoretical Development

Consider trees that occupy inventory plots sampled at intervals during which adults change in abundance due to survival of previously measured trees and ingrowth of new individuals that cross the minimum size threshold. Population growth rate can be expressed in terms of recruitment (per ha per yr) per adult abundance,

$$\rho_s = \frac{1}{a_s}\frac{dr_s}{dt} \tag{1}$$

where r_s is number of seedlings per ha of species s, t represents time (in years), and a_s indicates adult basal area (location i is suppressed to reduce clutter). Because it integrates information on size and numbers, adult abundance is typically expressed as basal area ($\mathrm{m}^2\ \mathrm{ha}^{-1}$). Recruitment is expressed as seedlings per ha per year, obtained from the ingrowth number, plot area, and sample interval of FIA (Sharma et al., 2021). It is divided by adult basal area following Equation 1 to generate seedlings per adult basal area per year ($\mathrm{m}^{-2}\ \mathrm{year}^{-1}$). Due to the small size of inventory plots, both tree basal area and recruitment are noisy variables. Recruits depend not only on adult abundances of the same species, but also on adults and recruits of other species (Zhu et al., 2015).

Generalized Joint Attribution Modeling (GJAM) allows us to jointly quantify CHI effects on both adults and recruitment due to its allowance for different data types and the dominance of zero values–most species are absent from most observations (Clark et al., 2017). From the fitted joint model we obtain a conditional distribution that isolates effects of CHI from adults, which can then be compared between species and with responses of tree abundance and fecundity.

Inputs to the model are predictors and responses $\{\mathbf{x}_i, \mathbf{y}_i\}_{i=1}^{n}$ for $i = 1, \ldots, n$ inventory plots. Predictors occupy the length-Q vector $\mathbf{x}_i$, including climate, habitat, and their interactions. Recruitment rates and adult basal areas of all S species occupy a length-$2S$ observation vector $\mathbf{y}_{is}$ consisting of S adult basal areas and S recruitment rates. Corresponding to the observation vector $\mathbf{y}_{is}$ is a latent vector $\mathbf{w}_i$ having elements w_{is} that are equal to y_{is} when $w_{is} \geq 0$ and negative otherwise (Clark et al., 2017). The latent w is *censored* at zero, allowing us to combine the continuous abundance with discrete zero values. For our application the basic GJAM model simplifies to

$$\mathbf{w}_i \sim MVN\left(\boldsymbol{\mu}_i, \boldsymbol{\Sigma}\right) \times \prod_{p=1}^{2S} I(w_{i,p} \leq 0)^{I(y_{i,p}=0)} I(w_{i,p} > 0)^{I(y_{i,p}=w_{i,p})} \tag{2}$$

where $\mathbf{w}_i = (\boldsymbol{\rho}_i', \mathbf{a}_i')'$ is a length-$2S$ vector holding the (uncensored, latent) abundances of species as S recruitment rates $\boldsymbol{\rho}_i$ (the discrete version of Equation 1) and S adult abundances $\mathbf{a}_i$ (basal area, $\mathrm{m}^2\ \mathrm{ha}^{-1}$), with mean vector $\boldsymbol{\mu}_i = \mathbf{B}\mathbf{x}_i$, and $2S \times Q$ coefficient matrix

$$\mathbf{B} = \begin{pmatrix} \mathbf{B}_\rho \\ \mathbf{B}_a \end{pmatrix} \tag{3}$$

The two components of $\mathbf{B}$ describe the effects of CHI on the recruitment and adult observations. The covariance matrix takes up additional dependence between all recruits and adults. The $2S \times 2S$ covariance can be partitioned as

$$\boldsymbol{\Sigma} = \begin{pmatrix} \boldsymbol{\Sigma}_{\rho,\rho} & \boldsymbol{\Sigma}_{\rho,a} \\ \boldsymbol{\Sigma}_{a,\rho} & \boldsymbol{\Sigma}_{a,a} \end{pmatrix} \tag{4}$$

This joint distribution of recruitment and adults allows us to isolate the contributions of adult abundances and CHI impacts on recruitment as a conditional distribution,

$$\boldsymbol{\rho}_i | \mathbf{a}_i \sim MVN(\boldsymbol{\mu}_{\rho,i}, \mathbf{P}) \tag{5}$$

$$\begin{aligned} \boldsymbol{\mu}_{\rho,i} &= \mathbf{B}_\rho \mathbf{x}_i + \mathbf{A}(\mathbf{a}_i - \mathbf{B}_a \mathbf{x}_i) \\ &= \mathbf{C}\mathbf{x}_i + \mathbf{A}\mathbf{a}_i \end{aligned} \tag{6}$$

$$\mathbf{P} = \boldsymbol{\Sigma}_{\rho,\rho} - \mathbf{A}\boldsymbol{\Sigma}_{a,\rho} \tag{7}$$

There are now two matrices of coefficients for recruitment rate, one $S \times S$ matrix for effects of adults, $\mathbf{A} = \boldsymbol{\Sigma}_{\rho,a}\boldsymbol{\Sigma}_{a,a}^{-1}$, and another $S \times Q$ matrix for effects of CHI, $\mathbf{C} = \mathbf{B}_\rho - \mathbf{A}\mathbf{B}_a$. Importantly, this capacity to condition on adult basal area offers an opportunity to compare the effects of CHI on seedling recruitment with that for fecundity, which, again, is necessarily conditioned on adult abundance. Following Clark et al. (2017), a joint sensitivity across all species to climate/habit covariates can be obtained using

$$\mathbf{f}_\rho = diag\left(\mathbf{C}'\mathbf{P}^{-1}\mathbf{C}\right) \tag{8}$$

The length-Q sensitivity vector $\mathbf{f}_\rho$ summarizes the importance of each covariate for conditional recruitment. Additionally, species correlation in response of recruitment to climate/habit can be quantified using response matrix

$$\mathbf{E}_\rho = \mathbf{C}\mathbf{V}\mathbf{C}' \tag{9}$$

where $\mathbf{V}$ is the covariance in predictors in the design matrix. Similar species can have similar responses to environment conditions (columns in $\mathbf{C}$) that can be amplified by large variation in $\mathbf{V}$, and vice versa. The $S \times S$ $\mathbf{E}_\rho$ matrix thus quantifies species correlation in their responses to climate/habitat conditions (Clark et al., 2017). Adult sensitivity $\mathbf{f}_a$ and response matrix $\mathbf{E}_a$ can be quantified in the same way using

$$\mathbf{f}_a = diag\left(\mathbf{B}_a'\boldsymbol{\Sigma}_{a,a}\mathbf{B}_a\right) \tag{10}$$

$$\mathbf{E}_a = \mathbf{B}_a\mathbf{V}\mathbf{B}_a' \tag{11}$$

TABLE 1 | Predictors used for fecundity estimate, and joint modeling of adults and recruits.

Predictors	Adults/Recruits	Fecundity	Definition and source
Diameter (*cm*)	No	Yes	MASTIF
Diameter squared (cm^2)	No	Yes	
Shade class	No	Yes	1–5 FIA/NEON classes from inventories
Stand age (year)	Yes	No	FIA
Site moisture	Yes	No	Site moisture level (xeric, mesic, and hydric) from FIA
Annual temperature (°C)	Yes	Yes	Average Temperature from terraClimate, CHELSA
Annual deficit (*mm*)	Yes	Yes	Accumulated $PET - P$ from terraClimate, CHELSA
Sand, clay (%)	Yes	Yes	Proportion of soil type by weight from soilgrids.org
Cation exchange capacity (*mmolc/kg*)	Yes	Yes	Soil fertility indicator by weight from soilgrids.org
Annual deficit × site moisture	Yes	No	Interaction between annual deficit (climate) and moisture (site)

Yes or No indicates whether or not the predictor is included in the analysis. PET represents potential evapotranspiration and P is precipitation, NEON is national ecological observatory network.

Data

Data used in this study include forest inventories (adult trees and recruits), fecundity data, soils, climate, and local habitat conditions (**Table 1**). Tree abundance were collected from 196,765 plots of the USDA Forest Inventory and Analysis (FIA) dataset in the United States (Gray et al., 2012), including over 4.6 million trees for 112 abundant species. Since the year 2009 (Woodall et al., 2009), FIA data that consistently samples forest trees across the demographic spectrum (seedlings to adults) and across space and time in all US forests have been used in numerous studies to examine the dynamics of range shifts (Zhu et al., 2011; Bell et al., 2014; Fei et al., 2017; Sharma et al., 2021). Basal area ($\mathrm{m}^2\ \mathrm{ha}^{-1}$) of adult trees ($\mathbf{a}$) and recruitment rate ($\boldsymbol{\rho}$) of small seedlings per adult basal area per year ($\mathrm{m}^{-2}\ \mathrm{year}^{-1}$) were evaluated using FIA. Adult tree basal area was calculated directly from diameter of individual trees. We defined numbers of recruits as live saplings with diameter between 2.5 cm and 12.7 cm and the FIA code RECONCILEDCD == 1 (i.e., an ingrowth tree) at forested and remeasured plots. Remeasured plots were identified using the Population Plot Stratum Assignment (PPSA) table (Woudenberg et al., 2010). We calculated recruitments per year by dividing the number of recruits by the sampling interval (REMPER in PPSA table) and then scaled it by the expansion factor, which depends on plot size, from the Population Stratum table (Woudenberg et al., 2010). Finally, we divided recruits per year by the adult basal area at each plot. We quantified recruitment success through recruitment rates instead of seedling abundances because seedlings are not individually tracked between censuses and thus cannot offer an estimate of rates. The K-Means algorithm (Hartigan and Wong, 1979) was used to aggregate plots on the basis of CHI and location into 1-ha clusters to increase the signal-to-noise ratio (Iverson and Prasad, 1998; Zhu et al., 2014).

Fecundity data were obtained from the Masting Inference and Forecasting (MASTIF) network (Clark et al., 2021), including 233,052 trees and 2,221,148 3-years from 149 species. Fecundity is compiled from two types of raw data, seed traps and crop counts (Clark et al., 2021). Fecundity sites are listed at the website MASTIF as detailed in Clark et al. (2019) and Clark et al. (2021).

Environmental covariates for modeling adult basal area, fecundity, and recruitment are summarized in **Table 1**. We obtained stand age and site moisture class from FIA field records, the latter characterized using local land form, topographical position, and soil (Woudenberg et al., 2010). Soil characteristics, including proportion of soil type (i.e., clay and sand) and cation exchange capacity (i.e., an indicator for soil fertility), were derived from Hengl et al. (2017). We calculated weighted average soil conditions based on uncertainty layers for three soil depths (i.e., 0–5 cm, 5–15 cm, and 15–30 cm). Monthly Climate data from Terraclimate (Abatzoglou et al., 2018) and CHELSA (Karger et al., 2017) were used to derive annual mean temperature and accumulated moisture deficit. Deficit was defined as the difference between potential evapotranspiration and precipitation at region scales, which differs from the moisture class that quantified plot-scale moisture availability to trees.

Analysis

Fecundity modeling required individual tree attributes, including diameter and shade class using the 5-point scale of FIA and NEON, in addition to site variables used for adults and recruits. The MASTIF model accommodates dependencies between individual trees and within trees over time using the R package MASTIF (Clark et al., 2019). Seed production for the 233,052 3-year observations in MASTIF was fitted to tree attributes and CHI.

As discussed in the section *Theoretical background*, adult abundances and recruitment, $\mathbf{a}$ and $\boldsymbol{\rho}$, were fitted jointly in GJAM, with summaries including joint sensitivity and species correlation in response to CHI. Similar to $\mathbf{E}_a$ in Equation 11 and $\mathbf{E}_\rho$ in Equation 9, the species correlation in fecundity was quantified as

$$\mathbf{E}_f = \mathbf{B}_f \mathbf{V}_f \mathbf{B}_f' \tag{12}$$

where $\mathbf{B}_f$ is the coefficient matrix of fecundity responses of each species to each predictor in $\mathbf{x}$, and $\mathbf{V}_f$ is the covariance of predictors. The fecundity sensitivity was quantified as

$$\mathbf{f}_f = diag\left(\mathbf{B}_f' \boldsymbol{\Sigma}_{f,f}^{-1} \mathbf{B}_f\right) \tag{13}$$

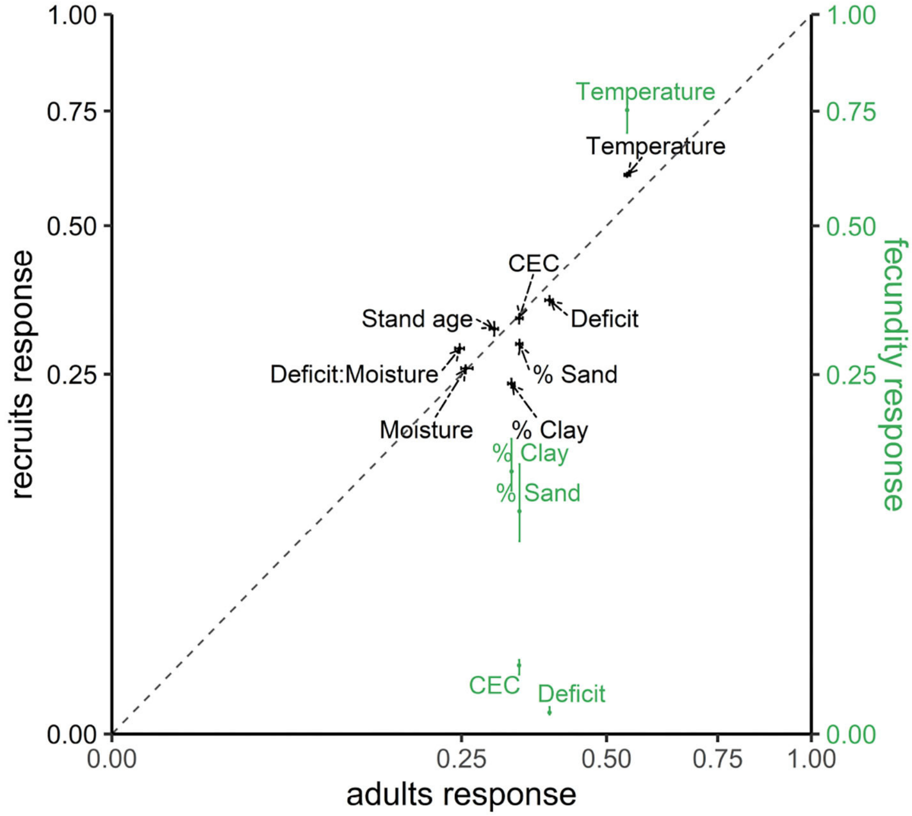

FIGURE 1 | Joint sensitivity taken over all species for adult abundances $\mathbf{f}_a$, *conditional* recruits $\mathbf{f}_\rho$ (left y-axis with black color), and fecundity $\mathbf{f}_f$ (right y-axis with green color). Sensitivity is shown as a fraction of the total variance explained for each variable. Posterior medians are show with 95% credible intervals (whiskers). The species-level sensitivity of fecundity to climate-habitat interactions (CHI) are detailed in **Supplementary Figure S2**.

where $\Sigma_{f,f}$ is the covariance matrix for fecundity.

To track community reorganization from adults to fecundity to recruits we summarized changes in the response matrix **E**. In this case, the community is defined in terms of species responses to predictors in the model. Hierarchical clustering was implemented on the 87 species that were included in both FIA and MASTIF sites using the R function *hclust* in the *stats* package (R Core Team, 2020). Adult abundances ($\mathbf{E}_a$), conditional recruitment ($\mathbf{E}_\rho$), and fecundity ($\mathbf{E}_f$) were clustered separately. Communities were identified by names of the most abundant species in clusters extracted from $\mathbf{E}_a$. We used an alluvial diagram (Rosvall and Bergstrom, 2010) to summarize the tendency for community reorganization with climate change across the three demographic stages (i.e., adults, fecundity, and recruits).

RESULTS

Taken over the entire map and all species, temperature is the most important source of variation in adults and conditional recruitment (black labels in **Figure 1**), and it is behind shade class (not shown) for fecundity (green labels in **Figure 1**). The other climate-related variable, moisture deficit, also plays a large role for adults and recruitment, but it contributes much less to variation in fecundity. Adult trees show higher sensitivities to soil texture (% sand and clay) and to deficit than does conditional recruitment (points are below the 1:1 line in **Figure 1**). Site moisture status and CEC show equivalent contributions to adults and recruitment. By contrast, temperature, stand age, and the deficit-moisture interaction have larger impacts on conditional recruitment than on adult abundance (**Figure 1**). While having high sensitivity to shade class and tree diameter (not shown), fecundity shows an even stronger response to temperature than do adults or recruitment (**Figure 1**). After temperature and individual tree attributes, soil-related variables have less effects on fecundity than recruitment and adults.

The high sensitivity to temperature and then moisture deficit in **Figure 1** results from large contrasts across $\mathbf{B}_a$ (adults) and **C** (conditional recruitment rate) coefficients for these variables in **Figure 2**. Variables that contribute small sensitivity in **Figure 1** are those for which there is limited contrast in responses across species.

The similarities in **Figure 2** between species define communities based on the responses to predictors that have important variation (**Figure 3**). For example, species in *ACSA-PIST* of **Figure 3a** share affinities for low temperatures, low CEC, and high moisture (bottom of **Figure 2a**). Similar affinities, but with many species-specific differences, characterize their recruitment rates (bottom of **Figure 2b**). Together these species

FIGURE 2 | Species responses to climate/habitat for **(a)** adults in $\mathbf{B}_a$ and **(b)** *conditional* recruits in C. Stars indicate that the 95% credible interval does not contain zero. Colors for the species names follow adult communities in **Figures 3a**, **4**, with horizontal lines separating clusters. Coefficient colors are scaled proportionally to the 97.5% of the estimated ranges for both adults and conditional recruits.

FIGURE 3 | The response matrices for **(a)** adult ($\mathbf{E}_a$), **(b)** fecundity ($\mathbf{E}_f$), and **(c)** *conditional* recruitment ($\mathbf{E}_\rho$). Rows in $\mathbf{E}_f$ and $\mathbf{E}_\rho$ are ordered by clusters estimated for adult responses $\mathbf{E}_a$, with communities separated by dashed lines. Community names are the first two letters of genus and species for the two most abundant species (see **Supplementary Figure S1** and **Supplementary Table S1**).

differences determine the community structure in **Figure 3c**. Overall, adult responses in matrix $\mathbf{E}_a$ cluster as clear species assemblages (red blocks in **Figure 3a** along the diagonal) with distinct biogeographical patterns (**Figure 4A**). From cool-moist to warm-dry in the West are *TSHE-THPL*, *PSME-PICO*, and *PIPO-ABCO*. From cool to warm in the East are *ACSA-PIST*, *ARCU-PRSE*, and *QUNI-ILOP*.

Conditional recruitment $\mathbf{E}_\rho$ does not find all six of the community types identified in adult basal area, instead separating southeastern forests as distinct from everything else (**Figures 3a,c**). The similarities come from the tendency for adult abundance and recruitment rate of the same species to respond similarly. This similarity was not a foregone conclusion from the fact that recruitment and adults occur in basically the same geographic spaces, because recruitment here is taken *conditional on* adult abundance. The conditional responses separate the effects of adult abundance, so there is opportunity for recruitment sensitivities to depart from those obtained for adults. The important differences result from lower climate sensitivity in recruitment rate than in adult distributions. The differences

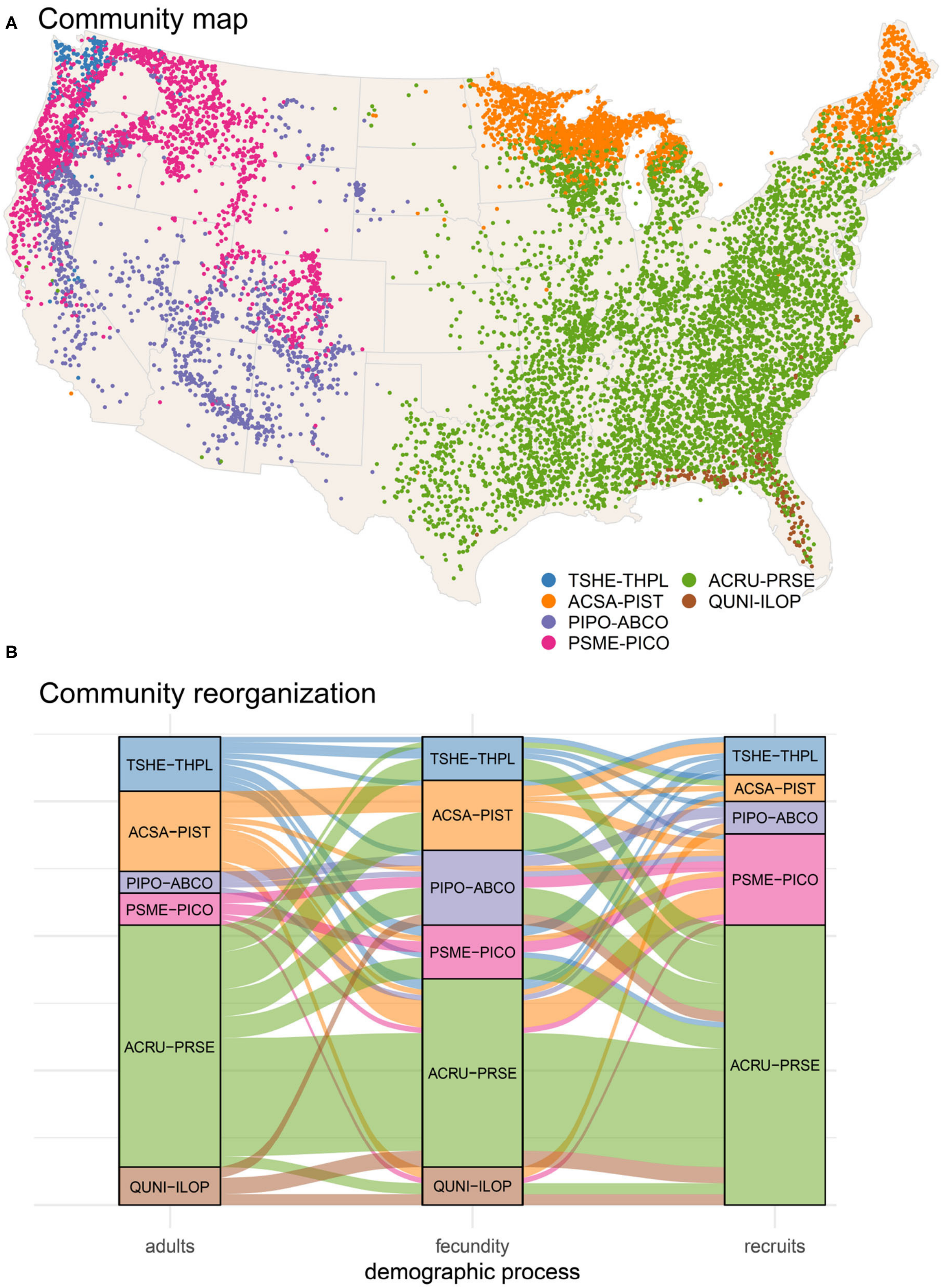

FIGURE 4 | Map of community assemblages **(A)** and reorganization as an alluvial diagram **(B)**. Community clustering is based on adult tree response matrix (**Figure 3a**). Separate maps for each type can be found in **Supplementary Figure S1**. **(B)** Shifts in assemblages across the three demographic stages (adult, fecundity, and *conditional* recruits) in eighty-seven species. Flows are color-coded by adult membership in communities mapped in **(A)**.

between **Figures 3a,c** would not have emerged from a standard, unconditional model, which would have simply showed that recruitment occurs where the adults are.

By contrast with recruitment, the fecundity response matrix $\mathbf{E}_f$ bears little resemblance to both adults and recruits (**Figure 3b**); fecundity response to CHI diverges from the life stages on either side of it. This divergence takes the form of a braided alluvial diagram in **Figure 4B**, where community reorganization occurs in 57% of species from adults to fecundity and in 64% of species from fecundity to recruits. The adult to fecundity divergence is followed by a partial re-coalescence, with 69% of species returning to the adult community at the recruitment stage. Species in the largest group *ARCU-PRSE* and *PIPO-ABCO* scatter across other groups from adults to fecundity, while many return to their adult groups at the recruitment stage. Despite this generally conservative tendency, nearly a third of all species (31%) change groups from adults to recruits. Recruits from the adult community *QUNI-ILOP* (Forida) merge with *ARCU-PRSE*, a shift toward conditions that are generally cooler than where adults are found. As adults, the community *PSME-PICO* combines western species (**Figure 4A**) with others from the Upper Midwest and Northeast (**Supplementary Figure S1**). The eastern and Midwestern species (e.g., *Abies balsamea*, *Betula papyrifera*, *Fraxinus nigra*, and *Larix laricina*) cluster as adults with *ACSA-PIST* but as recruits with *PSME-PICO*. Similarly, the eastern *Acer saccharum* and *Betula alleghaniensis* belong to *ACSA-PIST* as adults, whereas recruitment aligns with the predominantly western group *TSHE-THPL* (see also **Supplementary Figure S1**).

DISCUSSION

Three main patterns emerge from responses of recruitment stages that will influence the composition of twenty-first-century forests. At a coarse scale, similarities in adult and recruitment responses (**Figure 2**) suggest a degree of continuity from current to future forests. Secondly, the divergence of fecundity responses from those of both adults and recruitment, with its higher sensitivity to temperature and soil types (**Figure 1**), can be expected to bias the transition from adults to recruits for each species in different ways. Finally, the non-trivial differences between responses at different stages (31% of all species reorganize to different communities from adults to recruits) (**Figure 4**) reveal potential for change that cannot be fully anticipated from results presented here. A degree of coherence in niche shifts across the three life-history stages does not diminish the importance of inter-specific competition in influencing community dynamics, but it does indicate that species will be competing with different combinations of species.

Sensitivities quantified in this study show the basis for shifting forest distributions identified by Sharma et al. (2021). If warming has raised temperatures above those where tree populations recruited decades to centuries ago, then conditional recruitment should be occurring today in colder portions of the range and thus show less positive temperature responses than adults. We see this tendency for some species in the northeastern and northwestern *TSHE-THPL* (**Supplementary Figure S1**), indicated by brown shades for the species in **Figure 2b** (recruitment) than in **Figure 2a** (adults). These are also the communities tending to show a poleward shift in recruitment from adults (Sharma et al., 2021). The fact that recruitment rates for southwestern *PSME-PICO* are shifted to wetter (lower moisture deficit) parts of the range from adults (deep green for moist and brown for moisture deficit in **Figure 2b**) is consistent with a shift in regeneration to north and west of current populations (Sharma et al., 2021). The finding also provides evidence that the dieback-prone interior West (Allen et al., 2010) is already suffering from inadequate recruitment. Clearly, the devastating diebacks in this region are just the beginning of transformations that will critically depend on fecundity and seedling recruitment.

Across all species, fecundity exhibits the largest sensitivity to temperature and the lowest sensitivity to moisture deficit (**Figure 1**). High temperature generally increases fecundity in eastern forests (**Supplementary Figure S2**) and at least partially explains the fecundity hotspot in the warm southeastern North America (Clark et al., 2021). High recruitment rates are associated with younger stands compared to adult abundance (**Figure 2**), which could be caused by the increased seed availability where there are young and fast-growing trees (Clark et al., 2021). The fact that fecundity exhibits different responses to environment from those of adults and recruitment rate (**Figures 1**, **3**) highlights the importance of including seed production in understanding climate-driven migration (Sharma et al., 2021). These niche differences interpreted in parameter space ($\mathbf{B}_a$, $\mathbf{C}$, and $\mathbf{B}_f$) provide an alternative view of climate effects to distribution ranges (Lenoir et al., 2009; Zhu et al., 2011; Bell et al., 2014; Fei et al., 2017; Sharma et al., 2021).

Consistent responses to CEC suggest an important role for fertility gradients. The association of western *TSHE-THPL*, *PSME-PICO* communities with high CEC characterizes adult stages, but not seedling recruitments (**Figure 2**). Eastern communities span a range of CEC levels, but recruits are more strongly associated with lower CEC levels (deeper browns for *ARCU-PRSE* and *QUNI-ILOP* in **Figure 2b**). Positive responses to CEC can come with macroelements calcium, magnesium, and potassium that are essential for plant growth (Brady et al., 2008). On the other hand, vegetative growth promoted on fertile sites can reduce light availability and intensify canopy and understory light limitation on recruitment (Hubbell, 1999; Walters and Reich, 2000; Clark et al., 2012, 2014; Käber, 2021). Similarly, clay and sand fractions determine nutrient and moisture retention, which affects plant growth and potentially influences fecundity through the partition between growth and reproduction. Furthermore, the dominance of positive interactions between moisture deficit and local moisture class is consistent with topographic mediation of climate, particularly for recruits. This positive interaction means that local moisture has an increasingly positive effect the greater the climate deficit (Seyednasrollah and Clark, 2020). The high sensitivity of this interaction for recruitment, particularly in *PIPO-ABCO* and *ACSA-PIST*, is consistent with high seedling sensitivity to water availability compared to that of adults (Ibáñez et al., 2007; Dobrowski et al., 2015; Kueppers et al., 2017).

The conditional treatment of recruitment allows for potentially large differences in adult and recruitment habitats, so the similarities and differences found here are both meaningful. An unconditional analysis of recruitment would find high similarity between adults and recruits simply due to the fact that recruits will generally only be abundant where there are adults. These locations share the same covariate values, so recruitment differences from adults are limited to differences in their relative abundances across a species range, but constrained by the fact that the range itself is basically the same for both. Moreover, it would not account for the effects of adults on recruitment. By allowing for variation in adult abundance and then isolating environmental effects (given the adult effects), we could expect to find recruitment sensitivities that diverge from adults. We do in fact find substantial differences (**Figures 1**, **2**).

Rising temperatures, combined with an increased drought severity in many parts of U.S. forests, point to the urgent need to identify effective conservation strategies to maintain stability of forest ecosystems. The shifts from adults to fecundity are more severe than that from adults to recruits (**Figure 4B**), with a re-coalescence of communities as recruitment for many species revert to niche spaces that are similar to those of adults. Framed in a forest management context, while the fecundity stage may enable climate change-induced disruption of adult to recruit linkages, it may also afford opportunities to develop and implement conservation practices (Nagel et al., 2017) (e.g., silvicultural systems aligned with fecundity dynamics) that take advantage of this disruption to favor particular demographic trajectories across species to meet management objectives.

In summary, the relationships between three life history stages and climate-habitat interactions provide the underlying sensitivities needed to interpret changes in forest recruitment that are happening now and likely to shape future forests. The capacity to examine these stages independently and, in the case of recruitment, conditionally, provides new insight. Collectively, these results highlight species differences in the contribution to community reorganization and how it diverges between adults, seed production, and seedling recruitment. The three life history stages can each contribute to forest change in different ways.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

JSC designed the study and compiled the MASTIF and wrote the MSTIF model and software. TQ and JSC performed the statistical analysis and wrote the first draft of the manuscript. All authors contributed to the FIA data organization and contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.719141/full#supplementary-material

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