Chapter 8

Understanding climate change dynamics of tree species: implications for future forests

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Introduction

It is well established that the coming century's climate will affect forests in a myriad of ways ranging from growth, disturbance regimes (e.g., wildfires, insect pests, human land-use) and other biological processes that will impact their health, distribution, abundance, and ecosystem services they provide (Aitken et al., 2008; Bisbing et al., 2021; Parmesan, 2006; Price et al., 2013). Determining optimal human interventions to preserve forest health in anticipation of rapid change is a complex undertaking.

In this chapter, we examine aspects of this complexity and outline an integrated framework to address some current and future challenges facing forests. We start by providing a glimpse into the deep past—events that have shaped current forests—and then assess some general considerations that pertain to modeling the dynamics of tree species changes under climate change. In the process, we discuss the following topics: (1) estimating the realized niche, (2) assessing the suitability of data-driven statistical models for modeling habitat suitability (HQ), (3) estimating the migration potential of species, and (4) describing a multistaged approach to help capture the current and future dynamics of tree species under climate change. We provide examples from the eastern United States and Canada and present methods to address species vulnerabilities and adaptive capacities via species' regional summary tables. We also discuss several challenges that future forested ecosystems are likely to face, knowledge gaps associated with model building, management options like assisted migration, the potential role of climate change refugia, modeling challenges, and projected trends in major forest types around the globe. Even though our focus is mainly confined to eastern North America, we have tried to keep the narrative broad so that the lessons learned can be generalized to almost all temperate and boreal forest ecosystems.

A glimpse into the deep past

Only those who know the past, have a future. Wilhelm von Humboldt, 1767–1835

A broad perspective on the historical forces that have shaped global vegetation patterns helps provide a comprehensive background to gauge changes underway. In part, this entails peering into the deep past, and making sense of the paleoecological record to provide context and meaning to the vegetation changes that are happening today, and are likely to occur in the near future (Parmesan, 2006). This historical insight helps to inform model-building strategies and better frame management options by providing a greater appreciation of the processes involved.

Tracing the path that led to the eventual domination of plants on earth takes us back more than 3 billion years, when cyanobacteria acquired the ability to perform oxygenic photosynthesis (Blankenship, 2017; Cardona, 2019; Cardona et al., 2019). This important metabolic innovation eventually led to the Great Oxidation Event (~2.4 billion years ago),

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which further paved the way for more biological specializations (Demoulin et al., 2019; Sánchez-Baracaldo & Cardona, 2020; Schirrmeister et al., 2015). However, it was not until ~500 million years ago (mya), after the Cambrian explosion, that photosynthetic plants started to colonize land, led by nonvascular bryophytes, hornworts, mosses, and liverworts (Harrison & Morris, 2018; Kenrick & Crane, 1997). By ~450 mya, plants developed vascular tissues (pteridophytes: ferns, horsetails, and club mosses), and by ~370 mya started producing seeds (Meade et al., 2021), facilitating further seed and reproductive specializations found in gymnosperms and angiosperms (i.e., flowering plants).

Earth's forests have been shaped in deep time—by various geologic, climatic, biotic, and contingent historical forces since the gymnosperm trees first evolved ~360 mya (in the upper Devonian). The role of geologic forces in shaping the continents and their embedded terrain has resulted in biogeographic constraints to migration pathways and niches of various tree species. These forces created mountain ranges and other features that not only altered migration routes, but also greatly influenced regional climates, including glacial events that shaped the vegetation of various continents. The ascent of angiosperm trees, beginning ~150 mya in the Cretaceous and becoming dominant by ~100 mya, has been crucial in shaping the structure and composition of modern forests that we see today (Augusto et al., 2014). In the early Cretaceous (~113 mya), for example, angiosperms formed just 1% of the pollen records of the Atlantic coast of North America, but ~15 million years later, this percentage had risen to 40% (Thomas & Packman, 2007). Currently, only about 118 of the 679 tree species (17.5%) in North American forests are gymnosperms (Little, 1971; Ma et al., 2016; Tucker, 1983). This difference is more dramatic when comparing the number of angiosperm species (300,000−500,000) versus the mere 1000 gymnosperm species worldwide. This rapid rise of angiosperms in geologic time has generally restricted the gymnosperms to harsher, more fluctuating environments where they can still outcompete the angiosperms (Condamine et al., 2020). Thus pines (*Pinus* sp.), for example, are still an essential component of various forest ecosystems [e.g., the oak (*Quercus* sp.)-pine forests of the southeastern United States]. Also, large areas of northern temperate forest ecosystems and the higher elevation regions (e.g., in the Western US and Canada, and Europe) are still dominated by conifers [pines, spruces (*Picea* sp.), cypresses (*Cupressus* sp.), and firs (*Abies* sp.)], providing valuable economic and ecological benefits (Brodribb et al., 2012).

Glaciations and migration

The current Quaternary period, which encompasses ~2.6 million years, experienced more than 25 major glacial events—each lasting 50,000 −100,000 years. These events are closely tied to Milankovitch cycles, which are driven by the interplay of the earth's orbital eccentricity, obliquity, and precession (Ehlers et al., 2018; Marshall, 2009). The glacial stage typically ends with a rapid decline of ice sheets, followed by warmer interglacials lasting 10,000 − 20,000 years (Schoonmaker & Foster, 1991). While the forest extent and composition have changed in tune with Earth's climatic and geologic history in deep time, of particular relevance to the current forests in the temperate zone are changes that have taken place in the late Pleistocene and the Holocene in the Quaternary period, and especially since the last glacial maximum (LGM) ~18,000 years ago, after which ice started retreating in North America and Europe (Dyke, 2004; Kleman et al., 2010). By 10,000 years ago, when the ice started retreating without further major fluctuations, vegetation started taking advantage of increased niche-space provided by wetter and warmer conditions with comparatively minimal anthropogenic influence. The boreal vegetation that had been pushed south due to ice, or still existing in refugia, started advancing northward in North America, Europe, and Asia. Many of the hardwoods (angiosperms), which were confined to the south and/or inside glacial refugia also started taking advantage of the expanding suitable habitats that rapid climate change provided and migrated following the heels of the ice sheet, as did the conifers (Keppel et al., 2012; Stewart et al., 2010). While the general trend of migrations was from south to north, in North America and in Eurasia, not all tree species followed this simplistic route. Most species opportunistically colonized suitable habitats, but their final pace and route were modified by interspecific competition and other interacting disturbances. For example, in the United States, hickory entered Ohio 4000 years before beech, but beech arrived in southern New England 3000 years before hickory (Davis, 1983).

Implications for model building

The individualistic responses of tree species to historical climate changes should alert us that we are trying to capture a snapshot of change, amidst the interacting historical, ecological, and evolutionary forces operating under varying temporal and spatial scales (Fig. 8.1). Overlayed on these historical forest changes are two exacerbating factors unique to our current interglacial situation: the threat of ongoing, rapid, and sustained human-induced climate change due to fossil

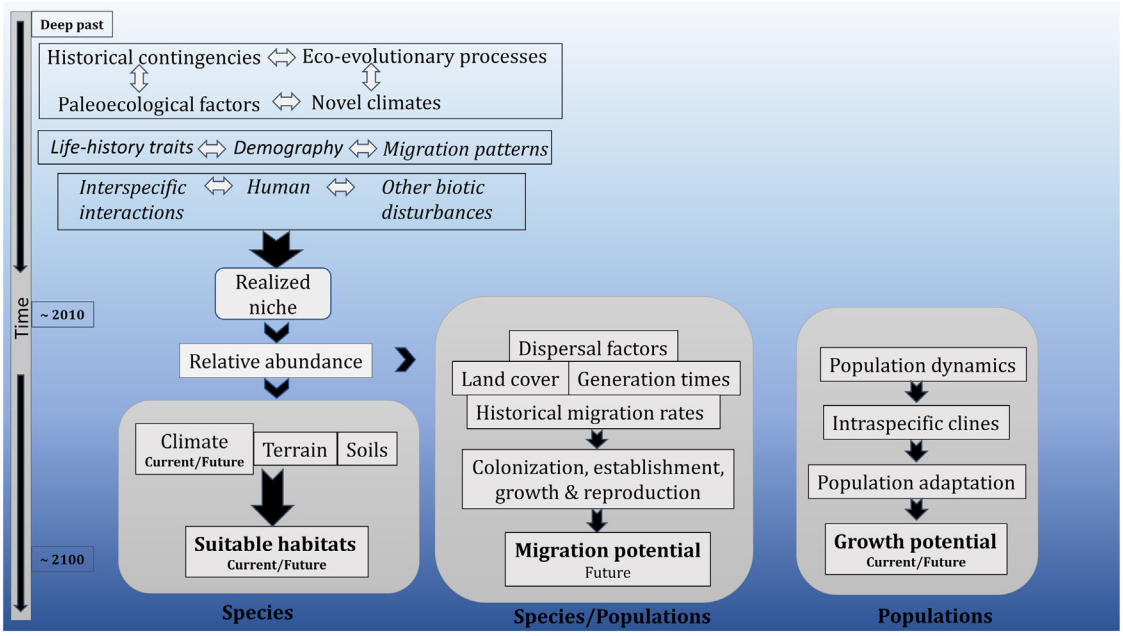

FIGURE 8.1 A schematic to demonstrate and aid in modeling various interacting historical and eco-evolutionary factors. The blue gradient conveys the passage of time, which is not to scale.

fuel emissions and the continued intensive, large-scale land-use changes wrought by large increases in human population and consumption (Mottl et al., 2021). Therefore, when one considers the current distribution of tree species, which have been recently reshaped by these drastic effects and novel constraints, most forest inventories capture the approximate realized niche as opposed to the fundamental niche (Hutchinson, 1957). The realized niche is the result of all the interacting disturbances that the species has historically faced, and all the recent disturbances it is facing (Chase & Leibold, 2003). We model the realized niche (derived from forest inventory analysis data) to project the fundamental niche via suitable habitats. This limitation is hard to overcome except for species with provenance test data from which we can predict fundamental climatic niches using response/transfer functions (Wang et al., 2010). However, for wide-ranging species, the realized niche can be assumed to be a close approximation of the fundamental niche (Booth, 2017).

There have been many attempts to model both biotic and abiotic changes and project the impacts on forested ecosystems (see Price et al. (2013) for a northern boreal synthesis/perspective). While these projected outcomes are important in shaping the direction of future forests, it is noteworthy that many tree species harbor large amounts of standing genetic variation and adaptive phenotypic plasticity acquired from their deep historical interactions that are open to natural selection and other forces of evolution—especially under rapid change (Clark et al., 2020; Huang, 2015; Nijhout et al., 2021). For example, the ancient origin of the genus *Pinus* goes back to the late Permian or the early Mesozoic (~250 mya). However, ~90% of the pine species we find today originated in the Neogene (23–2.6 mya). Pines in the southern hemisphere diverged earlier than those in the northern hemisphere (Leslie et al., 2012)—the latter showing higher rates of speciation and extinction, reflecting the complex climatic and migratory history compared to their counterparts in the south. Topographic heterogeneity, fire regimes, and aridity also played a major role in the diversification of pines in the northern hemisphere (Jin et al., 2021; Keeley, 2012). Many pine species have therefore been exposed to variable environments, and accumulated large amounts of standing genetic variation and adaptive phenotypic plasticity over the eons. These ongoing eco-evolutionary dynamics are hard to capture, especially because some contemporary evolutionary outcomes may ameliorate the effects of climate change, while others may not (Lamy, 2014; Nijhout et al., 2021). For example, Jin et al. (2021) speculate that pine's preference for warmer and relatively drier habitats may help them adapt to climate warming better than other genera. Additionally, we have to assess our current criteria of novel climates in light of novel environments tree species may have faced in deep time.

Given these realities, a useful macroecological modeling framework meant to capture many of these processes should: (1) forecast habitat changes, (2) estimate migration patterns, and (3) gauge intraspecific variability in response to future climate. In addition, it should be able to account for biotic interactions and other disturbance effects that are typically left out of such modeled forecasts (Fig. 8.1). However, in actual practice, we are constrained by various complex and challenging factors that accompany multivariate analysis.

Modeling approaches

Because of improved data availability and computational advances in recent decades, several approaches are available to address the complex challenge of forecasting suitable habitats and migration potential under climate change. The two main methods to predict multivariate phenomena are: (1) models that use dynamic vegetation processes (process-based); and (2) data-driven machine learning models. These competing approaches are often touted by their practitioners as better for specific tasks.

Process versus statistical machine learning models

There is a sizable literature base comparing mechanistic/process-based models and empirical-statistical distribution/niche models (e.g., Baker et al., 2018; Connolly et al., 2017; Kearney & Porter, 2009; Kearney et al., 2010). Theoretically, it is better to have parameters derived from causal processes to drive the simulation of real-world phenomena (because of the superior ability to extrapolate to new situations via a better mechanistic understanding of the feedback involved). However, such experiments and scaled-parameters are difficult to obtain, and many dynamic models must tackle multiple parameters that are sensitive to perturbation in multivariate settings. This is especially true concerning tree species with wide tolerances and typically exhibit Gene × Environment reaction norms that make their responses more dynamic. Therefore process-based models are best suited for physical problems that allow simulation under laboratory settings with fewer parameters (constraining the dimensionality problem). Also, process-based models are not exhaustively compared in the literature relative to statistical models (for both parametric and data-driven nonparametric, see Bachelet et al., 2015; Olsson & Jönsson, 2014; White et al., 2016).

Dynamic process-based models, however, can be useful for forecasting animal distribution patterns that exploit endothermal, ectothermal, or other biophysical requirements of specific species, and for simulating forest growth and competition across landscape scales (Gustafson et al., 2016). Also, hybrid process-driven simulation models are useful for several applications. For example, we have used a historically based migration model (SHIFT) to simulate future colonization likelihoods (CLs; Iverson et al., 2004; Prasad et al., 2013). Also, dynamic models like LANDIS (Scheller et al., 2007) are useful for simulating forest dynamics at varying spatial and temporal scales via functions of growth, succession, disturbances, and management scenarios (Brecka et al., 2020; Olson et al., 2021; Xiao et al., 2017).

For forecasting the HQ of multiple species across their entire range, macroscale empirical-statistical models that utilize data-driven nonparametric machine learning algorithms are better suited because they capture averaged emergent phenomena via correlative structures in the data (Fordham et al., 2018). However, care should be taken while interpreting these data-driven predictive models, and the limitations (e.g., spatial autocorrelation) and caveats (especially for future forecasts) need to be spelled out clearly (Dormann et al., 2011; Kühn & Dormann, 2012; Ploton et al., 2020).

In the following sections, we focus on macroscale analyses that attempt to capture a part of this changing reality and leave the unexplained variation to other studies that look at the dynamics from different scales, methodologies, and perspectives. We further develop an integrated, multistage modeling scheme (Prasad et al., 2016) to better understand future forest dynamics under climate change. Finally, we present various results related to this scheme; discuss strengths, limitations, and omissions related to the approach, and consider implications and management options for future forests.

Though the current effort is confined to continental North America, we believe it provides general guidelines for geographically varied studies with similar goals. We first note a few general principles: (1) the computation of relative abundance as a measure of the realized niche from forest inventory data, (2) the appropriateness of macroecological statistical models to gauge suitable habitats, and (3) the computation of migration potential using historical migration rates.

Estimating the realized niche

Forest inventory data typically include a variety of tree-related metrics (e.g., basal area, stem counts) taken from ground plots distributed across a region of interest (Woudenberg et al., 2010). Depending on the intensity and extent of the sampling method, these inventories can be used to aggregate plot-level data to the resolution of interest to calculate either relative or absolute measures of abundance. Alternatively, they can be aggregated to assess the presence/absence of tree species. Relative abundance allows one to calculate the relative importance value (RIV) of a species compared to all other species found in a plot using:

$$\mathrm{RIV}(x) = 50 \times \frac{\mathrm{BA}(x)}{\sum \mathrm{BA}(\text{all species in plot})} + 50 \times \frac{\mathrm{NS}(x)}{\sum \mathrm{NS}(\text{all species in plot})}$$

where x is the species, BA is the basal area in the plot, and NS is the number of stems (summed for overstory and understory trees). In monotypic stands, RIV could reach 100% (Iverson et al., 2008). RIV is a surrogate for accumulated growth and survival over the ages. It, therefore, provides a measure of where the species does best ecologically (at the current juncture), measured relative to all the other species in the plot. This is especially true for natural forested plots that have not been heavily influenced by human harvesting and reforestation activities. It is a reasonable measure for gauging the *species' response* to other abiotic and biotic influences (especially interspecific interactions) because these relative estimates portray the real importance of the tree species relative to the others and therefore approximate the realized niche of the species. However, as mentioned before, the limitation is that the realized niche is used to model a more general suitable habitat based on abiotic factors reflecting the fundamental niche. Measures of absolute abundance also suffer from this drawback. In addition, they do not capture interspecific interactions because they do not consider other species in the plot. Studies have employed presence/absence data to model future distributions when detailed inventories are unavailable. Such models can capture the general patterns associated with species' distributions but have been shown to lack the accuracy and detail provided by models trained using abundance data (Howard et al., 2014; see also Talluto et al., 2016). Other hybrid techniques account for multivariate responses of both discrete (presence/absence) and continuous (abundance) variables using joint species distribution models (Clark et al., 2017). However, the complexity entailed in interpreting these models limits their widespread use.

Multistage modeling framework

In order to capture tree species dynamics via assessments of the realized niche, several approaches are possible. One that we have previously used is a multistaged approach (Prasad et al., 2016), where we first model the species' HQ via relative abundance (RIV) using climatic, topographic, and edaphic variables to project currently modeled habitats to future climates (Fig. 8.2). Because not all projected suitable habitats can be colonized, we compute colonization likelihoods (CLs) based on a migration simulation model that uses historical tree migration rates as a basis for estimating colonizations in $\sim$100 years. Finally, we intersect and map combinations of future HQ and CLs to assess how these two interact in the future. It is useful to consider modeled results in the context of regional information about these factors (Boisvert-Marsh & de Blois, 2021; Iverson et al., 2012) because there still remains inherent residual variation due to biotic and other disturbance factors that could change modeled outcomes (even after accounting for the colonization of suitable habitats). Therefore, to handle this unexplained component, we employ a decision support framework where relevant biological and disturbance factors for the species (gleaned from the literature) are scored to potentially modify differing trends in modeled outcomes (Iverson, Prasad, et al., 2019; Matthews et al., 2011).

Efforts to develop publicly available trait-based databases (Boisvert-Marsh et al., 2020; Potter et al., 2017) are helping to document and inform models. Providing a portfolio of traits that may inform the direction and ability of a species to respond to changing conditions would be a valuable way of capturing some of this unexplained variance (Aubin et al., 2016; Matthews et al., 2011; Potter et al., 2017). There are many examples where species responses to disturbance agents, such as drought tolerance, can be quantified and tracked to show differential outcomes (Valladares & Niinemets, 2008). Further, primary integrators of competition, such as shade tolerance, produce repeatable partitioning of species along gradients of competition for light (Valladares & Niinemets, 2008). Because these considerations are difficult to incorporate into macroscale models, they are best used to supplement modeled results for managing forests

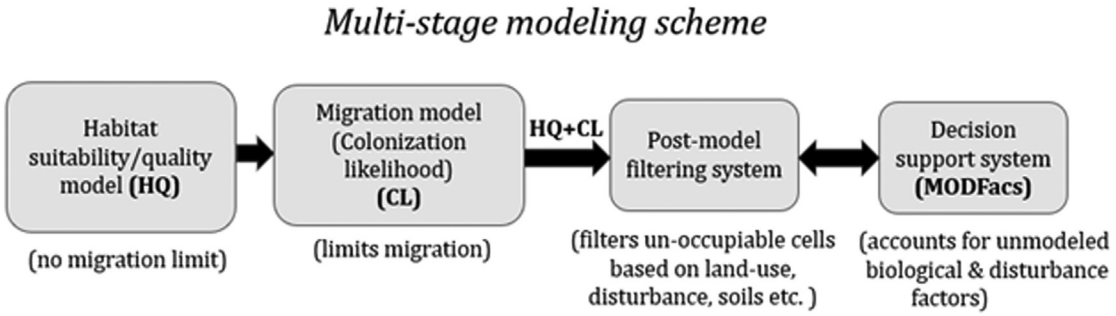

FIGURE 8.2 Multistage scheme to capture species dynamics via models and a scoring system. The current and future changes in HQ and colonization likelihoods can be evaluated based on more regional biological and disturbance dynamics. *HQ*, Habitat suitability.

at regional and local scales. However, some of these additional influences (e.g., traits, fire, disease, pest, regional/local climate, land-use, finer scale edaphic and topographic layers) can be obtained as GIS layers that can act as *postmodel* filters to bolster decision support (Fig. 8.2).

Modeling habitat suitability

Because of the recent advances in data-driven statistical methods, nonparametric ensemble learning algorithms used to classify or regress the data have become popular in various fields. While traditional regression modeling (and its various generalized incarnations) uses parametric distributional relationships, data-driven approaches find correlative patterns in the data and then allow prediction by minimizing the bias-variance ratio in the algorithms and making it less dependent on distributional assumptions (Elith et al., 2010). In this class of models, decision-tree-based approaches using recursive partitioning of data (Breiman et al., 1984) are beneficial for multivariate ecological problems. In addition to capturing correlative structure between the response and explanatory variables, they also incorporate nonlinearities and interactions without distributional assumptions. The flexibility associated with data-driven approaches comes with the cost of overfitting and attendant variance. Therefore the models may fit the training data well but not generalize well to newer prediction space (Hastie et al., 2009). However, they have proven to be quite robust with appropriate techniques to minimize bias and variance, like bagging, random forest, and boosting. They yield far better predictions than traditional parametric models for challenging multivariate problems. The techniques of Random Forest (RF, Breiman, 2001) and Stochastic Gradient Boosting (Friedman, 2002) are very popular for tackling complex ecological phenomena (Mellor et al., 2013; Prasad et al., 2006). Another drawback of machine learning approaches is that the relationships between the response and explanatory variables are less transparent than traditional generalized linear models—although many metrics are available to assist with model interpretation. RF, for example, provides pseudo R^2 for regression, out-of-bag residuals, and the relative importance of explanatory variables. In addition, metrics to exploit the hierarchical structuring of variables using the minimal depth of maximal subtrees within the models have been developed (Ishwaran et al., 2010) and applied to ecological settings (Adams & Matthews, 2022). While standard performance metrics are limited, there is sufficient information to combine with other statistics to determine reliability (Iverson et al., 2008; Peters et al., 2019). Recent efforts have been made to also make statistical machine learning models more explainable and interpretable while not sacrificing predictability (Chakraborty et al., 2021; Linardatos et al., 2020; Lou et al., 2012).

We have used RF to model the HQ of eastern US tree species (Iverson et al., 2008; Peters et al., 2019). More recently, we have used a newer approach termed MultiModel Ensemble (MME; Prasad, 2018) to model tree species that span US and Canada across their entire range, and for intraspecific analysis of white pine response to climate (Prasad & Leites, 2022; Prasad et al., 2020). The MME technique involves averaging the consensus predictions of multiple machine learning techniques that use similar base-learners (e.g., decision trees)—typically, variations of bagging and generalized gradient boosting methods. The MME approaches are best used where prediction uncertainty needs to be stabilized to yield more robust predictions that reflect the consensus (Araújo & New, 2007; Jones & Cheung, 2015; Martre et al., 2015) by averaging individual model errors (Zhang et al., 2015; Zhang & Lu, 2012). Only predictions where there was "consensus" among all models (i.e., where all models predicted nonzero values) are averaged to ensure that the main trends are captured, and the noise minimized.

Tree species migration

Migration patterns typically depend on complex interactions among abundance, habitat availability, life-history traits, dispersal mechanisms, climate, and human land-use. Tree populations subjected to climatic mismatch due to rapid climate change (impacts of climatic variability on physiological, ecological, and evolutionary processes at multiple levels)—(see Siefert et al., 2015; Vázquez et al., 2017) may be able to migrate to suitable habitats (provided access to new suitable habitats are available) in response to climate change. However, in the coming decades, historically adapted populations, especially those with a narrow endemic range, may face serious challenges (Aitken et al., 2008; Bisbing et al., 2021).

Many temperate tree species are wind-dispersed, with dispersal distances influenced by factors such as seed size and shape. Most tree seeds disperse relatively short distances each year (e.g., <100 m), though rare, long-distance dispersal (LDD) can occur in relation to biotic (e.g., bird) or abiotic (e.g., hurricane and derecho) events. Based on fossil pollen distribution, many tree species appear to have spread rapidly following ice retreat either from southern populations or smaller northern ones in micro-refugia (McLachlan et al., 2005). However, we cannot expect similar trajectories due to current abundance patterns and human-fragmented landscapes (Iverson et al., 2004). Historical estimates of tree migration vary from <10 to >100 km century^{-1} (Feurdean et al., 2013). Using optimistic migration rates of

50 km century^{-1}, we have estimated that in $\sim$ 100 years, only locations within 10−20 km of current range boundaries have a high likelihood of colonization (Iverson et al., 2004; Prasad et al., 2016). Therefore, without human-assisted migration, some tree species (those controlled primarily by climate) may be unable to keep pace with rapid climate change. However, some estimates based on recent empirical snapshots have shown higher transient rates from their abundance centers (Fei et al., 2017).

Our approach to simulating natural migration uses a lightly parameterized model, SHIFT, to estimate future colonizations based on historical tree migration rates. It uses species abundance estimates throughout the available range (i.e., source cells) to compute CLs in uncolonized cells (i.e., sinks—colonizable forested habitats both inside and beyond the current range). The migration model simulates LDD via a fat-tailed inverse power function under currently fragmented landscapes (Prasad et al., 2013, 2020). Each species is allowed to migrate based on its current distribution and generation time with no climatic constraints (indifferent to changes in climate) for approximately 100 years. This ensures that, despite having a common migration rate, the landscape is colonized based on individualistic species responses. The number of generations (model iterations) required to simulate $\sim$100 years of migration varies among species depending on their generation time. For example, SHIFT assumes that sugar maple has three generations per 100 years, or roughly 33 years/generation, and newly colonized cells can only contribute to colonization in the next generation since the propagules have to mature. The CLs are intersected with the modeled future suitable habitats to explore mapped combinations of HQ + CL, from which we can gauge potential migrations (CLs) under changing climates (see the following three sections for examples).

In our studies, we deliberately overestimated the migration response by making optimistic assumptions: a fairly generous historical migration rate of 50 km century^{-1}; inverse power function with a search window of 500 km (for stochastic long-distance events); no interspecific differences in dispersal rates; and all colonizable sink cells equally suitable for colonization. Another factor (not considered in our analysis) that makes our results optimistic is that, in addition to the colonization of suitable habitats, the colonized species should be able to overcome competitive exclusion and establish to adulthood (Thuiller et al., 2008). Even though these optimistic assumptions are compensated somewhat by the generally low abundance near species boundaries and the lower dispersal potential of animals for nonwind dispersed species, the declining rate of CLs with distance is remarkable (only 10−20 km from range boundaries have good likelihoods of colonization). This casts doubt on whether natural migration will be fast enough for narrowly endemic species seeking newer habitats due to climatic mismatches. However, there is some hope that historically observed rarer long-distance migration could mitigate the threat of extinction for some species (Clark et al., 1998).

Modeling species in the eastern United States

The multistage modeling scheme described above was applied to 125 tree species in the eastern United States, using US forest inventory data and RIV as the response (Iverson, Peters, et al., 2019; Peters et al., 2019). We modeled HQ and migration potential (CL) for most of the species and also accounted for unmodeled factors—(9 biological and 12 disturbance) via a scoring system. The relative abundance was modeled using 45 explanatory variables, including soils, climate, and topography (DISTRIB-II model—see Iverson, Peters, et al., 2019) to assess HQ. Finally, the future climates were evaluated for three GCM scenarios (CCSM4, GFDL, and Hadley). While these resulted in maps of HQ responses and reclassified combinations of HQ and CL, the ranges were truncated at the US national border—allowing only part of the full range to be analyzed. Nevertheless, these products have been used extensively in the United States for understanding the climate change response of tree species via the climate change tree atlas (https://www.fs.usda.gov/nrs/atlas/tree/ https://doi.org/10.2737/Climate-Change-Tree-Atlas-v4).

For example, post oak (*Quercus stellata*) which is currently widely distributed in the southern regions of the eastern US, is a slow-growing drought-tolerant oak. It currently occupies a variety of sites and soils, being most abundant on drier outcrops and ridges. Its acorns provide high-energy food to wildlife, and the wood being resistant to decay, is used for products such as railroad ties, construction timbers, and fenceposts.

Our eastern US models (https://www.fs.usda.gov/nrs/atlas/tree/835 and Fig. 8.3) show that suitable habitats for post oak increase under climate change, especially under RCP 8.5, with suitable habitats increasing northwards in the United States. The species is given a moderately good adaptability rating (unmodeled biological and disturbance factors) of 5.7 (ranges between 2.7 and 8.5 for 125 eastern US tree species) owing to its good drought tolerance and resistance to fire top-kill. However, post oak's intolerance to shade and susceptibility to insect pests and disease lowers its score despite its higher climatic adaptability.

Factoring in the migration potential of post oak by combining the CLs with HQ reveals that gaps within the current distribution as well as outside its current range get filled due to natural migration by the end of the century (Fig. 8.3).

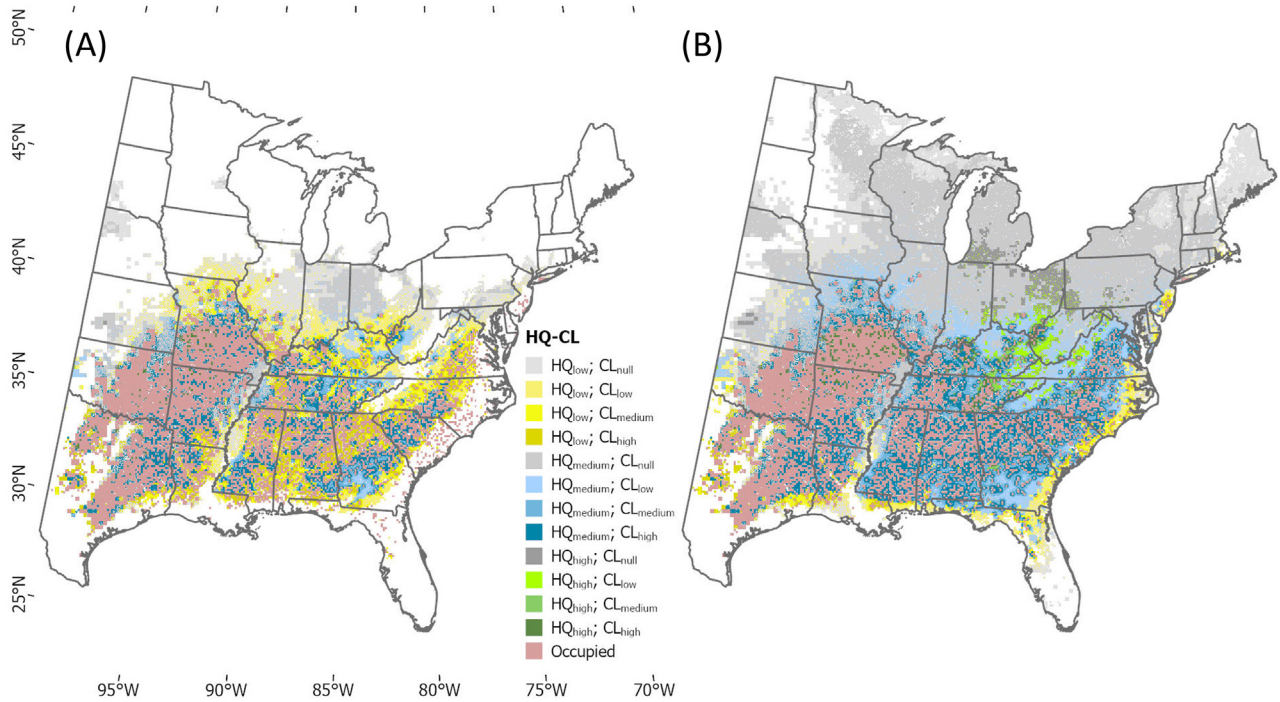

FIGURE 8.3 Combinations of modeled suitable habitats and colonization likelihoods (CL) for post oak in the eastern United States. (A) Average of 3 GCMs under moderate emissions (RCP 4.5); (B) Average of 3 GCMs under moderate emissions (RCP 4.5). HQ was reclassified to low, medium, and high, and CL into null, low, medium, and high classes. Various combinations of HQ−CL classes point to the type of suitable habitats colonized or not colonized (CLnull). The shades of gray (low to high suitability) indicate all those areas that are not naturally colonized by ∼2100.

Also, in the northern regions, even though suitable habitats are available, post oak is not colonized due to inability of the species to migrate naturally to these areas (areas shaded gray).

A major constraint with this analysis is that the ranges are truncated at the US−Canada border, not allowing the range-wide evaluation of the species under climate change, especially for more northern species. Therefore future suitable habitats and their migration potential are confined to within the US (southern parts of the distribution). In addition, the HQ model for the eastern US uses 45 environmental variables, with a preponderance of soil-related variables (30) compared to climate (7) and elevation (7). While this domination of soil variables can help constrain large movements in HQ (soil and elevation do not change from current to future climates), it can make the climatic response conservative for many tree species. For more regional analyses like the eastern US, including soil variables to constrain movement and capture the realized niche is justifiable. However, this constraint is not desirable for macroscale studies that project the entire species range to capture the overall climatic response. Therefore limiting the explanatory variables to climate, elevation, and terrain-derived variables is prudent when modeling entire species ranges.

Modeling the entire species range

Modeling tree HQ and migration under climate change is most effective at broad spatial extents, incorporating entire species ranges. Scale is important because truncation of species distribution data at political boundaries can produce artifacts in resulting model outputs, particularly when projecting species shifts under climate change. For example, since most of the tree species in Canada have at least a portion of their range in the United States, distribution models that do not incorporate data from the United States will tend to exaggerate habitat losses along the country's southern border under climate change. Similarly, truncation at the northern border leads to dismissing the future dynamics in Canada because many US species (even those that currently do not span borders) have the potential to find suitable habitats and migration potential in Canada under warming. However, sharing distribution data across political borders is often challenging, despite recent progress in open data-sharing initiatives such as the Global Biodiversity Information Facility (https://www.gbif.org/) and Global Forest Biodiversity Initiative (https://www.gfbinitiative.org/).

Cross-border datasets require significant effort to make distribution and/or environmental variables compatible. Prasad et al. (2020) combined US Forest Inventory plot data with the photo-plot data derived from Canada's National

Forest Inventory. This effort resulted in continental-scale relative abundance data for 25 tree species in eastern North America. While the merger was not seamless due to the differing nature of the national inventories, the effort nevertheless enabled the evaluation of climate change impacts on HQ and migration potential across the full range of the 25 target tree species (excluding Alaska, for which we did not have data). Using climatic and topographic variables across US and Canada, the climatic HQ was modeled using the MME approach described earlier, and the CLs of these habitats were computed using the migration model. We did not use soil variables because, as outlined in the previous section, climate variables are generally considered critical drivers at the macroscale (Toledo et al., 2011). Focusing on paper birch, a species that spans borders (Fig. 8.4), the combination of HQ and CL shows the regions where migration is possible (colored areas) and where suitable habitats are available and not currently occupied, but where the species cannot naturally migrate in ~100 years (gray areas; CL_{null}). The climatic habitat of paper birch is likely to move mainly to Canada, especially under the RCP 8.5 scenario (Fig. 8.4A).

In contrast, the milder RCP 4.5 (Fig. 8.4B) retains low to medium-quality habitats in the United States. A compensating factor for the US is that climatically suitable habitats are likely to be available in Alaska, which is warming rapidly—making that a possible test bed for assisted migration and reciprocal transplant experiments. Because our analysis did not include Alaskan inventory (due to its nonavailability in FIA at the time of analysis), this pattern could potentially apply to many species not currently present in Alaska. For many of the 25 species, northern ranges experienced habitat gains, while the southern ranges were relatively stable, although experiencing reduced habitat quality. As can be expected for wide-ranging species, only a small portion of the suitable climatic habitats will be colonized naturally by the end of the century, even under the optimistic migration rate of 50 km $century^{-1}$, pointing to the need for assisted migration for ecologically vulnerable or commercially important tree species (Fig. 8.5).

Regional summary tables

Evaluation of individual species provides rich insight into the nature of the HQ and CL dynamics under climate change. However, we frequently want to evaluate a suite of species together regionally, to understand how they respond to the changing climate. To this end, we have evaluated and summarized the vulnerability, adaptability, and migration potential of all modeled tree species in the eastern United States (125) within various regions of interest, including 1×1-degree grids, National Forests, National Parks, HUC6 watersheds, Ecoregions, National Climate Assessment regions, Eastern US States, and Urban Areas (Iverson, Prasad, et al., 2019). Details are provided in the form of tabular outputs that list species-level information related to distribution, model reliability, areal percentages, abundance estimates,

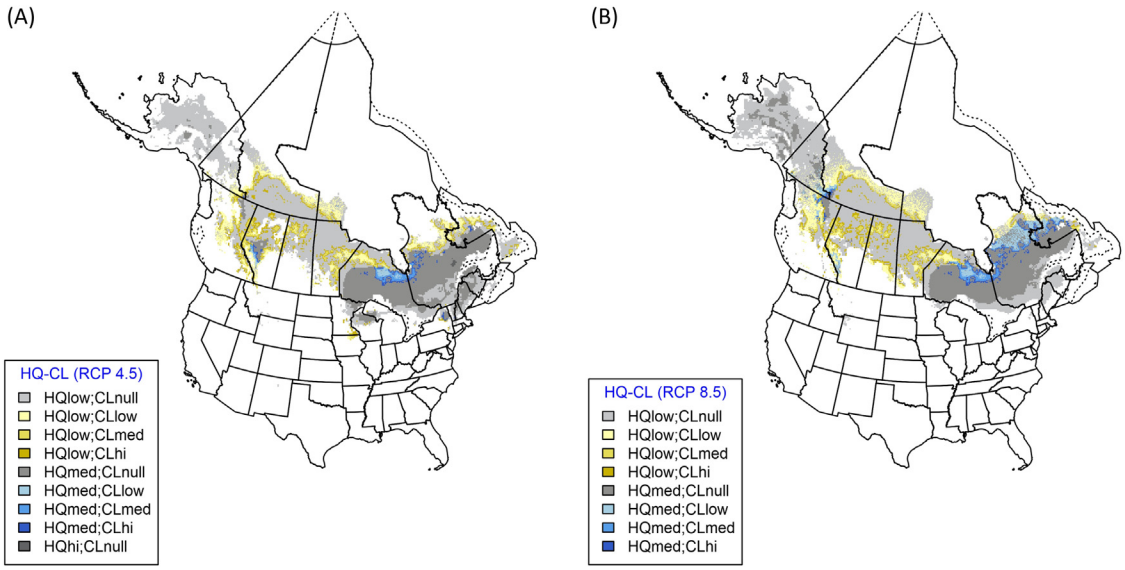

FIGURE 8.4 Combinations of modeled suitable habitats and colonization likelihoods (CL) for paper birch across the eastern US and Canada. HQ was reclassified to low, medium, and high, and CL into null, low, medium, and high classes. Various combinations of HQ–CL classes point to the type of suitable habitats colonized or not colonized (CL_{null}). The shades of gray (low to high suitability) indicate all those areas that are not naturally colonized by ~2100.

FIGURE 8.5 Paper Birch is known for its white bark that curls and peels when fully mature. *Credit: Photo by Mary Sharon Moore from Pixabay.*

adaptability and capability ratings, and the likelihood of species migrating naturally into the area (under current and future climate scenarios in the United States). The table values are derived from combinations of the three components of the multistage modeling scheme—(1) HQ model, (2) migration model, and (3) adaptability, the latter based on scoring from 12 disturbance and 9 biological factors (Iverson, Prasad, et al., 2019). These tables are best explored online (https://www.fs.usda.gov/nrs/atlas/combined/resources/summaries/), where further resources are available to interpret them. However, here we provide an example showing part of the table for the Midwestern US states (Illinois, Indiana, Iowa, Michigan, Minnesota, Missouri, Ohio, and Wisconsin), where many species find their northern edge within the United States (Table 8.1). For example, six of the seven most abundant species in the region, including two maples and three oaks, are modeled to have good or very good potential to cope or persist into the future; only *Populus tremuloides* (the top species) may exhibit declines. Five of the seven species also are modeled to potentially infill or internally migrate within their current range within the next 100 years or so. Many of the next tier of species, however, have been modeled to have a relatively poor capability to cope or persist—species such as *Pinus resinosa, Pinus strobus, Abies balsamea, Picea mariana, Fraxinus nigra*, or *Larix laricina*. It must be emphasized, however, that the summary tables are best used with local knowledge and other ancillary information (including other models) to assess the realistic potential for further management actions. For example, though we include a severe impact of emerald ash borer (EAB) in the adaptability scoring, the other 20 adaptability (i.e., modification) factors and increasing change class models for ash still provide for a relatively higher capability than expected; the manager would not typically include ash in future planting unless EAB-resistant strains become widely available. Also, other regions with smaller geographic areas overlapping the chosen region (currently, Midwestern US States), for example, Ecoregional vulnerability assessment, USDA EcoMap, or even 1×1-degree grids (https://www.fs.usda.gov/nrs/atlas/combined/resources/summaries/) can be used in parallel to assess similarities and differences.

Challenges, knowledge gaps, and lessons learned

The modeled results from both species distribution models (SDMs) and migration simulations address macroscale spatial trends under future climates that are best used by managers as a general guide to tweak management based on additional information at finer scales. In general, the modeled results for the United States and Canada exhibited (1) north/north-western shifts in climatically suitable habitats; (2) limited natural migration (10−20 km from outer range, with a reasonable chance of colonization assuming a historically optimistic migration scenario of 50 km century^{-1}); (3) lower habitat quality in the southern portion of the species range; and (4) vulnerability of narrowly endemic tree species. These results can also be used in conjunction with regional results of dynamic models like Landis (Scheller et al., 2007) to bolster confidence in species vulnerability ratings (Iverson et al., 2017). It is generally better to compare correspondence among different models rather than trying to integrate models with different philosophies. Below, we address various factors (underscored in different section headings) that fall under the rubric of "challenges and knowledge gaps and lessons learned" that will be relevant to future forests.

TABLE 8.1 A portion (24 of 135 total species, sorted by decreasing current abundance) of the summary table of tree species present now or potentially in the future within the eight states of the Midwestern US.

Common Name	Scientific Name	MR	ChngCl45	ChngCl85	Adap	Abund	Capabil45	Capabil85	SHIFT45	SHIFT85
quaking aspen	Populus tremuloides	High	Sm. dec.	Sm. dec.	Medium	Common	Poor	Poor	Infill +	Infill +
red maple	Acer rubrum	High	No change	No change	High	Common	Good	Good	Infill ++	Infill ++
sugar maple	Acer saccharum	High	No change	No change	High	Common	Good	Good	Infill ++	Infill ++
white oak	Quercus alba	Medium	Sm. inc.	No change	High	Common	Very Good	Good	Infill ++	Infill ++
American elm	Ulmus americana	Medium	Sm. inc.	Sm. inc.	Medium	Common	Good	Good		
black oak	Quercus velutina	High	Sm. inc.	Sm. inc.	Medium	Common	Good	Good	Infill ++	Infill ++
northern red oak	Quercus rubra	Medium	Sm. inc.	No change	High	Common	Very Good	Good		
black cherry	Prunus serotina	Medium	Sm. inc.	Sm. inc.	Low	Common	Fair	Fair		
red pine	Pinus resinosa	Medium	No change	No change	Low	Common	Poor	Poor		
green ash	Fraxinus pennsylvanica	Low	Sm. inc.	Lg. inc.	Medium	Common	Good	Very Good	Infill ++	Infill ++
balsam fir	Abies balsamea	High	Lg. dec.	Sm. dec.	Low	Common	Very Poor	Poor		Infill +
northern white-cedar	Thuja occidentalis	High	No change	No change	Medium	Common	Fair	Fair	Infill +	Infill +
paper birch	Betula papyrifera	High	No change	Sm. dec.	Medium	Common	Fair	Poor		
eastern white pine	Pinus strobus	High	No change	No change	Low	Common	Poor	Poor		
American basswood	Tilia americana	Medium	Sm. inc.	No change	Medium	Common	Good	Fair		
white ash	Fraxinus americana	Medium	Sm. inc.	Sm. inc.	Low	Common	Fair	Fair	Infill +	Infill +
black spruce	Picea mariana	High	Sm. dec.	Sm. dec.	Medium	Common	Poor	Poor	Infill +	Infill +
black ash	Fraxinus nigra	Medium	No change	No change	Low	Common	Poor	Poor		
tamarack (native)	Larix laricina	High	No change	No change	Low	Common	Poor	Poor	Infill +	Infill +
bur oak	Quercus macrocarpa	Medium	Sm. inc.	Sm. inc.	High	Common	Very Good	Very Good	Infill ++	Infill ++
post oak	Quercus stellata	High	No change	Sm. inc.	High	Common	Good	Very Good	Infill ++	Infill ++
boxelder	Acer negundo	Low	Sm. inc.	Sm. inc.	High	Common	Very Good	Very Good	Infill ++	Infill ++
eastern redcedar	Juniperus virginiana	Medium	Lg. inc.	Lg. inc.	Medium	Common	Very Good	Very Good	Infill ++	Infill ++
black walnut	Juglans nigra	Low	Sm. inc.	Sm. inc.	Medium	Common	Good	Good		

MR is the model reliability (how reliable is the model for the species), ChngCl45 and ChngCl85 assess the change in HQ under RCP 4.5 and RCP 8.5, Adap is adaptability as defined by the adaptability scores (from literature), Abund denotes abundance according to tree density and basal area (abundant, common, rare or absent), Capabil45 and Capabil85 estimate the capability of the species to cope or persist into the future based on ChngCl, Adap, Abund, and SHIFT45 and SHIFT85 show migration potentials for the RCP 4.5 and RCP 8.5 scenario—species can "infill" within their current range or "migrate" (not shown here) into the region (+ and ++ denoting the strength of the likelihoods). *HQ*, Habitat suitability.

Current trends

Investigations assessing potential future impacts based on empirical observations capture only static snapshots of dynamic biophysical processes, but they raise important issues. Studies based on empirical observations from existing inventories in the United States (Fei et al., 2017; Zhu et al., 2012, 2014) and Canada (Boisvert-Marsh et al., 2014) show some interesting trends. For example, results from the United States showed more westward shifts of angiosperms (hardwoods) and more poleward shifts of gymnosperms (conifers), stressing the importance of moisture in recent and potential future tree dynamics (Fei et al., 2017). In eastern Canada, hardwood species exhibited the expected northward shifts, while coniferous species tended to exhibit southward shifts (Boisvert-Marsh et al., 2014). For most species, juveniles preferred a more optimal climate compared to adults, indicating faster population turnover rather than tree migration (Boisvert-Marsh et al., 2014; Zhu et al., 2014). In the western United States, the current composition and structure of many tree species are showing declines compared to their historic variability (with widespread shifts in the size structure) due to a century of fire suppression, drought-induced mortality (Allen et al., 2015), and intensive harvesting (Stanke et al., 2021). In addition, tree species have responded to spatially differential warming and moisture availability in the past 30−60 years (McNulty et al., 2013; Zhang et al., 2019; https://www.ncdc.noaa.gov/temp-and-precip/us-trends/). It is difficult to disentangle the effects of climate change from other biotic and abiotic disturbances, including human-induced land-use changes (Boisvert-Marsh et al., 2014) due to these multiple interacting forces and changes in population demographics (Stanke et al., 2021; Woodall & Weiskittel, 2021). For example, red maple's (i.e., *Acer rubrum*) range has increased in the eastern United States, with a corresponding decrease in oaks due to factors primarily unrelated to climate change in the recent past (Dyer & Hutchinson, 2019; McEwan et al., 2011). Similarly, the impact of EAB on ash trees in the eastern United States and Canada has been mainly unrelated to climate (Klooster et al., 2018). In Europe, because of more limited potential for migration due to dispersal and geographic constraints (Svenning & Skov, 2004), the impact of climate change may be more dire for many tree species (Dyderski et al., 2018), including significant changes in tree species compositions (Buras & Menzel, 2019) (Fig. 8.6).

Biome shifts

Biome shifts, in which forested lands are converted to shrub or grasslands, or where hardwoods replace conifers, represent more severe forms of divergence from historical conditions, and may already be occurring in some regions. These

FIGURE 8.6 A red maple (Acer rubrum) on the Superior National Forest, Minnesota. *Credit: U.S. Department of Agriculture, U.S. Forest Service.*

shifts are expected to be most evident at ecotones where different biomes converge (Evans & Brown, 2017), and where changing climate conditions (typically warmer and drier) may cause increased stress for some trailing edge species and opportunities for some leading edge species (Seidl et al., 2017; Svenning & Sandel, 2013). Regionally, warmer and drier conditions may promote certain species over others. For example, in the US Midwest and Northeast, oak, hickory, and pine species are likely to gain suitable habitat at the expense of more mesic species like maple and beech, reversing current trends (Janowiak et al., 2018; Swanston et al., 2018). Furthermore, drought conditions along the southern boundary of the boreal forest in western Canada over the past several decades have resulted in growth losses and mortality events that appear to be shifting these forests toward an open, aspen parkland cover type (Birch et al., 2019; Hogg, 1994; Michaelian et al., 2011). These drought-related impacts may be exacerbated by climate-induced regional fire and insect outbreaks, further pushing some forests down novel successional pathways (Birch et al., 2019). Future drought-related response depends on the persistence of water deficits (Vicente-Serrano et al., 2013), which are harder to predict because of higher variability in precipitation forecasts relative to temperatures in GCM scenarios. Despite significant changes in some regions currently, it is noteworthy that the resilience of boreal forests has historically remained high, with a reasonably stable tree species pool over the last 8000 years, despite large fluctuations in climate and disturbance (Blarquez et al., 2014; Gauthier et al., 2015).

Biome shifts are difficult to predict at the global scale, but some broad trends are attributable to changes in seasonal temperature, precipitation patterns, and climatic extremes. Paleoecological records indicate that extensive ecosystem transformations occurred due to climatic warming after the last ice age (i.e., glacial to interglacial transition, Nolan et al., 2018). Forest types defined from practical (i.e., silvicultural) and current ecological considerations are likely to include novel assemblages as species compositions change due to climatic, disturbance, and land-use changes. Using trait-environment models (linking climate to plant traits and plant traits to biomes), Boonman et al. (2022) estimated that tropical and subtropical biomes will expand: forests by 18%−22%, grasslands by 9%−14% and xeric shrublands by 5%−8%. However, their projections for tundra, temperate, and boreal forests were dismal—with projected contractions of 30%−34%, 16%−21%, and 3.6%−7.2%, respectively. They also project 70%−75% of the current distribution of temperate broadleaved and mixed forests and grasslands to shift northward. Such a large and sweeping analysis across global biomes naturally comes with caveats and seem to contradict studies more regional in scope (Iverson, Peters, et al., 2019); for example, Boonman et al. (2022) did not include biotic feedback or land-use changes. Nonetheless, these trait-environment correlation analyses appear to capture extant environmental variation and have corroborated some of the primary biome shifts projected by dynamic global vegetation models (DGVMs; Gonzalez et al., 2010; Sitch et al., 2008).

Based on satellite imagery, it was estimated that 27% of global permanent forest loss was caused by land-use change for commodity production (Curtis et al., 2018). Other significant impacts resulting in areas not permanently deforested were forestry (26%), shifting agriculture (24%), and wildfire (23%). These large-scale impacts show that it is not just climate change in isolation that will influence ecosystems, but the interaction of human activities and other types of biotic disturbances in conjunction with climate change that will cause the most significant impact in vulnerable geographic regions.

Intraspecific aspects

Distribution modeling is typically undertaken at the species level; however, genetic studies have demonstrated climate-driven, intraspecific variation for a variety of tree traits—particularly those related to growth, phenology, and cold tolerance (Leites et al., 2019). Consequently, intraspecific units (e.g., subspecies, climatypes (e.g., cold, intermediate, and warm), populations) may respond uniquely to climate perturbations and thus may represent more suitable taxonomic units for distribution modeling under climate change (Pearman et al., 2010; Hällfors et al., 2016). For example, delineating white pine (*Pinus strobus*) climatypes and mapping combinations of modeled suitable habitats and growth potential enabled the matching of genotypes and climate, helping evaluate assisted migration potential and locating regional vulnerabilities (Prasad & Leites, 2022).

Provenance trials, which measure growth and mortality through time of various seed sources (provenances) planted at various test sites (common gardens) across the range of a species, have been widely used to elucidate population-level growth and mortality responses to climate change (Leites et al., 2012; O'Neill et al., 2014; Rehfeldt et al., 1999; Wang et al., 2010; Yang et al., 2015; Pedlar & McKenney, 2017; Pedlar et al., 2021). Despite their value for climate change research, range-wide provenance data exist for only a limited number of (typically) major timber species (Risk et al., 2021), which limits their potential application in this area. In a rare multispecies provenance study, Pedlar and McKenney (2017) assembled provenance data for five northern conifers. They reported a consistent growth response

where populations from across the geographic range of a species appear to grow well at temperatures characteristic of the southern portion of the range, indicating significant potential for a positive growth response to climate warming in cold-origin populations. Further work is needed to examine whether this pattern extends beyond this assemblage of northern conifer species owing to tradeoffs between survival and cold hardiness among populations (Sebastian-Azcona et al., 2018). However, modern genomic analyses have demonstrated significant value for elucidating intraspecific climate responses. For example, identifying haplotypes linked to evolutionary lineages of ponderosa pine (*Pinus ponderosa*) revealed the importance of geographic variation in vulnerability to climate change (Maguire et al., 2018; Shinneman et al., 2016). Similarly, evaluating ecological differences among population groups identified from genetic clusters (inferred from molecular markers) revealed significant intraspecific differences in vulnerability for eastern hemlock (*Tsuga canadensis*) (Prasad & Potter, 2017).

Phenotypic plasticity (physiological, morphological, and phenological) and ecophysiological strategies have become a significant focus on evolutionary ecology and genetics because of intraspecific responses, and are likely to play important roles under rapid climate change (Dorado-Liñán et al., 2019; Loehle, 2018; Maguire et al., 2018). Plasticity (where a genotype (G) has a differential response based on the environment (E)) reflects G × E effects exposed via reaction norms (on which differential selective pressures can operate). Because the acquired standing genetic variation over the eons is mainly the product of past mutations, and can be selected upon, we could be witnessing a more dynamic picture of adaptation under future climates (Henn et al., 2018) once we include plastic responses of tree species.

Studying the differential response of populations may be helpful for reasons other than the "growth response." Future climate changes may alter this emphasis because most provenance studies are based mainly on commercial tree growth considerations. For example, if fast-growing populations are found to be more disease-prone in the future, we may need to identify other aspects of plastic G × E responses related to forest health that are currently under studied (Li et al., 2017). In addition, the multidimensional aspects of the adaptive capacity of tree species and the multiple scales in which they operate point to the need for better cross-collaboration among disciplines to document and elaborate finer aspects of "adaptive variability" among species (Royer-Tardif et al., 2021).

Assisted migration

Results from species distribution and migration models point to the potential role of assisted migration in climate change adaptation efforts, because many tree species may not be able to keep pace with projected changes in climate. Also, interspecific exclusions and the possibility of nonequilibrium with climate (especially for more endemic species) does not equate to the realized niche for many species because of inherent plasticity. Therefore some tree species can occupy climatic niches far larger than their current distributions (Sáenz-Romero et al., 2020).

Specifically, the HQ−CL maps presented here (Figs. 8.3 and 8.4) identify potential locations for various assisted migration objectives (Aitken & Bemmels, 2016; Pedlar et al., 2012; Prasad et al., 2020). Within-range movements represent a relatively low-risk form of assisted migration that could help better align population-level climate preferences with projected future climate (Ste-Marie et al., 2011). Such efforts could use HQ−CL outputs that identify general infilling opportunities within extant range limits (Prasad et al., 2020). However, the projected magnitude of climate change coupled with limited adaptive variation across species' ranges suggests that extra-range movements may also be necessary (Pedlar et al., 2021). To this end, HQ−CL maps identify potential planting zones that could mimic natural migration patterns at northern/upslope range limits. Such efforts may be required where natural migration rates are slowed due to human-made and/or natural barriers. The HQ−CL maps also identify locations well outside current range limits with little chance of being naturally colonized. However, they may be climatically suitable in the future, although local and on-ground knowledge is needed to match species to the site. Similarly, combinations of habitat quality with growth potential (GP) based on intraspecific studies that align genotypes with climate can be helpful in formulating assisted migration strategies (Prasad & Leites, 2022). Such movements (including assisted gene flow) may be of interest for certain species and regions but have been the source of ongoing ethical debates and would require careful assessments before being undertaken at scale (Champagne et al., 2021; McLachlan et al., 2007; Pelai et al., 2021; Schwartz et al., 2012).

Role of refugia

There is fossil evidence to suggest that both European and North American tree species survived repeated glacial cycles of the Quaternary by persisting in climatic refugia—both in the ice-free southern regions and in portions of the higher latitudes which remained ice-free. Buffered from extreme climates, they served as source populations for subsequent

re-colonizations when more favorable climates returned (Hampe et al., 2013; Keppel et al., 2012; Provan & Bennett, 2008). Many previous estimates of long-distance migration rates were lowered because of these high-latitude refugial populations (McLachlan et al., 2005; Napier et al., 2019), providing more credible scenarios of species migration under climate change. Some studies, however, caution that refugia with small "relict" fragmented populations may not have the same potential for initiating new populations compared to larger populations to the south (Edwards et al., 2014; Fernandez et al., 2021; Tzedakis et al., 2013).

Identifying relevant landscape features, species traits, and biotic influences that buffer tree species from anticipated rapid warming and moisture deficits will be crucial for healthy future forests (Hampe & Jump, 2011; McLaughlin et al., 2017). Also, identifying both in situ climate refugia (currently occupied by species expected to remain suitable under climate change) and ex situ refugia (regions beyond current species' ranges expected to remain suitable) will be important, with the former being especially important for narrow-range species with limited dispersal abilities (Beaumont et al., 2019). Studies that combine the power of SDMs with phylogenetic, paleoclimatic, geomorphological, and biogeographic perspectives (Dobrowski, 2011; Edwards et al., 2014; Fernandez et al., 2021; Meineri & Hylander, 2017; Napier et al., 2019; Roberts & Hamann, 2015; Stralberg et al., 2018) are pivotal for a more comprehensive view on the role of refugia in future policies (Keppel et al., 2012; Morelli et al., 2016; Stralberg et al., 2020)—including a particular emphasis on protecting endemic regions throughout the globe linked to stable climatic refugia (Eigenbrod et al., 2015; Harrison & Noss, 2017).

Climatic equilibrium

Historical and current climatic and biotic pressures, along with contingent eco-evolutionary factors, together broadly determine the distribution and abundance patterns of tree species (Davis, 1983; Schoonmaker & Foster, 1991). While wide-ranging tree species are generally thought to be in equilibrium with historical climate (Webb, 1986), this may not be the case for all species—particularly those with narrow ranges (Seliger et al., 2021). For example, Svenning and Skov (2004) concluded that "*European tree species ranges appear strongly controlled by geographical dispersal constraints on post-glacial expansion as well as climate*." In addition, for several temperate and northern tree species, reciprocal transplant experiments have shown that specific populations are growing under suboptimal climate conditions (Namkoong, 2001; Pedlar & McKenney, 2017; Rehfeldt et al., 2018; Thomson & Parker, 2008); implying that populations are not necessarily matched to their geographic location. Even North American broadleaved tree species, which are generally assumed to be in equilibrium with climate, show distinct geographic patterns that can be traced to the current climate and lagged immigration from glacial refugia (Ordonez & Svenning, 2016). These factors, therefore, constrain the ability of SDMs and other modeling approaches to forecast changes because they assume equilibrium with climate (i.e., the realized niches of species correspond well with their fundamental niches).

Modeling issues and challenges

In addition to the challenges associated with the model internals and the constraints on SDMs discussed previously, several ancillary issues related to the data, scale, and spatial and temporal transferability of results are important when gauging the strengths and limitations of modeled results.

Data availability and computational constraints have primarily been the main limitations to the spatial resolution of ecological models. From 1990 to 2010, environmental data represented at a resolution of 20 km were more manageable with computer capabilities (e.g., storage and computational speeds) for subcontinental to continental extents. However, advances in remote sensing (Pettorelli et al., 2014) and computers have made high-resolution environmental data available, which makes the density of on-ground inventory data and our confidence to interpolate/extrapolate the most significant limiting factors in modeling at finer spatial resolutions. Unfortunately, a finer resolution is not always better for macroscale studies because the scale of the response variable (in our case, relative abundance) should match the explanatory variables for the models to work well (Manzoor et al., 2018). For example, in the United States, FIA sampling density results in roughly one plot per 5 km in forested regions. However, their spatial density varies across the country due to random sampling inside the systematic hexagonal grid of $\sim 24\ \text{km}^2\ \text{hexagon}^{-1}$ (Weiskittel et al., 2012). We have determined that our HQ models generally yield good response for abundance at 20×20 km. However, a 10×10 km cell resolution in more densely sampled areas may be acceptable with adequate plots per cell. In our case, averaging FIA plots to a 20×20 km cell resolution resulted in a better model fit overall compared to the 10×10 km resolution. However, the differential sampling density of plots in many inventories calls for more judicious approaches. For example, Peters et al. (2019) modeled individual species abundance across the eastern United States using a hybrid lattice (Stevens, 1997; Tsui & Brimicombe, 1997) of 10×10 and 20×20 km cells to take advantage of the differential

sampling intensity of FIA plots across the eastern United States, while still maintaining a good match with the response.

Choosing which environmental features to include as explanatory variables is not easy given data availability, quality, spatial extents, resolutions, and relevance to the modeling problem of interest (e.g., Austin & Van Niel, 2011; Chauvier et al., 2021; Williams et al., 2012; Zurell et al., 2020). While newer data-driven prediction techniques have sophisticated algorithms for extracting important features from many explanatory variables, these can still pose problems for ecological interpretability and prediction. For example, soil properties are significant explanatory variables for tree distributions. However, their relevance varies with scale. Many tree species show varying abundance locally and sometimes regionally due to edaphic factors. Therefore one must be cautious about how many and what type of soil variables to include in macroscale modeling frameworks. In addition, high-quality soil data are lacking for many forested regions worldwide. For example, soil surveys in Canada and the United States have traditionally focused on potential agricultural land. In Canada, the soil survey focus remains agricultural, and soils are mapped at a very coarse resolution (1:1,000,000). Therefore these maps are of limited use for modeling forest species shifts under climate change. While the Natural Resources Conservation Service (NRCS) in the United States has invested in soil surveys and has compiled an extensive database at 1:24,000 resolution, the NRCS has not yet mapped wall-to-wall at this resolution across the continental United States.

For this reason, the data applicability to forest trees is still secondary relative to agriculture and development. Because of some of these constraints, it may be necessary to pay more attention to which soil variables are relevant in the model a priori to ensure that multivariate modeling artifacts do not result in excessive importance of soils and lead to more favorable results under climate change. However, it should be noted that relevant soil variables help capture interactions between climate and soil that would be useful in understanding finer-scale changes in abundance. In addition, the interactions between microclimate and soils will be significant for more regional and local studies.

Concerning climate variables, it is essential to include seasonal variables that indicate heat-moisture balances that will be crucial for vegetation response in the future (Harvey et al., 2020). For mountainous areas, the role of topographic variables and their interaction with climate and terrain water-holding capacity is important (Title & Bemmels, 2018). Models should be fine-tuned to disentangle these confounding effects for better interpretation. Staging models to capture climatic influences initially, then adding other explanatory variables into models is helpful to disentangle climatic effects from other variables. The residual variability to be explained after the climatic influence is captured can be tackled at later stages of the modeling process by accounting for relevant ecological variables and other scale-related issues. Our multistage modeling scheme is amenable to this approach.

Also, the future climate scenarios we have considered represent the plausible lower (RCP 4.5) and upper (RCP 8.5) bounds of future greenhouse gas emissions. It may be preferable to start planning and implementation with milder future scenarios (e.g., RCP 4.5 or equivalent) when dealing with assisted migration and seed transfer protocols, not to prescribe drastic solutions that deviate too much from the current normals, and allow for a greater chance of initial survival successes. However, experimentation and field testing with planting according to the more drastic (e.g., RCP 8.5) scenarios would also be appropriate to indicate the procedures that may be needed in the future should the "business as usual" scenarios play out globally.

The temporal and spatial transferability of HQ models have been questioned (Charney et al., 2021; Dobrowski et al., 2011; Randin et al., 2006). Many biotic interactions, such as spatial autocorrelation artifacts, are not typically considered when extrapolating in time and space—mainly because of data incompatibility, model complexity, and computational constraints. However, these need not be significant limitations if the caveats are well-described, and postmodeling steps are taken to address them. For example, postmodel processing can filter out some incompatibilities in predictions using higher-resolution land-use maps (Dewitz, 2019). Finer scale local maps can also be used to constrain the predictions to what is ecologically relevant. Our multistage modeling approach can incorporate these additional postmodel features to make the macroscale modeled results more helpful in addressing local-scale issues.

The techniques we have outlined here for modeling species abundance can, in principle, be applied to any area of interest; however, regional variation in data availability may necessitate modifications to this approach. We used regression-tree-based methods to model species abundance as a function of a suite of environmental variables. If abundance data are unavailable, it may be possible to employ presence/absence data, which are more readily available. For example, crowd-sourced/citizen-science data (Boho et al., 2020; Mahecha et al., 2021; Pärtel et al., 2021), herbarium records, and documented data for commercially important tree species are becoming increasingly available. In place of regression-tree-based approaches, classification-tree ensembles and logistic regression are well suited to model presence/absence data, while the machine learning software MaxEnt (Phillips & Dudík, 2008; Phillips et al., 2017) has proven useful for modeling presence-only data. In addition, climate and terrain data are available for almost all regions

of the globe, as well as coarse soil data (Abatzoglou, 2013; Hengl et al., 2017). However, a global macroscale modeling effort encompassing entire tree species ranges will present more significant challenges requiring more international cooperation. These challenges are especially great in continents outside North America and Australia, where scores of countries are typically involved. Organizations like the United Nations Food and Agriculture Organization's tropical forest assessment (Keenan et al., 2015; Morales-Hidalgo et al., 2015) can offer countrywide forest area data to help achieve this goal.

Conclusion

In this chapter, we traced the role of climate and other eco-evolutionary forces on forests starting from the deep past. We provided a few examples of (1) data-driven HQ models based on empirical data, (2) a migration simulation model calibrated with historical migration rates, and (3) accounted for unmodeled biological and disturbance factors—which constitute our multistage modeling scheme. We also discussed the various issues and considerations arising from the model building that is relevant to the health of future forests. It should be clear from our deliberations that multiple modeling approaches are necessary to assess future uncertainties—including dynamic process-based and agent-based models. All modeling exercises involve tradeoffs, trying to approximate reality in a socially useful manner. Despite tremendous improvements in data quality and computational capabilities, striving to achieve optimal balance among generality, realism, and accuracy in model building is still relevant today (Levins, 1966, 1993). Valuable insights and sensible management guidelines will emerge based on the strengths and limitations of various techniques, viewpoints, and approaches (Iverson et al., 2017). The complexity due to nonlinearities, uncertainties, and sometimes contradictory responses of forest ecosystems to both abiotic and biotic disturbances call for a more thoughtful and comprehensive approach to management, stressing adaptation strategies based on species vulnerability that aligns with long-term management objectives (Case & Lawler, 2016; Glick et al., 2011). Management strategies crafted using these concepts by bringing together various agents, players, and stakeholders, show promise for maintaining the health of future forests amidst multiple demands and disturbances (Foden et al., 2019; Janowiak et al., 2018; Swanston et al., 2018). This is all the more necessary when dealing with current and future uncertainties associated with anticipated rapid climate change, which can result in novel forested landscapes and other unknowns. We stress that future climate change will often be confounded with rapid human-caused land-use changes, and other biotic and abiotic disturbances. Future forests will most likely be shaped by these interacting forces and the resulting feedback responses.

References

Abatzoglou, J. T. (2013). Development of gridded surface meteorological data for ecological applications and modelling. *International Journal of Climatology*, *33*(1), 121−131. Available from https://doi.org/10.1002/joc.3413.

Adams, B. T., & Matthews, S. N. (2022). Feature-dependent group structures and hierarchical songbird-habitat relationships in a managed forest landscape. *Ecological Indicators*, *136*, 108717. Available from https://doi.org/10.1016/j.ecolind.2022.108717.

Aitken, S. N., & Bemmels, J. B. (2016). Time to get moving: Assisted gene flow of forest trees. *Evolutionary Applications*, *9*, 271−290. Available from https://doi.org/10.1111/eva.12293.

Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T., & Curtis-McLane, S. (2008). Adaptation, migration or extirpation: Climate change outcomes for tree populations. *Evolutionary Applications*, *1*, 95−111. Available from https://doi.org/10.1111/j.1752-4571.2007.00013.x.

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, *6*, art129. Available from https://doi.org/10.1890/ES15-00203.1.

Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, *22*, 42−47. Available from https://doi.org/10.1016/j.tree.2006.09.010.

Aubin, I., Munson, A. D., Cardou, F., et al. (2016). Traits to stay, traits to move: A review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. *Environmental Review*, *24*, 164−186. Available from https://doi.org/10.1139/er-2015-0072.

Augusto, L., Davies, T. J., Delzon, S., & De Schrijver, A. (2014). The enigma of the rise of angiosperms: Can we untie the knot? *Ecology Letters*, *17*, 1326−1338. Available from https://doi.org/10.1111/ele.12323.

Austin, M. P., & Van Niel, K. P. (2011). Improving species distribution models for climate change studies: Variable selection and scale. *Journal of Biogeography*, *38*(1), 1−8.

Bachelet, D., et al. (2015). Challenges and limitations of using a DGVM for local to regional applications. In D. Bachelet, & D. Turner (Eds.), *Global vegetation dynamics: Concepts and applications in the MC1 model*. John Wiley & Sons, Inc.

Baker, R. E., Peña, J.-M., Jayamohan, J., & Jérusalem, A. (2018). Mechanistic models versus machine learning, a fight worth fighting for the biological community? *Biology Letters*, *14*, 20170660. Available from https://doi.org/10.1098/rsbl.2017.0660.

Beaumont, L. J., Esperón-Rodríguez, M., Nipperess David, A., et al. (2019). Incorporating future climate uncertainty into the identification of climate change refugia for threatened species. *Biological Conservation*, *237*, 230−237. Available from https://doi.org/10.1016/j.biocon.2019.07.013.

Birch, J. D., Lutz, J. A., Hogg, E. H., et al. (2019). Decline of an ecotone forest: 50 years of demography in the southern boreal forest. *Ecosphere*, *10*, e02698. Available from https://doi.org/10.1002/ecs2.2698.

Bisbing, S. M., Urza, A. K., Buma, B. J., et al. (2021). Can long-lived species keep pace with climate change? Evidence of local persistence potential in a widespread conifer. *Diversity and Distributions*, *27*, 296−312. Available from https://doi.org/10.1111/ddi.13191.

Blankenship, R. E. (2017). How Cyanobacteria went green. *Science (New York, N.Y.)*, *355*, 1372−1373. Available from https://doi.org/10.1126/science.aam9365.

Blarquez, O., Carcaillet, C., Frejaville, T., & Bergeron, Y. (2014). Disentangling the trajectories of alpha, beta and gamma plant diversity of North American boreal ecoregions since 15,500 years. *Frontiers in Ecology and Evolution*, *2*. Available from https://doi.org/10.3389/fevo.2014.00006.

Boho, D., Rzanny, M., Wäldchen, J., et al. (2020). Flora capture: A citizen science application for collecting structured plant observations. *BMC Bioinformatics*, *21*, 576. Available from https://doi.org/10.1186/s12859-020-03920-9.

Boisvert-Marsh, L., & Blois, S. (2021). Unravelling potential northward migration pathways for tree species under climate change. *Journal of Biogeography*, *48*, 1088−1100. Available from https://doi.org/10.1111/jbi.14060.

Boisvert-Marsh, L., Périé, C., & de Blois, S. (2014). Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. *Ecosphere*, *5*(art83). Available from https://doi.org/10.1890/ES14-00111.1.

Boisvert-Marsh, L., Royer-Tardif, S., Nolet, P., Doyon, F., & Aubin, I. (2020). Using a trait-based approach to compare tree species sensitivity to climate change stressors in Eastern Canada and inform adaptation practices. *Forests*, *11*(9).

Boonman, C. C. F., Huijbregts, M. A. J., Benítez-López, A., et al. (2022). Trait-based projections of climate change effects on global biome distributions. *Diversity and Distributions*, *28*, 25−37. Available from https://doi.org/10.1111/ddi.13431.

Booth, T. H. (2017). Assessing species climatic requirements beyond the realized niche: Some lessons mainly from tree species distribution modelling. *Climatic Change*, *145*, 259−271. Available from https://doi.org/10.1007/s10584-017-2107-9.

Brecka, A. F. J., Boulanger, Y., Searle, E. B., et al. (2020). Sustainability of Canada's forestry sector may be compromised by impending climate change. *Forest Ecology and Management*, *474*, 118352. Available from https://doi.org/10.1016/j.foreco.2020.118352.

Breiman, L. (2001). Random forest. *Machine Learning*, *45*(1), 5−32.

Breiman, L., Friedman, J., Stone, C. J., & Olshen, R. A. (1984). *Classification and regression trees*. Boca Raton, FL: CRC Press.

Brodribb, T. J., Pittermann, J., & Coomes, D. A. (2012). Elegance versus speed: Examining the competition between conifer and angiosperm trees. *International Journal of Plant Sciences*, *173*, 673−694. Available from https://doi.org/10.1086/666005.

Buras, A., & Menzel, A. (2019). Projecting tree species composition changes of European forests for 2061−2090 under RCP 4.5 and RCP 8.5 scenarios. *Frontiers in Plant Science*, *9*, 1986. Available from https://doi.org/10.3389/fpls.2018.01986.

Cardona, T. (2019). Thinking twice about the evolution of photosynthesis. *Open Biology*, *9*, 180246. Available from https://doi.org/10.1098/rsob.180246.

Cardona, T., Sánchez-Baracaldo, P., Rutherford, A. W., & Larkum, A. W. (2019). Early Archean origin of Photosystem II. *Geobiology*, *17*, 127−150. Available from https://doi.org/10.1111/gbi.12322.

Case, M. J., & Lawler, J. J. (2016). Relative vulnerability to climate change of trees in western North America. *Climatic Change*, *136*, 367−379. Available from https://doi.org/10.1007/s10584-016-1608-2.

Chakraborty, D., Basagaoglu, H., & Winterle, J. (2021). Interpretable vs. noninterpretable machine learning models for data-driven hydro-climatological process modeling. *Expert Systems with Applications*, *170*, 114498. Available from https://doi.org/10.1016/j.eswa.2020.114498.

Champagne, E., Royo, A. A., Tremblay, J.-P., & Raymond, P. (2021). Tree assisted migration in a browsed landscape: Can we predict susceptibility to herbivores. *Forest Ecology and Management*, *498*, 119576. Available from https://doi.org/10.1016/j.foreco.2021.119576.

Charney, N. D., Record, S., Gerstner, B. E., et al. (2021). A test of species distribution model transferability across environmental and geographic space for 108 Western North American tree species. *Frontiers in Ecology and Evolution*, *9*, 689295. Available from https://doi.org/10.3389/fevo.2021.689295.

Chase, J. M., & Leibold, M. A. (2003). *Ecological niches: Linking classical and contemporary approaches*. University of Chicago Press.

Chauvier, Y., Thuiller, W., Brun, P., et al. (2021). Influence of climate, soil, and land cover on plant species distribution in the European Alps. *Ecological Monographs*, *91*(2).

Clark, J. S., Fastie, C., Hurtt, G., et al. (1998). Reid's paradox of rapid plant migration. *Bioscience*, *48*, 13−24. Available from https://doi.org/10.2307/1313224.

Clark, J. S., Nemergut, D., Seyednasrollah, B., et al. (2017). Generalized joint attribute modeling for biodiversity analysis: Median-zero, multivariate, multifarious data. *Ecological Monographs*, *87*, 34−56. Available from https://doi.org/10.1002/ecm.1241.

Clark, A. D., Deffner, D., Laland, K., et al. (2020). Niche construction affects the variability and strength of natural selection. *The American Naturalist*, *195*, 16−30. Available from https://doi.org/10.1086/706196.

Condamine, F. L., Silvestro, D., Koppelhus, E. B., & Antonelli, A. (2020). The rise of angiosperms pushed conifers to decline during global cooling. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 28867−28875. Available from https://doi.org/10.1073/pnas.2005571117.

Connolly, S. R., Keith, S. A., Colwell, R. K., & Rahbek, C. (2017). Process, mechanism, and modeling in macroecology. *Trends in Ecology & Evolution*, *32*, 835−844. Available from https://doi.org/10.1016/j.tree.2017.08.011.

Curtis, P. G., Slay, C. M., Harris, N. L., et al. (2018). Classifying drivers of global forest loss. *Science (New York, N.Y.)*, *361*, 1108−1111. Available from https://doi.org/10.1126/science.aau3445.

Davis, M. B. (1983). Quaternary history of deciduous forests of Eastern North America and Europe. *Annals of the Missouri Botanical Garden*, *70*, 550. Available from https://doi.org/10.2307/2992086.

Demoulin, C. F., Lara, Y. J., Cornet, L., et al. (2019). Cyanobacteria evolution: Insight from the fossil record. *Free Radical Biology and Medicine*, *140*, 206−223. Available from https://doi.org/10.1016/j.freeradbiomed.2019.05.007.

Dewitz, J.. (2019). *National Land Cover Database (NLCD) 2016 products: U.S. Geological Survey data release*. https://doi.org/10.5066/P96HHBIEDewitz.

Dobrowski, S. Z. (2011). A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology*, *17*, 1022−1035. Available from https://doi.org/10.1111/j.1365-2486.2010.02263.x.

Dobrowski, S. Z., Thorne, J. H., Greenberg, J. A., et al. (2011). Modeling plant ranges over 75 years of climate change in California, USA: Temporal transferability and species traits. *Ecological Monographs*, *81*, 241−257. Available from https://doi.org/10.1890/10-1325.1.

Dorado-Liñán, I., Piovesan, G., Martínez-Sancho, E., et al. (2019). Geographical adaptation prevails over species-specific determinism in trees' vulnerability to climate change at Mediterranean rear-edge forests. *Global Change Biology*, *25*, 1296−1314. Available from https://doi.org/10.1111/gcb.14544.

Dormann, C. F., Schymanski, S. J., Cabral, J., et al. (2011). Correlation and process in species distribution models: Bridging a dichotomy. *Journal of Biogeography*, *13*.

Dyderski, M. K., Paź, S., Frelich, L. E., & Jagodziński, A. M. (2018). How much does climate change threaten European forest tree species distributions. *Global Change Biology*, *24*, 1150−1163. Available from https://doi.org/10.1111/gcb.13925.

Dyke, A. S. (2004). *An outline of North American deglaciation with emphasis on central and northern Canada. Developments in quaternary sciences* (pp. 373−424). Elsevier.

Dyer, J. M., & Hutchinson, T. F. (2019). Topography and soils-based mapping reveals fine-scale compositional shifts over two centuries within a central Appalachian landscape. *Forest Ecology and Management*, *433*, 33−42. Available from https://doi.org/10.1016/j.foreco.2018.10.052.

Edwards, M. E., Armbruster, W. S., & Elias, S. E. (2014). Constraints on post-glacial boreal tree expansion out of far-northern refugia: Genetic constraints on post-glacial boreal tree expansion. *Global Ecology and Biogeography*, *23*, 1198−1208. Available from https://doi.org/10.1111/geb.12213.

Ehlers, J., Hughes, P.L., & Gibbard, P.L. (2016). The ice age (548 pp.). Chichester: Wiley-Blackwell.

Eigenbrod, F., Gonzalez, P., Dash, J., & Steyl, I. (2015). Vulnerability of ecosystems to climate change moderated by habitat intactness. *Global Change Biology*, *21*, 275−286. Available from https://doi.org/10.1111/gcb.12669.

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, *1*, 330−342.

Evans, P., & Brown, C. D. (2017). The boreal−temperate forest ecotone response to climate change. *Environmental Review*, *25*, 423−431. Available from https://doi.org/10.1139/er-2017-0009.

Fei, S., Desprez, J. M., Potter, K. M., et al. (2017). Divergence of species responses to climate change. *Science Advances*, *3*, e1603055. Available from https://doi.org/10.1126/sciadv.1603055.

Fernandez, M. C., Hu, F. S., Gavin, D. G., et al. (2021). A tale of two conifers: Migration across a dispersal barrier outpaced regional expansion from refugia. *Journal of Biogeography*, *48*, 2133−2143. Available from https://doi.org/10.1111/jbi.14209.

Feurdean, A., Bhagwat, S. A., Willis, K. J., et al. (2013). Tree migration-rates: Narrowing the gap between inferred post-glacial rates and projected rates. *PLoS One*, *8*, e71797. Available from https://doi.org/10.1371/journal.pone.0071797.

Foden, W. B., Young, B. E., Akçakaya, H. R., et al. (2019). Climate change vulnerability assessment of species. *WIREs Climate Change*, *10*. Available from https://doi.org/10.1002/wcc.551.

Fordham, D. A., Bertelsmeier, C., Brook, B. W., et al. (2018). How complex should models be? Comparing correlative and mechanistic range dynamics models. *Global Change Biology*, *24*, 1357−1370. Available from https://doi.org/10.1111/gcb.13935.

Friedman, J. H. (2002). Stochastic gradient boosting. *Computational Statistics & Data Analysis*, *38*, 367−378. Available from https://doi.org/10.1016/S0167-9473(01)00065-2.

Gauthier, S., Bernier, P., Kuuluvainen, T., et al. (2015). Boreal forest health and global change. *Science (New York, N.Y.)*, *349*, 819−822. Available from https://doi.org/10.1126/science.aaa9092.

Glick, P., Stein, B. A., & Edelson, N. A. (2011). *Scanning the conservation horizon: A guide to climate change vulnerability assessment*. Washington, DC: National Wildlife Federation.

Gonzalez, P., Neilson, R. P., Lenihan, J. M., & Drapek, R. J. (2010). Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change: Global vulnerability to climate change. *Global Ecology and Biogeography*, *19*, 755−768. Available from https://doi.org/10.1111/j.1466-8238.2010.00558.x.

Gustafson, E. J., De Bruijn, A. M. G., Miranda, B. R., & Sturtevant, B. R. (2016). Implications of mechanistic modeling of drought effects on growth and competition in forest landscape models. *Ecosphere*, 7. Available from https://doi.org/10.1002/ecs2.1253.

Hällfors, M. H., Liao, J., Dzurisin, J., et al. (2016). Addressing potential local adaptation in species distribution models: Implications for conservation under climate change. *Ecological Applications: A Publication of the Ecological Society of America*, *26*, 1154−1169. Available from https://doi.org/10.1890/15-0926.

Hampe, A., & Jump, A. S. (2011). Climate relicts: Past, present, future. *Annual Review of Ecology, Evolution, and Systematics*, *42*, 313−333. Available from https://doi.org/10.1146/annurev-ecolsys-102710-145015.

Hampe, A., Rodríguez-Sánchez, F., Dobrowski, S., et al. (2013). Climate refugia: From the last glacial maximum to the twenty-first century. *The New Phytologist*, *197*, 16−18. Available from https://doi.org/10.1111/nph.12059.

Harrison, S., & Noss, R. (2017). Endemism hotspots are linked to stable climatic refugia. *Annals of Botony*, *119*, 207−214. Available from https://doi.org/10.1093/aob/mcw248.

Harrison, C. J., & Morris, J. L. (2018). The origin and early evolution of vascular plant shoots and leaves. *Philosophical Transactions of the Royal Society B*, *373*, 20160496. Available from https://doi.org/10.1098/rstb.2016.0496.

Harvey, J. E., Smiljanic, M., Scharnweber, T., et al. (2020). Tree growth influenced by warming winter climate and summer moisture availability in northern temperate forests. *Global Change Biology*, *26*, 2505−2518. Available from https://doi.org/10.1111/gcb.14966.

Hastie, T., Tibshirani, R., & Friedman, J. (2009). *The elements of statistical learning* (2nd ed.). New York, NY: Springer Science.

Hengl, T., Mendes de Jesus, J., Heuvelink, G. B. M., et al. (2017). SoilGrids250m: Global gridded soil information based on machine learning. *PLoS One*, *12*(2), e0169748. Available from https://doi.org/10.1371/journal.pone.0169748.

Henn, J. J., Buzzard, V., Enquist, B. J., et al. (2018). Intraspecific trait variation and phenotypic plasticity mediate alpine plant species response to climate change. *Frontiers in Plant Science*, *9*, 1548. Available from https://doi.org/10.3389/fpls.2018.01548.

Hogg, E. H. (1994). Climate and the southern limit of the western Canadian boreal forest. *Canadian Journal of Forest Research*, *24*, 1835−1845.

Howard, C., Stephens, P. A., Pearce-Higgins, J. W., Gregory, R. D., & Willis, S. G. (2014). Improving species distribution models: The value of data on abundance. *Methods in Ecology and Evolution*, *5*(6), 506−513.

Huang, J. P. (2015). Revisiting rapid phenotypic evolution in sticklebacks: Integrative thinking of standing genetic variation and phenotypic plasticity. *Frontiers in Ecology and Evolution*, *3*(47), 1−4. Available from https://doi.org/10.3389/fevo.2015.00047.

Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415−427.

Ishwaran, H., Kogalur, U. B., Gorodeski, E. Z., Minn, A. J., & Lauer, M. S. (2010). High-dimensional variable selection for survival data. *Journal of American Statistical Association*, *105*, 205−217. Available from https://doi.org/10.1198/jasa.2009.tm08622.

Iverson, L. R., Schwartz, M. W., & Prasad, A. M. (2004). How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography*, *11*.

Iverson, L. R., Prasad, A. M., Matthews, S. N., & Peters, M. (2008). Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management*, *254*, 390−406. Available from https://doi.org/10.1016/j.foreco.2007.07.023.

Iverson, L. R., Matthews, S. N., Prasad, A. M., Peters, M. P., & Yohe, G. (2012). Development of risk matrices for evaluating climatic change responses of forested habitats. *Climatic Change*, *114*(2), 231−243.

Iverson, L. R., Thompson, F. R., Matthews, S., et al. (2017). Multi-model comparison on the effects of climate change on tree species in the eastern U.S.: Results from an enhanced niche model and process-based ecosystem and landscape models. *Landscape Ecology*, *32*, 1327−1346. Available from https://doi.org/10.1007/s10980-016-0404-8.

Iverson, L., Peters, M., Prasad, A., & Matthews, S. (2019). Analysis of climate change impacts on tree species of the Eastern US: Results of DISTRIB-II modeling. *Forests*, *10*, 302. Available from https://doi.org/10.3390/f10040302.

Iverson, L. R., Prasad, A. M., Peters, M. P., & Matthews, S. N. (2019). Facilitating adaptive forest management under climate change: A spatially specific synthesis of 125 species for habitat changes and assisted migration over the Eastern United States. *Forests*, *10*, 989. Available from https://doi.org/10.3390/f10110989.

Janowiak, M.K., D'Amato, A.W., & Swanston, C.W., et al. (2018). *New England and northern New York forest ecosystem vulnerability assessment and synthesis: A report from the New England Climate Change Response Framework project*. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA

Jin, W.-T., Gernandt, D. S., Wehenkel, C., et al. (2021). Phylogenomic and ecological analyses reveal the spatiotemporal evolution of global pines. *Proceedings of the National Academy of Sciences of the United States of America*, *118*. Available from https://doi.org/10.1073/pnas.2022302118, e2022302118.

Jones, M. C., & Cheung, W. W. L. (2015). Multi-model ensemble projections of climate change effects on global marine biodiversity. *ICES Journal of Marine Science*, *72*, 741−752. Available from https://doi.org/10.1093/icesjms/fsu172.

Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, *12*, 334−350. Available from https://doi.org/10.1111/j.1461-0248.2008.01277.x.

Kearney, M. R., Wintle, B. A., & Porter, W. P. (2010). Correlative and mechanistic models of species distribution provide congruent forecasts under climate change: Congruence of correlative and mechanistic distribution models. *Conservation Letters*, *3*, 203−213. Available from https://doi.org/10.1111/j.1755-263X.2010.00097.x.

Keeley, J. E. (2012). Ecology and evolution of pine life histories. *Annals of Forest Science*, *69*, 445−453. Available from https://doi.org/10.1007/s13595-012-0201-8.

Keenan, R. J., Reams, G. A., Achard, F., et al. (2015). Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. *Forest Ecology and Management*, *352*, 9−20. Available from https://doi.org/10.1016/j.foreco.2015.06.014.

Kenrick, P., & Crane, P. R. (1997). The origin and early evolution of plants on land. *Nature*, *389*, 33−39. Available from https://doi.org/10.1038/37918.

Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., et al. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, *21*, 393−404. Available from https://doi.org/10.1111/j.1466-8238.2011.00686.x.

Kleman, J., Jansson, K., De Angelis, H., et al. (2010). North American Ice Sheet build-up during the last glacial cycle, 115−21kyr. *Quaternary Science Reviews*, *29*, 2036−2051. Available from https://doi.org/10.1016/j.quascirev.2010.04.021.

Klooster, W., Gandhi, K., Long, L., et al. (2018). Ecological impacts of Emerald Ash Borer in forests at the epicenter of the invasion in North America. *Forests*, *9*, 250. Available from https://doi.org/10.3390/f9050250.

Kühn, I., & Dormann, C. F. (2012). Less than eight (and a half) misconceptions of spatial analysis: Correspondence. *Journal of Biogeography*, *39*, 995−998. Available from https://doi.org/10.1111/j.1365-2699.2012.02707.x.

Lamy, J., Delzon, S., Bouche, P. S., et al. (2014). Limited genetic variability and phenotypic plasticity detected for cavitation resistance in a Mediterranean pine. *The New Phytologist*, *201*, 874−886. Available from https://doi.org/10.1111/nph.12556.

Leites, L. P., Rehfeldt, G. E., Robinson, A. P., et al. (2012). Possibilities and limitations of using historic provenance tests to infer forest species growth responses to climate change: Growth-climate responses. *Natural Resource Modeling*, *25*, 409−433. Available from https://doi.org/10.1111/j.1939-7445.2012.00129.x.

Leites, L. P., Rehfeldt, G. E., & Steiner, K. C. (2019). Adaptation to climate in five eastern North America broadleaf deciduous species: Growth clines and evidence of the growth-cold tolerance trade-off. *Perspectives in Plant Ecology, Evolution and Systematics*, *37*, 64−72. Available from https://doi.org/10.1016/j.ppees.2019.02.002.

Leslie, A. B., Beaulieu, J. M., Rai, H. S., et al. (2012). Hemisphere-scale differences in conifer evolutionary dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 16217−16221. Available from https://doi.org/10.1073/pnas.1213621109.

Levins, R. (1966). The strategy of model building in population biology. *American Scientist*, *54*, 421−431.

Levins, R. (1993). A response to Orzack and Sober: Formal analysis and the fluidity of science. *The Quarterly Review of Biology*, *68*, 547−555.

Li, Y., Suontama, M., Burdon, R. D., & Dungey, H. S. (2017). Genotype by environment interactions in forest tree breeding: Review of methodology and perspectives on research and application. *Tree Genetics & Genomes*, *13*(60). Available from https://doi.org/10.1007/s11295-017-1144-x.

Linardatos, P., Papastefanopoulos, V., & Kotsiantis, S. (2020). Explainable AI: A review of machine learning interpretability methods. *Entropy*, *23*, 18. Available from https://doi.org/10.3390/e23010018.

Little, E.L. Jr. (1971). *Atlas of United States trees, vol 1. Conifers and important hardwoods*. USDA Forest Service Miscellaneous Publication 1146, Washington, DC.

Loehle, C. (2018). Disequilibrium and relaxation times for species responses to climate change. *Ecological Modelling*, *384*, 23−29.

Lou, Y., Caruana, R., & Gehrke, J. (2012). *Intelligible models for classification and regression. Proceedings of the 18th ACM SIGKDD international conference on Knowledge discovery and data mining − KDD'12* (p. 150) Beijing, China: ACM Press.

Ma, Z., Sandel, B., & Svenning, J.-C. (2016). Phylogenetic assemblage structure of North American trees is more strongly shaped by glacial-interglacial climate variability in gymnosperms than in angiosperms. *Ecology and Evolution*, *6*, 3092−3106. Available from https://doi.org/10.1002/ece3.2100.

Maguire, K. C., Shinneman, D. J., Potter, K. M., & Hipkins, V. D. (2018). Intraspecific niche models for ponderosa pine (*Pinus ponderosa*) suggest potential variability in population-level response to climate change. *Systematic Biology*, *67*, 965−978. Available from https://doi.org/10.1093/sysbio/syy017.

Mahecha, M. D., Rzanny, M., Kraemer, G., et al. (2021). Crowd-sourced plant occurrence data provide a reliable description of macroecological gradients. *Ecography*, *44*, 1131−1142. Available from https://doi.org/10.1111/ecog.05492.

Manzoor, S. A., Griffiths, G., & Lukac, M. (2018). Species distribution model transferability and model grain size − finer may not always be better. *Scientific Reports*, *8*, 7168. Available from https://doi.org/10.1038/s41598-018-25437-1.

Marshall, S. J. (2009). Glaciations, quaternary. In V. Gornitz (Ed.), *Encyclopedia of paleoclimatology and ancient environments*. Dordrecht: Springer, Encyclopedia of Earth Sciences Series. Available from https://doi.org/10.1007/978-1-4020-4411-3_97.

Martre, P., Wallach, D., Asseng, S., et al. (2015). Multimodel ensembles of wheat growth: Many models are better than one. *Global Change Biology*, *21*, 911−925. Available from https://doi.org/10.1111/gcb.12768.

Matthews, S. N., Iverson, L. R., Prasad, A. M., Peters, M. P., & Rodewald, P. G. (2011). Modifying climate change habitat models using tree species-specific assessments of model uncertainty and life history-factors. *Forest Ecology and Management*, *262*(8), 1460−1472. Available from https://doi.org/10.1016/j.foreco.2011.06.047.

McEwan, R. W., Dyer, J. M., & Pederson, N. (2011). Multiple interacting ecosystem drivers: Toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography*, *34*, 244−256. Available from https://doi.org/10.1111/j.1600-0587.2010.06390.x.

McLachlan, J. S., Clark, J. S., & Manos, P. S. (2005). Molecular indicators of tree migration capacity under rapid climate change. *Ecology*, *86*, 2088−2098. Available from https://doi.org/10.1890/04-1036.

McLachlan, J. S., Hellmann, J. J., & Schwartz, M. W. (2007). A framework for debate of assisted migration in an era of climate change. *Conservation Biology*, *21*, 297−302. Available from https://doi.org/10.1111/j.1523-1739.2007.00676.x.

McLaughlin, B. C., Ackerly, D. D., Klos, P. Z., et al. (2017). Hydrologic refugia, plants, and climate change. *Global Change Biology*, *23*, 2941−2961. Available from https://doi.org/10.1111/gcb.13629.

McNulty, S., Caldwell, P., Doyle, T. W., Johnsen, K., Liu, Y., Mohan, J., . . . Sun, G. (2013). Forests and climate change in the Southeast USA. In K. Ingram, K. Dow, L. Carter, & J. Anderson (Eds.), *Climate of the Southeast United States: Variability, change, impacts, and vulnerability* (pp. 165−189). Washington, DC: Island Press.

Meade, L. E., Plackett, A. R. G., & Hilton, J. (2021). Reconstructing development of the earliest seed integuments raises a new hypothesis for the evolution of ancestral seed-bearing structures. *The New Phytologist*, *229*, 1782−1794. Available from https://doi.org/10.1111/nph.16792.

Meineri, E., & Hylander, K. (2017). Fine-grain, large-domain climate models based on climate station and comprehensive topographic information improve microrefugia detection. *Ecography*, *40*, 1003−1013.

Mellor, A., Haywood, A., Stone, C., & Jones, S. (2013). The performance of random forests in an operational setting for large area sclerophyll forest classification. *Remote Sensing*, *5*, 2838−2856.

Michaelian, M., Hogg, E. H., Hall, R. J., & Arsenault, E. (2011). Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest: Aspen mortality following severe drought. *Global Change Biology*, *17*, 2084−2094. Available from https://doi.org/10.1111/j.1365-2486.2010.02357.x.

Morales-Hidalgo, D., Oswalt, S. N., & Somanathan, E. (2015). Status and trends in global primary forest, protected areas, and areas designated for conservation of biodiversity from the Global Forest Resources Assessment 2015. *Forest Ecology and Management*, *352*, 68−77. Available from https://doi.org/10.1016/j.foreco.2015.06.011.

Morelli, T. L., Daly, C., Dobrowski, S. Z., et al. (2016). Managing climate change refugia for climate adaptation. *PLoS One*, *11*, e0159909. Available from https://doi.org/10.1371/journal.pone.0159909.

Mottl, O., Flantua, S. G. A., Bhatta, K. P., et al. (2021). Global acceleration in rates of vegetation change over the past 18,000 years. *Science (New York, N.Y.)*, *372*, 860–864. Available from https://doi.org/10.1126/science.abg1685.

Namkoong, G. (2001). Forest genetics: pattern and complexity. *Canadian Journal of Forest Research. Journal Canadien de la Recherche Forestiere*, *31*, 623–632. Available from https://doi.org/10.1139/x00-166.

Napier, J. D., de Lafontaine, G., Heath, K. D., & Hu, F. S. (2019). Rethinking long-term vegetation dynamics: Multiple glacial refugia and local expansion of a species complex. *Ecography*, *42*, 1056–1067. Available from https://doi.org/10.1111/ecog.04243.

Nijhout, H. F., Kudla, A. M., & Hazelwood, C. C. (2021). *Genetic assimilation and accommodation: Models and mechanisms. Current topics in developmental biology* (pp. 337–369). Elsevier.

Nolan, C., Overpeck, J. T., Allen, J. R. M., et al. (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science (New York, N.Y.)*, *361*, 920–923. Available from https://doi.org/10.1126/science.aan5360.

O'Neill, G. A., Stoehr, M., & Jaquish, B. (2014). Quantifying safe seed transfer distance and impacts of tree breeding on adaptation. *Forest Ecology and Management*, *328*, 122–130. Available from https://doi.org/10.1016/j.foreco.2014.05.039.

Olson, S. K., Smithwick, E. A. H., Lucash, M. S., et al. (2021). Landscape-scale forest reorganization following insect invasion and harvest under future climate change scenarios. *Ecosystems*. Available from https://doi.org/10.1007/s10021-021-00616-w.

Olsson, C., & Jönsson, A. M. (2014). Process-based models not always better than empirical models for simulating budburst of Norway spruce and birch in Europe. *Global Change Biology*, *20*, 3492–3507. Available from https://doi.org/10.1111/gcb.12593.

Ordonez, A., & Svenning, J.-C. (2016). Functional diversity of North American broad-leaved trees is codetermined by past and current environmental factors. *Ecosphere*, 7. Available from https://doi.org/10.1002/ecs2.1237.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 637–669. Available from https://doi.org/10.1146/annurev.ecolsys.37.091305.110100.

Pärtel, J., Pärtel, M., & Wäldchen, J. (2021). Plant image identification application demonstrates high accuracy in Northern Europe. *AoB PLANTS*, *13*, plab050. Available from https://doi.org/10.1093/aobpla/plab050.

Pearman, P. B., D'Amen, M., Graham, C. H., Thuiller, W., & Zimmermann, N. E. (2010). Within-taxon niche structure: Niche conservatism, divergence and predicted effects of climate change. *Ecography*, *33*(6), 990–1003. Available from https://doi.org/10.1111/j.1600-0587.2010.06443.x.

Pedlar, J. H., & McKenney, D. W. (2017). Assessing the anticipated growth response of northern conifer populations to a warming climate. *Scientific Reports*, 7. Available from https://doi.org/10.1038/srep43881.

Pedlar, J. H., McKenney, D. W., Aubin, I., et al. (2012). Placing foresy in the assisted migration debate. *Bioscience*, *62*, 835–842. Available from https://doi.org/10.1525/bio.2012.62.9.10.

Pedlar, J. H., McKenney, D. W., & Lu, P. (2021). Critical seed transfer distances for selected tree species in eastern North America. *Journal of Ecology*, *109*, 2271–2283. Available from https://doi.org/10.1111/1365-2745.13605.

Pelai, R., Hagerman, S. M., & Kozak, R. (2021). Whose expertise counts? Assisted migration and the politics of knowledge in British Columbia's public forests. *Land Use Policy*, *103*, 105296. Available from https://doi.org/10.1016/j.landusepol.2021.105296.

Peters, M. P., Iverson, L. R., Prasad, A. M., & Matthews, S. N. (2019). Utilizing the density of inventory samples to define a hybrid lattice for species distribution models: DISTRIB-II for 135 eastern U.S. trees. *Ecology and Evolution*, *9*(15), 8876–8899. Available from https://doi.org/10.1002/ece3.5445.

Pettorelli, N., Laurance, W. F., O'Brien, T. G., Wegmann, M., Nagendra, H., & Turner, W. (2014). Satellite remote sensing for applied ecologists: Opportunities and challenges. *Journal of Applied Ecology*, *51*(4), 839–848. Available from https://doi.org/10.1111/1365-2664.12261.

Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography*, *31*(2), 161–175. Available from https://doi.org/10.1111/j.0906-7590.2008.5203.x.

Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., & Blair, M. E. (2017). Opening the black box: An open-source release of Maxent. *Ecography*, *40*(7), 887–893. Available from https://doi.org/10.1111/ecog.03049.

Ploton, P., Mortier, F., Réjou-Méchain, M., et al. (2020). Spatial validation reveals poor predictive performance of large-scale ecological mapping models. *Nature Communications*, *11*, 4540. Available from https://doi.org/10.1038/s41467-020-18321-y.

Potter, K. M., Crane, B. S., & Hargrove, W. W. (2017). A United States national prioritization framework for tree species vulnerability to climate change. *New Forests*, *48*, 275–300. Available from https://doi.org/10.1007/s11056-017-9569-5.

Prasad, A. M. (2018). Machine learning for macroscale ecological niche modeling – A multi-model, multi-response ensemble technique for tree species management under climate change. In G. R. Humphries, D. R. Magness, & F. Huettmann (Eds.), *Machine learning for ecology and sustainable natural resource management*. Cham, Switzerland: Springer International Publishing.

Prasad, A., & Leites, L. (2022). Ecological analysis of intraspecific variability of eastern white pine (*Pinus strobus*) under climate change by combining provenance and demographic data. *Landscape Ecology*, *37*, 109–128. Available from https://doi.org/10.1007/s10980-021-01333-4.

Prasad, A. M., & Potter, K. M. (2017). Macro-scale assessment of demographic and environmental variation within genetically derived evolutionary lineages of eastern hemlock (*Tsuga canadensis*), an imperiled conifer of the eastern United States. *Biodiversity and Conservation*, *26*, 2223–2249. Available from https://doi.org/10.1007/s10531-017-1354-4.

Prasad, A. M., Gardiner, J. D., Iverson, L. R., et al. (2013). Exploring tree species colonization potentials using a spatially explicit simulation model: implications for four oaks under climate change. *Global Change Biology*, *19*, 2196–2208. Available from https://doi.org/10.1111/gcb.12204.

Prasad, A. M., Iverson, L. R., & Liaw, A. (2006). Newer classification and regression tree techniques: Bagging and random forests for ecological prediction. *Ecosystems*, *9*, 181–199. Available from https://doi.org/10.1007/s10021-005-0054-1.

Prasad, A. M., Iverson, L. R., Matthews, S. N., & Peters, M. P. (2016). A multistage decision support framework to guide tree species management under climate change via habitat suitability and colonization models, and a knowledge-based scoring system. *Landscape Ecology*, *31*, 2187–2204. Available from https://doi.org/10.1007/s10980-016-0369-7.

Prasad, A., Pedlar, J., Peters, M., et al. (2020). Combining US and Canadian forest inventories to assess habitat suitability and migration potential of 25 tree species under climate change. *Diversity and Distributions*, *26*, 1142–1159. Available from https://doi.org/10.1111/ddi.13078.

Price, D. T., Alfaro, R. I., Brown, K. J., et al. (2013). Anticipating the consequences of climate change for Canada's boreal forest ecosystems. *Environmental Reviews*, *21*, 322–365. Available from https://doi.org/10.1139/er-2013-0042.

Provan, J., & Bennett, K. (2008). Phylogeographic insights into cryptic glacial refugia. *Trends in Ecology & Evolution*, *23*, 564–571. Available from https://doi.org/10.1016/j.tree.2008.06.010.

Randin, C. F., Dirnböck, T., Dullinger, S., et al. (2006). Are niche-based species distribution models transferable in space. *Journal of Biogeography*, *33*, 1689–1703. Available from https://doi.org/10.1111/j.1365-2699.2006.01466.x.

Rehfeldt, G. E., Leites, L. P., Joyce, D. G., & Weiskittel, A. R. (2018). Role of population genetics in guiding ecological responses to climate. *Global Change Biology*, *24*, 858–868. Available from https://doi.org/10.1111/gcb.13883.

Rehfeldt, G. E., Ying, C. C., Spittlehouse, D. L., & Hamilton, D. A. (1999). Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecological Monographs*, *69*, 375–407.

Risk, C., McKenney, D. W., Pedlar, J., & Lu, P. (2021). A compilation of North American tree provenance trials and relevant historical climate data for seven species. *Scientific Data*, *8*, 29. Available from https://doi.org/10.1038/s41597-021-00820-2.

Roberts, D. R., & Hamann, A. (2015). Glacial refugia and modern genetic diversity of 22 western North American tree species. *Proceedings of the Royal Society B*, *282*, 20142903. Available from https://doi.org/10.1098/rspb.2014.2903.

Royer-Tardif, S., Boisvert-Marsh, L., Godbout, J., et al. (2021). Finding common ground: Toward comparable indicators of adaptive capacity of tree species to a changing climate. *Ecology and Evolution*, ece3.8024. Available from https://doi.org/10.1002/ece3.8024.

Sáenz-Romero, C., O'Neill, G., Aitken, S. N., & Lindig-Cisneros, R. (2020). Assisted migration field tests in Canada and Mexico: Lessons, limitations, and challenges. *Forests*, *12*(9). Available from https://doi.org/10.3390/f12010009.

Sánchez-Baracaldo, P., & Cardona, T. (2020). On the origin of oxygenic photosynthesis and Cyanobacteria. *The New Phytologist*, *225*, 1440–1446. Available from https://doi.org/10.1111/nph.16249.

Scheller, R. M., Domingo, J. B., Sturtevant, B. R., et al. (2007). Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling*, *201*, 409–419. Available from https://doi.org/10.1016/j.ecolmodel.2006.10.009.

Schirrmeister, B. E., Gugger, M., & Donoghue, P. C. J. (2015). Cyanobacteria and the Great Oxidation Event: Evidence from genes and fossils. *Palaeontology*, *58*, 769–785. Available from https://doi.org/10.1111/pala.12178.

Schoonmaker, P. K., & Foster, D. R. (1991). Some implications of paleoecology for contemporary ecology. *Botanical Review*, *57*, 204–245.

Schwartz, M. W., Hellmann, J. J., McLachlan, J. M., et al. (2012). Managed relocation: Integrating the scientific, regulatory, and ethical challenges. *Bioscience*, *62*, 732–743. Available from https://doi.org/10.1525/bio.2012.62.8.6.

Sebastian-Azcona, J., Hacke, U. G., & Hamann, A. (2018). Adaptations of white spruce to climate: strong intraspecific differences in cold hardiness linked to survival. *Ecology and Evolution*, *8*, 1758–1768. Available from https://doi.org/10.1002/ece3.3796.

Seidl, R., Thom, D., Kautz, M., et al. (2017). Forest disturbances under climate change. *Nature Climate Change*, *7*, 395–402. Available from https://doi.org/10.1038/nclimate3303.

Seliger, B. J., McGill, B. J., Svenning, J., & Gill, J. L. (2021). Widespread underfilling of the potential ranges of North American trees. *Journal of Biogeography*, *48*, 359–371. Available from https://doi.org/10.1111/jbi.14001.

Shinneman, D. J., Means, R. E., Potter, K. M., & Hipkins, V. D. (2016). Exploring climate niches of ponderosa pine (*Pinus ponderosa* Douglas ex Lawson) haplotypes in the Western United States: Implications for evolutionary history and conservation. *PLoS One*, *11*, e0151811. Available from https://doi.org/10.1371/journal.pone.0151811.

Siefert, A., Lesser, M. R., & Fridley, J. D. (2015). How do climate and dispersal traits limit ranges of tree species along latitudinal and elevational gradients?: Latitudinal and elevational range limits. *Global Ecology and Biogeography*, *24*, 581–593. Available from https://doi.org/10.1111/geb.12287.

Sitch, S., Huntingford, C., Gedney, N., et al. (2008). Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs): Uncertainty in land carbon cycle feedbacks. *Global Change Biology*, *14*, 2015–2039. Available from https://doi.org/10.1111/j.1365-2486.2008.01626.x.

Stanke, H., Finley, A. O., Domke, G. M., et al. (2021). Over half of western United States' most abundant tree species in decline. *Nature Communications*, *12*, 451. Available from https://doi.org/10.1038/s41467-020-20678-z.

Ste-Marie, C., Nelson, E., Dabros, A., & Bonneau, M. E. (2011). Assisted migration: Introduction to a multifaceted concept. *The Forestry Chronicle*, *87*(6), 724–730.

Stevens, D. L. (1997). Variable density grid-based sampling designs for continuous spatial populations. *Environmetrics (London, Ont.)*, *8*(3), 167–195.

Stewart, J. R., Lister, A. M., Barnes, I., & Dalén, L. (2010). Refugia revisited: Individualistic responses of species in space and time. *Proceedings of the Royal Society B*, *277*, 661–671. Available from https://doi.org/10.1098/rspb.2009.1272.

Stralberg, D., Arseneault, D., Baltzer, J. L., et al. (2020). Climate-change refugia in boreal North America: What, where, and for how long? *Frontiers in Ecology and the Environment*, *18*, 261–270. Available from https://doi.org/10.1002/fee.2188.

Stralberg, D., Carroll, C., Pedlar, J. H., et al. (2018). Macrorefugia for North American trees and songbirds: Climatic limiting factors and multi-scale topographic influences. *Global Ecology and Biogeography*, *27*, 690–703. Available from https://doi.org/10.1111/geb.12731.

Svenning, J.-C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, *100*, 1266–1286. Available from https://doi.org/10.3732/ajb.1200469.

Svenning, J.-C., & Skov, F. (2004). Limited filling of the potential range in European tree species: Limited range filling in European trees. *Ecology Letters*, *7*, 565–573. Available from https://doi.org/10.1111/j.1461-0248.2004.00614.x.

Swanston, C., Brandt, L. A., Janowiak, M. K., et al. (2018). Vulnerability of forests of the Midwest and Northeast United States to climate change. *Climatic Change*, *146*, 103–116. Available from https://doi.org/10.1007/s10584-017-2065-2.

Talluto, M. V., Boulangeat, I., Ameztegui, A., Aubin, I., Berteaux, D., Butler, A., … Gravel, D. (2016). Integrated models of species ranges. *Global Ecology and Biogeography*, *25*(2), 238–249. Available from https://doi.org/10.1111/geb.12395.

Thomas, P., & Packman, J. (2007). *Ecology of woodlands and forests: Description, dynamics and diversity*. Cambridge University Press. Available from https://doi.org/10.1017/CBO9780511805578.

Thomson, A. M., & Parker, W. H. (2008). Boreal forest provenance tests used to predict optimal growth and response to climate change. 1. Jack pine. *Canadian Journal of Forest Research*, *38*, 157–170.

Thuiller, W., Albert, C., Araújo, M. B., et al. (2008). Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, *9*, 137–152. Available from https://doi.org/10.1016/j.ppees.2007.09.004.

Title, P. O., & Bemmels, J. B. (2018). Envirem: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. *Ecography*, *41*, 291–307. Available from https://doi.org/10.1111/ecog.02880.

Toledo, M., Poorter, L., Peña-Claros, M., et al. (2011). Climate is a stronger driver of tree and forest growth rates than soil and disturbance: Climate drives tree and forest growth. *Journal of Ecology*, *99*, 254–264. Available from https://doi.org/10.1111/j.1365-2745.2010.01741.x.

Tsui, P. H., & Brimicombe, A. J. (1997). Adaptive Recursive Tessellations (ART) for geographical information systems. *International Journal of Geographical Information Science*, *11*(3), 247–263. Available from https://doi.org/10.1080/136588197242383.

Tucker, A. O. (1983). Atlas of United-States trees, Vol 6 – Little.El. *Bulletin of the Torrey Botonical Club*, *110*, 103.

Tzedakis, P. C., Emerson, B. C., & Hewitt, G. M. (2013). Cryptic or mystic? Glacial tree refugia in northern Europe. *Trends in Ecology & Evolution*, *28*, 696–704. Available from https://doi.org/10.1016/j.tree.2013.09.001.

Valladares, F., & Niinemets, Ü. (2008). Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics*, *39*, 237–257. Available from https://doi.org/10.1146/annurev.ecolsys.39.110707.173506.

Vázquez, D. P., Gianoli, E., Morris, W. F., & Bozinovic, F. (2017). Ecological and evolutionary impacts of changing climatic variability: Impacts of changing climatic variability. *Biological Reviews*, *92*, 22–42. Available from https://doi.org/10.1111/brv.12216.

Vicente-Serrano S.M., Gouveia C., Camarero J.J., et al. (2013) Response of vegetation to drought time-scales across global land biomes. Proceedings of the National Academy of Sciences of the United States of America 110:52–57. https://doi.org/10.1073/pnas.1207068110

Wang, T., O'Neill, G. A., & Aitken, S. N. (2010). Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecological Applications*, *20*, 153–163. Available from https://doi.org/10.1890/08-2257.1.

Webb, T. (1986). Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio*, *67*, 75–91. Available from https://doi.org/10.1007/BF00037359.

Weiskittel, A. R., Crookston, N. L., & Rehfeldt, G. E. (2012). Projected future suitable habitat and productivity of Douglas-fir in western North America. *Schweizerische Zeitschrift fur Forstwesen*, *163*, 70–78. Available from https://doi.org/10.3188/szf.2012.0070.

White, A., Tolman, M., Thames, H. D., et al. (2016). The limitations of model-based experimental design and parameter estimation in sloppy systems. *PLoS Computational Biology*, *12*, e1005227. Available from https://doi.org/10.1371/journal.pcbi.1005227.

Williams, K. J., Belbin, L., Austin, M. P., Stein, J. L., & Ferrier, S. (2012). Which environmental variables should I use in my biodiversity model? *International Journal of Geographical Information Science*, *26*(11), 2009–2047.

Woodall, C. W., & Weiskittel, A. R. (2021). Relative density of United States forests has shifted to higher levels over last two decades with important implications for future dynamics. *Scientific Reports*, *11*, 18848. Available from https://doi.org/10.1038/s41598-021-98244-w.

Woudenberg, S.W., Conkling, B.L., O'Connell, B.M., LaPoint, E.B., Turner, J.A., & Waddell, K.L. (2010). *The forest inventory and analysis database: Database description and user's manual version 4.0 for Phase 2* (Gen. Tech. Rep. RMRSGTR-245). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, p. 336.

Xiao, J., Liang, Y., He, H. S., et al. (2017). The formulations of site-scale processes affect landscape-scale forest change predictions: A comparison between LANDIS PRO and LANDIS-II forest landscape models. *Landscape Ecology*, *32*, 1347–1363. Available from https://doi.org/10.1007/s10980-016-0442-2.

Yang, J., Pedlar, J. H., McKenney, D. W., & Weersink, A. (2015). The development of universal response functions to facilitate climate-smart regeneration of black spruce and white pine in Ontario, Canada. *Forest Ecology and Management*, *339*, 34–43. Available from https://doi.org/10.1016/j.foreco.2014.12.001.

Zhang, G., & Lu, Y. (2012). Bias-corrected random forests in regression. *Journal of Applied Statistics*, *39*, 151–160. Available from https://doi.org/10.1080/02664763.2011.578621.

Zhang, L., Liu, S., Sun, P., et al. (2015). Consensus Forecasting of Species Distributions: The Effects of Niche Model Performance and Niche Properties. *PLoS One*, *10*, e0120056. Available from https://doi.org/10.1371/journal.pone.0120056.

Zhang, X., Flato, G., Kirchmeier-Young, M., et al. (2019). Changes in temperature and precipitation across Canada. In E. Bush, & D. S. Lemmen (Eds.), *Canada's changing climate report* (pp. 112–193). Ottawa, Ontario: Government of Canada.

Zhu, K., Woodall, C. W., & Clark, J. S. (2012). Failure to migrate: Lack of tree range expansion in response to climate change. *Global Change Biology*, *18*, 1042–1052. Available from https://doi.org/10.1111/j.1365-2486.2011.02571.x.

Zhu, K., Woodall, C. W., Ghosh, S., et al. (2014). Dual impacts of climate change: Forest migration and turnover through life history. *Global Change Biology*, *20*, 251–264. Available from https://doi.org/10.1111/gcb.12382.

Zurell, D., Franklin, J., König, C., et al. (2020). A standard protocol for reporting species distribution models. *Ecography*, *43*(9), 1261–1277. Available from https://doi.org/10.1111/ecog.04960.