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## Toward an improved conceptual understanding of North American tree species distributions

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**Abstract.** Species distributions have often been assumed to represent climatic limitations, yet recent evidence has challenged these assumptions and emphasized the potential importance of biotic interactions, dispersal limitation, and disturbance. Despite significant investigation into these factors, an integrated understanding of where and when they may be important is lacking. Here, we review evidence for the factors underlying the historical and contemporary distributions of North American tree species and argue that a cohesive conceptual framework must be informed by an understanding of species ecological and evolutionary history. We further demonstrate that available evidence offers little indication of a significant, independent influence of biotic interactions or dispersal limitation on species distributions. Disturbance may provide important constraints on distributions in limited contexts. Overall, historic and contemporary evidence suggests that species distributions are strongly influenced by climate, yet examples of disequilibrium with climate abound. We propose that differences among life stages and the impacts of human land use may contribute to explain these inconsistencies and are deserving of greater research attention.

**Key words:** biotic interactions; climate; dispersal limitation; distribution; disturbance; land use; paleoecology; range; recruitment; seedlings; temperate; trees.

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### INTRODUCTION

The patterns and processes of species distributions form a major research theme in ecology. Understanding the factors underlying observed distribution patterns has important implications for species conservation and climate change predictions, yet efforts to identify and quantify these factors are often complicated by inconsistencies in species' relationships with their occupied environment. Specifically, species distributions have often been shown to be well explained by broad-scale

climatic factors, indicating strong climatic control on species distribution patterns (Woodward 1987, Brown et al. 1996, Soberón and Nakamura 2009). Strong correlations between bioclimatic factors and tree species distributions have been observed across North America both today (Rehfeldt et al. 2006, Morin et al. 2007, Boucher-Lalonde et al. 2012, Bell et al. 2014, Morueta-Holme et al. 2016) and in the past (COHMAP Members 1988, Prentice et al. 1991, Davis and Shaw 2001, Shuman et al. 2004). However, among ecologists, it is broadly maintained that species distributions

rarely occur in equilibrium with climate (e.g., Araújo et al. 2005, Svenning and Sandel 2013, Worth et al. 2014, Blois 2014, Svenning et al. 2015). Evidence in support of this hypothesis comes in the form of range shift studies, which often document failure of many species to migrate at a rate concurrent with the rate of contemporary climate change (Lenoir et al. 2010, Corlett and Westcott 2013), and some biogeographic analyses and theory that indicate historic legacies and lagged responses to past climate changes (Svenning et al. 2015, Ordonez and Svenning 2016). Across North America, limited climate tracking has been recorded among tree species in California (Serradiaz et al. 2015), at the Alaska treeline (Dial et al. 2015), in western North American forests (Gray and Hamann 2013, Bell et al. 2013), and among eastern North American tree species (Woodall et al. 2009, Murphy et al. 2010, Zhu et al. 2012, Boisvert-Marsh et al. 2014). In response to evidence for failure of species distributions to maintain equilibrium with contemporary climate, alternative factors including biotic interactions, dispersal limitation, and disturbance have been proposed as influential underlying drivers of species distribution patterns (e.g., Austin 2002, HilleRisLambers et al. 2013, Svenning 2014, Siefert et al. 2015), yet it is unclear whether these processes can influence patterns observed over the coarse spatial (>1 km<sup>2</sup>) and long temporal scales (e.g., 30-yr normals) over which distributions are typically characterized (Soberón and Nakamura 2009, Wiens 2011). In particular, if such processes vary according to local environmental gradients, their heterogeneous effects may be averaged out when evaluating broad-scale biodiversity patterns, such as occurrence, at coarse spatiotemporal resolutions (Whittaker et al. 2001, Pearson and Dawson 2003). Yet, if the cumulative impact of local processes is sufficient to alter population dynamics in a manner that is detectable at coarse spatiotemporal resolutions (e.g., exclude species from a large patch of suitable habitat), such processes may contribute to explain the observed disequilibrium between species occurrence and climate (Pulliam 2000, Holt 2009).

While theoretical evidence for the potential influences of these alternative factors on species distributions has emerged (e.g., Case et al. 2005, Godsoe and Harmon 2012, Araújo and Rozenfeld 2014, Godsoe et al. 2015), few consistencies have

arisen in empirical studies and the precise contexts in which these factors influence distributions remain unclear. As a result, ecologists lack a cohesive framework to guide investigations of species distributions (Cassini 2011). Without a better conceptual understanding of the factors underlying species distribution patterns and observed climate disequilibrium, progress on models that can ascribe processes to patterns will be hampered, and predictions of species distributions across time and space will remain highly uncertain and inconsistent.

Global generalizations of the factors underlying distributions may be impossible due to substantial variation in species environmental tolerances, dispersal ability, and ecological and evolutionary history, yet regional trends may emerge among species with shared life history characteristics. We focus here on North American tree species in an attempt to provide an improved understanding of when and where certain factors may contribute to distribution patterns. Specifically, we review evidence regarding the historical and contemporary distributions of North American tree species (Fig. 1) and emphasize the importance of historical context for understanding current species distribution patterns. We note that the scope of this review does not permit us to fully review studies addressing future distribution projections, and we instead emphasize historical and contemporary patterns. Biogeographers and ecologists alike have often argued for greater integration of historical biogeography and macroecology on the basis that species' ecological and evolutionary history provides a great deal of context for understanding current distribution patterns (e.g., Brown et al. 1996, Ricklefs 2004, Jackson et al. 2009, Lavergne et al. 2010). The historical environment of a species exerts selective pressures that have shaped the traits that underlie species responses to current environmental conditions; these responses then determine the environments in which a species can and cannot persist (Brown et al. 1996).

North American tree species have a unique historical legacy characterized by strong climate variability and repeated periods of glaciation (Williams et al. 2004). This legacy has undoubtedly influenced how species currently respond to climate, dispersal barriers, natural disturbance regimes, and co-occurring species (Bennett 1990, Davis and Shaw 2001). We provide a review of

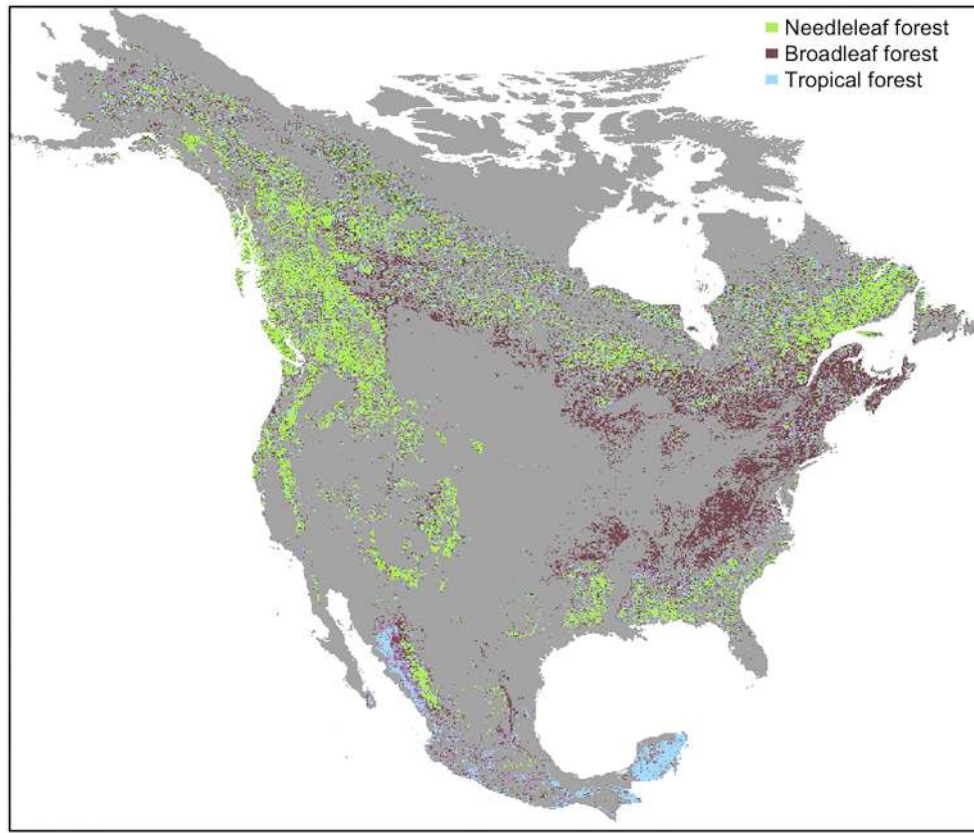


Fig. 1. The distribution of major forest types across North America. Data represent 2010 land-cover estimates from MODIS satellite imagery (<http://modis.gsfc.nasa.gov/>).

the history of North American tree species distributions and propose that species are generally well adapted to respond predominantly to climate and have generally maintained a historical dynamic equilibrium with climate. We then review the contemporary evidence for the roles of biotic interactions, dispersal limitation, and disturbance in shaping the distributions of North American tree species. We emphasize that our discussion of biotic interactions is limited to interspecific interactions occurring within the same trophic level such as competition and facilitation, which reflects the focus of the majority of empirical work available on the subject. Finally, we suggest avenues for further research that may address knowledge gaps and contribute to an improved conceptual understanding of the distributions of North American tree species.

We limit our review to examples involving North American trees precisely because of the

distinct ecological and evolutionary history of these species that allow us to infer some level of shared historical legacy. While North America, Europe, and Asia all share many tree taxa and have a joint history of glaciation (Manchester 1999, Mucina and Wardell-Johnson 2011), North American flora exhibits several key distinctions. First, North America is characterized by fewer large topographic barriers, and as a result, exhibits lower diversity than similar floristic regions in Europe and Asia (Newton et al. 1999, Xiang et al. 2004, Jaramilla-Correa et al. 2009). Additionally, Europe and Asia have much longer histories of human influence and habitat modification, with profound implications for species distributions. Precisely because of the strong influence of historical legacies on contemporary distribution patterns, distributions of European and Asian tree species may be expected to respond more strongly to different underlying factors than those

that are deemed to be particularly important for North American trees.

We also note that this review emphasizes broad-scale patterns and responses, particularly those that are observed across a species' range and at decadal to millennial time scales. We emphasize these scales specifically because tree species distributions, both past and present, are typically evaluated at coarse spatial resolutions ( $\geq 1 \text{ km}^2$ ) and longer temporal scales (30-yr climate normals for contemporary evaluations,  $\geq 100 \text{ yr}$  for paleoecological investigations). While a variety of patterns and responses may be observed at finer resolutions, these may more closely reflect locally heterogeneous conditions and are highly dependent upon the local ecological context, rather than the general distribution-level trends that we wish to characterize.

## HISTORICAL CONTEXT

North American trees have persisted through periods of dramatic climate fluctuations (Fig. 2). Their responses have involved rapid range shifts, contractions, expansions, range-wide changes in abundance, and frequent shuffling of species assemblages (Williams et al. 2004). Persistence through these periods of extreme environmental variability provides evidence that their traits have conferred rapid climate tracking, including through high fecundity, prominent dispersal mechanisms, rapid colonization ability, and high levels of local adaptation and phenotypic plasticity (Davis and Shaw 2001, Jaramilla-Correa et al. 2009). Plentiful evidence suggests that climate has historically been the dominant factor driving North American tree species distributions (COHMAP Members 1988, Prentice et al. 1991, Williams et al. 2002, Shuman et al. 2004, Nelson and Hu 2008, Ordonez and Williams 2013, Blonder et al. 2015) and that past environmental pressures have selected for species and traits that continue to respond strongly to climate (Ricklefs 2004). While historical contingencies have left some detectable imprints on the contemporary distributions of North American tree species across a wide range of spatial scales (McLachlan et al. 2005, Jackson et al. 2009, Jaramilla-Correa et al. 2009, Berland et al. 2011, Hampe and Jump 2011, Ordonez and Svenning 2016), paleoecological data support a primary dynamic equilibrium

between climate and the distributions of extant tree taxa, which depends more upon species' climate niches than on the sequence of past events (Webb 1986).

### *Climate change and distribution shifts*

North American tree species have evolved over the last  $>2.8$  million years in the context of a rapidly changing climate marked by repeated glacial cycles. Some past climate changes in North America occurred rapidly with temperatures changing by  $>3^\circ\text{C}/\text{century}$  (Levesque et al. 1997), and at times drove glacial and interglacial transitions within one to several human generations (Harrison and Goñi 2010). Factors such as instabilities in North Atlantic circulation and heat transport, sea ice extent, and feedbacks among the oceans, atmosphere, and land surface drove these rapid changes (Clark et al. 2001b, Claussen 2009, Clark 2012), which were superimposed on longer glacial–interglacial trends controlled by orbital, greenhouse gas, and ice sheet change (COHMAP Members 1988, Braconnot et al. 2007, Shakun et al. 2012). Each interglacial and glacial period has featured unique climates compared to other periods (Bartlein 1997), and individual regions followed particular climate trajectories with many different combinations of seasonal temperatures and precipitation rates (Fig. 2; Braconnot et al. 2007, Shuman and Marsicek 2016). For example, a location in the modern mixed deciduous forest of Massachusetts would have experienced climates over the last 11,000 yr that today have analogous conditions in Manitoba, Minnesota, Wisconsin, Michigan, and New York before achieving its current state over the last 2000 yr (squares, Fig. 2G), whereas a location in central Minnesota may have experienced historical climates that today only extend from South Dakota to Manitoba (circles, Fig. 2G; Jacobson and Grimm 1986).

These climatic shifts involved substantial variation in both temperature and precipitation regimes. Changes in moisture availability may have been at least as important as temperature for creating some particularly high climate velocities (Loarie et al. 2009). Ice cores and tree-ring records not only reveal annual to decadal changes in temperatures of  $4^\circ\text{C}$  or more over the past millennium (Willis et al. 2000, Mann et al. 2009), but they also provide evidence of droughts



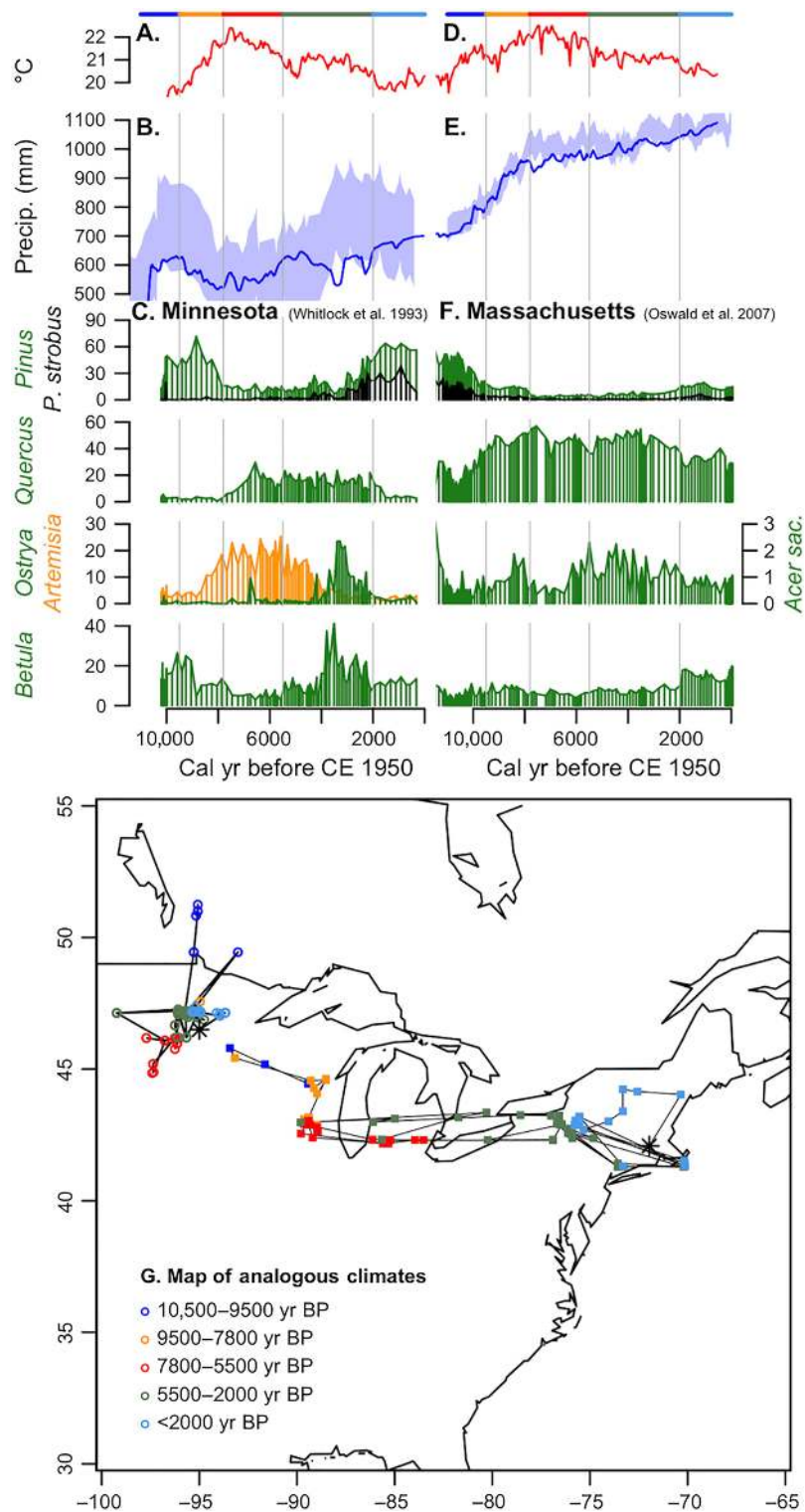


Fig. 2. Regional temperature and effective precipitation histories from the north-central and northeast United States (Shuman and Marsicek 2016) with Holocene fossil pollen percentages from representative sites in each

(Fig. 2. Continued)

region: Elk Lake, Minnesota (A–C; Whitlock et al. 1993), and Blood Pond, Massachusetts (D–F; Oswald et al. 2007). To evaluate how closely plant assemblages tracked the climate changes, effective precipitation was inferred both from regional lake-level changes (dark blue lines; Shuman and Marsicek 2016) and from fossil pollen percentages (light blue bands; Bartlein and Whitlock 1993, Marsicek et al. 2013). The map (G) shows the median locations of modern climates analogs for different times in the past at each location (based on regional paleoclimate data derived from Shuman and Marsicek 2016). The modern locations of the fossil pollen records are shown as stars. The analogous locations to past Minnesota climates are marked by circles and to past Massachusetts climates by squares, and indicate where a plant population would have had to move to grow under the same climate conditions through time. Color bars at the top of the time series indicate periods that correspond to the similarly colored locations on the map (G).

and multi-decade “megadroughts,” which were more severe than any experienced within the historic record of the past 150 yr (Cook et al. 2004). Tree species exhibited biotic velocities similar to the climate velocities, which is consistent with a direct linkage between climate and species distributions (Ordonez and Williams 2013).

These changes interacted with the multivariate climate requirements of tree taxa in different ways across various times and places (Webb 1986, Shuman et al. 2002b, Veloz et al. 2012). In many cases, the outcomes of continuous changes in the relationships between climate variables resulted in the formation of repeated periods of no-analog climates, which have no modern equivalents, and the development of novel mixtures of taxa (Jackson and Overpeck 2000, Williams and Jackson 2007). Yet, similar individual species–climate relationships have persisted despite different regional sequences of climate changes and vegetation phases (Fig. 2A–F) and substantially different climate velocities (Fig. 2G). For example, white pine (*Pinus strobus*) populations were most abundant in Massachusetts at ca. 11,000–9000 yr BP (black, Fig. 2F) when warm-season temperatures and effective annual precipitation were like central Minnesota today (Fig. 2G) where white pines only spread as the modern conditions developed in the last two millennia (black, Fig. 2C; Jacobson 1979, Whitlock et al. 1993, Oswald et al. 2007).

The fossil pollen record consistently demonstrates rapid movement of North American vegetation in response to millennial-scale climate variability, with little to no discernable lag between tree distributions and climate within the temporal limits of the sampling and dating resolution (~100 yr; Prentice et al. 1991, Jackson and

Overpeck 2000, Williams et al. 2002, Harrison and Goñi 2010, Jiménez-Moreno et al. 2010, Blonder et al. 2015). Blonder et al. (2017) propose that comparisons of climates inferred from fossil pollen and other independent lines of evidence can be used to assess the magnitudes of disequilibrium between plant communities and climate, and in multiple regions, such comparisons show a close relationship, which could only exist if the individual taxa had conservative niches and if their distributions did not substantially lag behind changes in their optimal climates. For example, pollen assemblages (e.g., blue bands in Fig. 2B, E) and lake-level changes (e.g., blue lines in Fig. 2B, E) indicate similar sequences and magnitudes of hydrologic changes during the Holocene, with only minor and non-significant differences in both the mid-continent (Bartlein and Whitlock 1993) and in the northeast United States (Marsicek et al. 2013).

Lags have most often been inferred only in the absence of independent climate data (Davis 1969, Davis et al. 1986), and the multivariate climate history, including simultaneous changes in seasonal temperatures and moisture balance, has rarely been adequately constrained (Ordonez and Williams 2013). Climate variables changed at heterogeneous rates during periods of dramatic climate shifts, and simultaneous consideration of tree distribution shifts relative to fast-changing and slow-changing variables has generally revealed that the rate of northward expansion during periods of glacial retreat closely paced the rate of climate change (Ordonez and Williams 2013). Yet, limited cases exist where historical contingencies including limited dispersal capacity, disturbance and successional histories, seed

sources, and available habitat have interacted with multivariate changes in climate to produce lagged responses of species distributions to climatic changes (Lyford et al. 2003, Gavin and Hu 2006, Gray et al. 2006, Berland et al. 2011). For example, western hemlock (*Tsuga heterophylla*) expanded within its interior range in the mountains of inland British Columbia >1000 yr after suitable temperatures developed, and climate envelope models continue to overpredict its modern distribution (Gavin and Hu 2006, Chase et al. 2008). This lag may represent the interactions of climate history with a topographically complex dispersal pathway, exclusion by fire, and the long lifespan of the species (Chase et al. 2008). Related processes may explain why Ordonez and Svenning (2016) detect that both past and present climate are important predictors of the diversity of traits of North American broadleaf trees. However, other similar lags originally attributed to slow dispersal, such as the slow dispersal of *Fagus grandifolia* across the Great Lakes region or into the northeast United States (e.g., Davis 1969, Davis et al. 1986), are most likely to be explained by multivariate climate changes and trajectories (Shuman et al. 2004).

Spatial and temporal scale may also be an important consideration in evaluating rates of change in tree distributions relative to climate change, as larger/longer resolutions will average out much of the heterogeneity in response rates that may be observed at smaller/shorter resolutions. Available evidence indicates that most North American tree distributions closely tracked climate change at centennial time scales, yet it is possible that dispersal limitations may have generated disequilibrium at sub-centennial time scales (Webb 1986, Prentice et al. 1991, Ordonez and Williams 2013). Adaptive potential, lifespan, and dispersal ability may all interact with climate change to generate different response rates across multiple time scales (Davis 1984). However, evaluation of tree communities relative to regional pools indicates a close match between community and regional responses throughout the late-Quaternary glacial–interglacial climate shifts at centennial time scales and both strongly reflect climatic influences, suggesting that similar rates of climate change responses were generated at both large and small spatial resolutions (Blonder et al. 2015).

Responses to rapid multivariate climate changes have generally involved changes in the abundance of locally extant taxa (Webb 1986), with leading and trailing edge populations responding at different rates. For many North American trees, the rate of northward expansion was faster than the rate of decline at southern edges, indicating greater climate sensitivity of northern populations (Ordonez and Williams 2013). These patterns produced accelerated shifts in tree distributions over large areas, such as when spruce (*Picea*) populations retreated from the northeast and north-central United States at ca. 11,700 yr BP at the end of the cold Younger Dryas interval (Lindbladh et al. 2007, Gonzales and Grimm 2009, Shuman et al. 2009b). Short dispersal distances from local microsites facilitated the rapid increases in species at their advancing margins (Bennett et al. 1991, Clark et al. 2001a, b, Williams et al. 2004, McLachlan et al. 2005). Rapid changes in North American moisture gradients, such as in response to the retreat of the Laurentide ice sheet by ca. 8000 yr BP, which dried western areas as eastern areas became humid (Fig. 2B, E), also contributed to strong west-to-east climate velocities (Fig. 2G) and to shifts in the distributions of key taxa, including white pine (Fig. 2F; Shuman et al. 2002a, Shuman and Marsicek 2016). In general, paleoecological evidence supports rapid changes in tree distributions that corresponded closely with climatic variability, and reveals a primary climatic control on the distributions of many North American tree species (Dean et al. 1984, Shuman et al. 2002b, 2004, Grimm et al. 2006, Yu 2007, Minckley et al. 2012, Ordonez and Williams 2013).

#### *Niche conservatism*

For the responses described above to have played out, the fundamental niche boundaries of many plant species were likely conserved over evolutionary time (Huntley et al. 1989, Jackson and Overpeck 2000). In fact, phylogenetic analyses have identified niche conservatism as a strong driver of richness patterns specifically among North American trees (Jaramilla-Correa et al. 2009, Qian et al. 2015). Low rates of diversification in North American plants relative to similar floristic regions imply a prominent strategy of ecological generalization, which may be



realized either through high phenotypic plasticity or through local adaptation (Davis and Shaw 2001, Xiang et al. 2004, Lavergne et al. 2010). Indeed, generalist species have a demonstrated ability to persist in the face of extreme climatic fluctuations and to spread rapidly in periods of favorable climate (Jackson et al. 2009). Generalization appears to have been promoted by frequent isolation during periods of glaciation, paired with recurrent long-distance gene flow and large ancestral populations (Willis et al. 2000, Jiménez-Moreno et al. 2010). These conditions supported strategies that enabled species to succeed in a variety of habitats, while at the same time preventing reproductive isolation (Jaramilla-Correa et al. 2009). Such a strategy may be typified by the history of lodgepole pine (*Pinus contorta*), which has one of the broadest climate niches of North American species (Williams 2006), and has persisted in many places in western North America through a wide range of climate changes after expanding its distribution rapidly after deglaciation (Cwynar and MacDonald 1987, Minckley et al. 2012). Yet, other taxa, such as *Pinus resinosa*, appear to have responded to frequent climatic changes by maintaining specific, narrow fundamental niches and, thus, only spread to a given location when the optimal conditions developed (Webb 1986, Huntley et al. 1989, Walter and Epperson 2001, Shuman et al. 2004). Such patterns are consistent with genetic pauperization resulting from isolation in small and distant glacial refugia (Jaramilla-Correa et al. 2009). While the precise genetic strategies utilized by North American trees in response to past climatic changes vary, niche conservatism prevailed across a wide variety of taxa, indicating limited genetic response to climatic changes. Diversification in North American trees, even in the presence of repeated periods of historical isolation, may have been hampered by long generation times, large populations, and high investment in reproduction. These traits enabled the persistence of North American trees through dramatic climate changes, yet required that responses involve increases and decreases in regional importance as their realized niche space changed with climate change (Veloz et al. 2012). Ultimately, evidence for stable climatic niches over time reflects the ability of North American tree species to respond rapidly to climate

changes via distribution changes. Species have generally responded either by tracking climatic changes rapidly (Williams et al. 2004) or by persisting in unique microsites within their ranges (McLachlan et al. 2005, Hampe and Jump 2011).

#### *Dispersal and colonization*

Rapid dispersal of tree species in response to climate appears to be a critical control on the timing of past distribution changes (Lyford et al. 2003, Shuman et al. 2004, 2009b, Gray et al. 2006, Nelson et al. 2006). The first major Northern Hemisphere glaciations at the beginning of the Quaternary probably acted as a selective filter on the flora of North America, favoring species with strong dispersal traits that allowed them to sufficiently track their optimal climate zones (Davis and Shaw 2001, Bennett 2004). In particular, extinctions at the beginning of the Pleistocene favored flora that were capable of responding to ice ages via migration (Svenning et al. 2015). Retreat of tree populations during glacial periods restricted species primarily to populations in southern regions of the continent, and dispersal from these southern populations, including infrequent yet important long-distance dispersal events, facilitated rapid range expansion during periods of deglaciation (Jackson and Overpeck 2000). The genetic structure of many North American tree species indicates that post-glacial expansion involved both gradual expansion of a migrating front and long-distance dispersal (Ibrahim et al. 1996, Petit et al. 1997, Bialozyt et al. 2006). Rapid post-glacial colonization generally appears to have been attained by both dispersal from southern populations and colonization from isolated northern refugial populations (Clark et al. 2001a, b, Ricklefs 2004, McLachlan et al. 2005). Refugial populations of *Picea* and *Pinus* taxa have been recorded at the edges of ice sheets in Alaska and western North America, and dispersal from these populations appears to match the relatively rapid rate of glacial retreat (Fastie 1995, Jackson and Overpeck 2000, Williams et al. 2004). In order to keep pace with glacial retreat, refugial populations readily and rapidly colonized newly available habitat.

Records of rapid post-glacial range expansion involving migration from southern populations and colonization from northern refugia in pace with glacial retreat suggest well-developed

mechanisms of dispersal and colonization among North American tree species. Strong dispersal mechanisms, such as high fecundity, high seed release height, dispersive seed traits (e.g., low mass, winged seeds), and rapid colonization ability can evolve in response to rapid climate changes and enable species to track climate closely, and these traits are evident in many North American tree species (Clark 1998, Davis and Shaw 2001, Thomas et al. 2001, Fenner and Thompson 2004, Aitken et al. 2008, Massot et al. 2008, Lavergne et al. 2010). Alternatively or in conjunction with rapid climate tracking, dispersal capacity can evolve to maintain disjunct metapopulations at regional scales, which is consistent with the occurrence of rapid dispersal from glacial refugial populations and the maintenance of genetic diversity within isolated refugial populations (Jaramilla-Correa et al. 2009, Lavergne et al. 2010, Kubisch et al. 2013). Low rates of diversification despite isolation of refugial populations indicate recurrent long-distance gene flow, particularly among some ancient genera such as *Abies*, *Picea*, *Pinus*, *Populus*, *Prunus*, and *Quercus*, reinforcing the high dispersal capacity of many North American tree species (Martinsen et al. 2001, Jaramilla-Correa et al. 2009). Overall, the ability of North American tree species to rapidly disperse and colonize habitat is consistent with previously reviewed evidence arguing that North American tree species exhibit traits and strategies that enable strong and rapid responses to climate.

#### *Individualistic species responses to climate*

Biotic interactions, particularly interspecific competition, have often been hypothesized as underlying drivers of contemporary tree distributions. Yet, historical context indicates little to no evidence for an independent role of interspecific interactions in shaping past tree distributions, bringing into question the potential for such factors to contribute to contemporary distributions. Due to rapid glacial cycles, formation of no-analog climates, and repeated instances of range expansion, contraction, and shuffling, North American tree species have rarely co-existed for substantial enough periods of time to drive evolution of niche partitioning or adaptation to co-occurring species (Case et al. 2005, Thompson 2005, Araújo et al. 2011), and contemporary

communities bear the imprint of historical mechanisms of species sorting (Ricklefs 2004, Wiens 2011; P. E. Copenhaver-Parry and D. M. Bell, *unpublished manuscript*). North American tree species have undergone repeated periods of community shuffling in response to past climate change, underscoring the individualistic responses to climate exhibited by tree species at millennial time scales (Jacobson et al. 1987, Graham and Grimm 1990, Williams et al. 2004).

Multivariate climate history drove the repeated disaggregation of existing communities as species responded to different dimensions of changing climate, resulting in repeated formation of locally to globally novel communities (Jackson and Overpeck 2000, Williams and Jackson 2007). Such communities persisted for short periods of time (e.g., *Betula–Ostrya* assemblages from ~4000 to 3000 yr BP in Minnesota, Whitlock et al. 1993; Fig. 2C) before again disaggregating in response to the next major climate fluctuation, resulting in a lack of opportunity for coevolution among species (Lavergne et al. 2010, Blois et al. 2013).

This frequent reshuffling along with limited biotic pressure for diversification is consistent with evidence for relatively low rates of diversification over time, and the lack of contemporary evidence for niche filling (Ricklefs 2004, Wiens 2011). This suggests that competition was not an important force structuring historic species distributions (Williams et al. 2004, Blois et al. 2014). In fact, past North American species associations can be overwhelmingly attributed to climatic limitations and, in some cases, dispersal, with little evidence for the influence of biotic interactions (Blois et al. 2014). However, biotic interactions may have exerted a secondary influence on some species distributions in finer-scale contexts. For example, the spread of temperate deciduous species along the prairie–forest ecotones of Minnesota’s Big Woods region was associated with climatic changes following the onset of the cold Little Ice Age (McAndrews 1968, Grimm 1984, Umbanhowar 2004, Shuman et al. 2009a), yet the finer-scale patterns of species spread were likely influenced by successional competition and fire regimes (Berland et al. 2011).

Ultimately, North American tree species appear to have responded individually to climate, forming stable associations among species only in association with suitable climate

conditions. The evolution of competitive or facilitative relationships among co-occurring species, therefore, appears to have had only a secondary, and often minimal, effect on species distributions. This evidence, combined with the historical context of rapidly fluctuating and variable climate, rapid distribution shifts, niche conservatism, and strong dispersal and colonization mechanisms, indicates that North American tree species have experienced conditions that favor strong climatic responses, resulting in primary climatic control on species distributions and maintaining a historic dynamic equilibrium between tree distributions and climate. However, we have noted several important counter-examples to these general conclusions, and some lines of evidence suggest that past conditions may have produced important legacies for North American trees such as delayed-range infilling (Svenning et al. 2015, Ordonez and Svenning 2016). Yet, past distributions and assemblages appear to be predictable based on modern realized climate niches (Fig. 2). Thus, we note that some unresolved inconsistencies remain in our understanding of past climatic responses and historical legacies.

## CONTEMPORARY EVIDENCE

Consistent with expectations generated from the paleoecological record, contemporary distributions of North American tree species are typically well predicted by climate at broad spatial scales (Rehfeldt et al. 2006, Morin et al. 2007, Boucher-Lalonde et al. 2012, Boisvert-Marsh et al. 2014, Morueta-Holme et al. 2015). In particular, the impact of temperature and precipitation extremes on phenology has been shown to limit distributions and generate sharp range boundaries (Pither 2003, Morin et al. 2007, Boucher-Lalonde et al. 2012). However, many species fail to occupy all climatically suitable space, and many species distributions are ringed by climatically suitable areas that remain unoccupied, indicating that alternative factors may also have important influences on species distributions (Fig. 3a). Most hypotheses regarding the factors driving disequilibrium of contemporary species distributions with climate emphasize the potential importance of biotic interactions, dispersal limitation, and natural disturbances (Fig. 3b–d;

e.g., Austin 2002, Case et al. 2005, Wiens 2011, Godsoe and Harmon 2012, Wisz et al. 2013, Araújo and Rozenfeld 2014, Svenning et al. 2014). All of these factors may exclude species from climatically suitable space, yet their tendency to do so over a large enough region and with consistent spatial structure to impact species distributions at a relevant scale of analysis has been questioned (Soberón and Nakamura 2009, Wiens 2011). Further, as reviewed earlier, the paleoecological record offers no strong evidence for a general importance of any of these factors on historic species distributions, which brings into question the likelihood that species would exhibit traits that facilitate a strong distribution-level response to any of these factors under current climate.

Indeed, increasing empirical evidence addressing each of these hypothesized factors suggests that the direct effects of biotic interactions, dispersal limitation, and disturbance on North American tree species distributions may be limited, particularly at the coarse spatial resolutions over which distributions are typically analyzed. Consideration of biotic interactions in species distribution models and range models of North American trees has generally failed to improve predictions beyond those made using bioclimatic factors alone, indicating that interactions may be too weak to scale up to the level of the distribution or that interactions are tightly correlated with climate (Copenhaver-Parry et al. 2016, Gutiérrez et al. 2016, Morueta-Holme et al. 2016; P. E. Copenhaver-Parry and Bell, *unpublished manuscript*). Similarly, dispersal limitation, in most instances, does not fully explain failure of species to migrate in concert with current rates of climate change (Woodall et al. 2009, Murphy et al. 2010, Zhu et al. 2012), though few studies have tested dispersal limitation directly. Disturbance appears to drive temporal instability in species distributions and may influence distributions in key contexts where disturbance regimes reach either particularly high or low frequencies, yet most of the effects of disturbance are not independent of climate (Coops et al. 2005, Franklin et al. 2005, Whitman et al. 2015). Distribution patterns expected to be generated by each of the above factors also deviate from observed species distributions, particularly when distributions are considered in climatic space (Fig. 3; P. E. Copenhaver-Parry and Bell, *unpublished manuscript*).

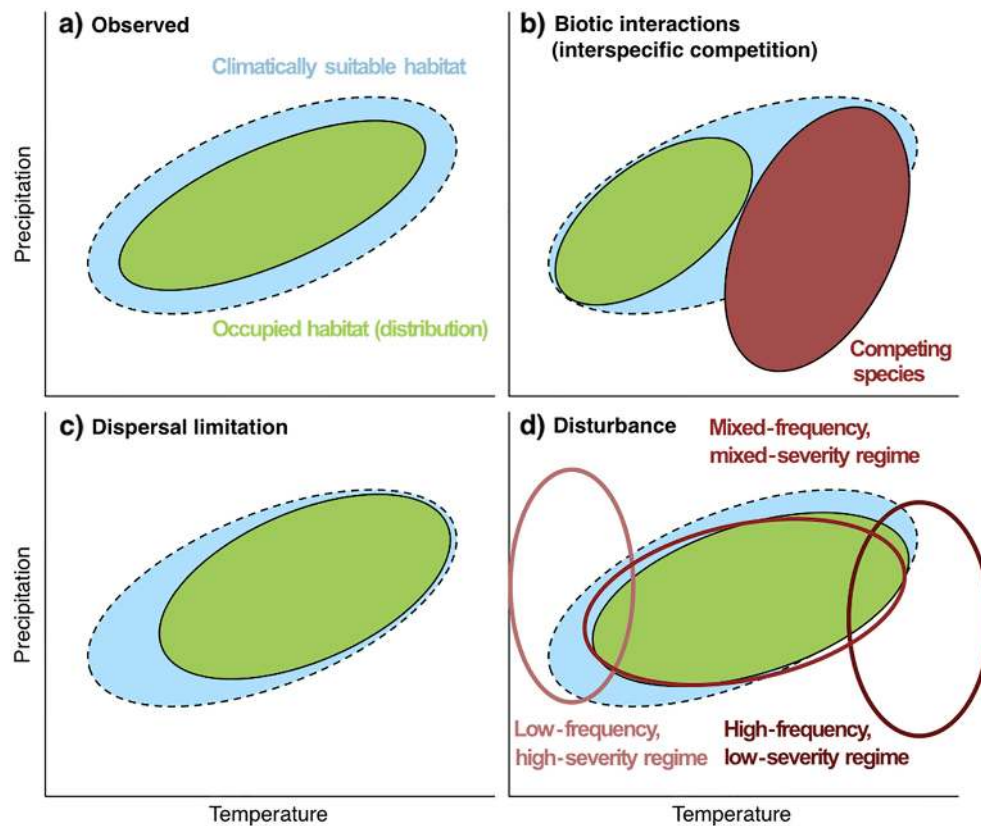


Fig. 3. Schematic representation of the expected impacts of interspecific competition (b), dispersal limitation (c), and disturbance (d) relative to observed patterns (a) on a hypothetical species distribution represented in climatic space. Many North American tree species distributions have been found to be ringed by unoccupied but climatically suitable habitat (a), which is inconsistent with the hypothesized effects of alternative ecological processes. While a variety of biotic interactions may impact species distributions in various ways, the most commonly investigated interaction, interspecific competition, is hypothesized to generate a pattern of exclusion from regions where the competing species occurs (b). The most apparent result of dispersal limitation would be failure of species to migrate in pace with climate change, which has generally moved in a poleward direction (c). Disturbance may generate temporal instability in species distributions, or may constrain species to habitats characterized by the disturbance regimes to which they are adapted (d), yet disturbance regimes are often driven by and thus closely correlated with climate.

Overall, the available evidence regarding the distributions of North American trees demonstrates that historical species distributions have responded primarily to climate and that contemporary distributions bear the imprints of interspecific biotic interactions, dispersal limitation, and disturbance only in limited contexts. This may be seen to confirm the long-held assumption that North American tree species distributions are driven primarily by climate (Woodward 1987), yet considerable evidence demonstrates that many species are failing to track

contemporary climate change (Woodall et al. 2009, Murphy et al. 2010, Zhu et al. 2012, Gray and Hamann 2013, Boisvert-Marsh et al. 2014, Dial et al. 2015, Serra-Diaz et al. 2015). To be sure, contemporary climate change differs from events observed in the Pleistocene (Malcolm et al. 2002, Aitken et al. 2008). Specifically, current rates of climate change exceed the rates of many past climate change events and species responses are currently being played out over a dramatically human-altered landscape (Corlett and Westcott 2013). While these differences may



generate patterns that differ from those observed in the past, integrating historical and contemporary evidence can provide an improved understanding of the processes that underlie such patterns. Available evidence suggests that alternative non-climatic factors may be important in explaining observed climate disequilibrium. To this end, we provide a broad treatment of the contemporary evidence addressing the influences of biotic interactions, dispersal limitation, and disturbance on tree distributions. Given the general lack of evidence for a widespread importance of these factors on contemporary North American tree distributions, we also review two alternative processes, life stage and human land use, that may contribute to explain disequilibrium and may be important considerations for generating projections of future distributions.

### *Biotic interactions*

Ecologists have long investigated the role of biotic interactions among communities at local extents, yet recent research trajectories have emphasized new tools and approaches to evaluate biotic interactions across the broader spatial scales at which species distributions are characterized, resulting in a high amount of research emphasis on the influence of biotic interactions on species distributions. Biotic interactions may include a variety of species relationships (i.e., predator–prey, herbivory, competition, facilitation, parasitism, microbial symbioses; see Van der Putten et al. 2010, Lankau et al. 2015, Katz and Ibáñez 2016), yet most research related to species distributions and biotic interactions has focused on interspecific interactions occurring within the same trophic level, such as competition and facilitation; our usage of the term “biotic interactions” throughout this review reflects that emphasis. Interspecific biotic interactions arise from resource–consumer dynamics operating between individual organisms, making them inherently local (Soberón and Nakamura 2009, McGill 2010, Clark et al. 2014, Sandel 2015). These local processes are theorized to scale up to the level of the species distribution by altering demographic rates and resultant population dynamics sufficiently to exclude species from regions of climatic suitability or to extend distributions beyond climatic limits (Svenning et al. 2014). When the sum and strength of such

interactions is sufficient and consistent across a large spatial extent, biotic interactions may produce effects that observably impact species distributions (Fig. 3; Araújo and Rozenfeld 2014, Godsoe et al. 2015, Sandel 2015). Because of inherent scale dependencies in the processes of biotic interactions and the scale of inference (species distribution), appropriate methods for evaluating the influence of biotic interactions on species distributions have remained unclear and inference from any one approach may be limited. Yet, when existing empirical evidence gleaned from a variety of approaches is taken as a whole, the collective findings demonstrate that biotic interactions appear to primarily impact patterns observed at local spatial scales for North American trees, and may only scale up to affect species distributions in rare contexts.

Species distributions may co-vary strongly across environmental gradients, yet patterns of covariance are overwhelmingly attributable to shared or divergent environmental responses, rather than biotic interactions, phylogenetic relatedness, or trait divergence (Clark et al. 2014, Morueta-Holme et al. 2016; P. E. Copenhaver-Parry and Bell, *unpublished manuscript*). In particular, joint species distribution models (Pollock et al. 2014) reveal a substantial contribution of climate to species co-occurrence patterns (Clark et al. 2014), while at the same time demonstrating that local processes, including biotic interactions, play a minimal role in explaining species co-occurrence (P. E. Copenhaver-Parry and Bell, *unpublished manuscript*). For example, *Abies lasiocarpa* and *Picea engelmannii* show a strong association across their distributions (Fig. 4a, b), and much of this association can be explained by shared responses to climate. *Abies lasiocarpa* and *P. engelmannii* associations may also bear the imprint of facilitation, although the contribution of this association to observed distribution patterns is minimal (Fig. 4c–f). Despite this weak biotic effect, *A. lasiocarpa* and *P. engelmannii* distributions exhibit a stronger influence of biotic interactions than other western tree species pairs, underscoring the overwhelming influence of climate on tree species distributions (P. E. Copenhaver-Parry and Bell, *unpublished manuscript*).

Biotic interactions appear to be most important in determining local composition patterns and stand dynamics, while broader-scale distribution

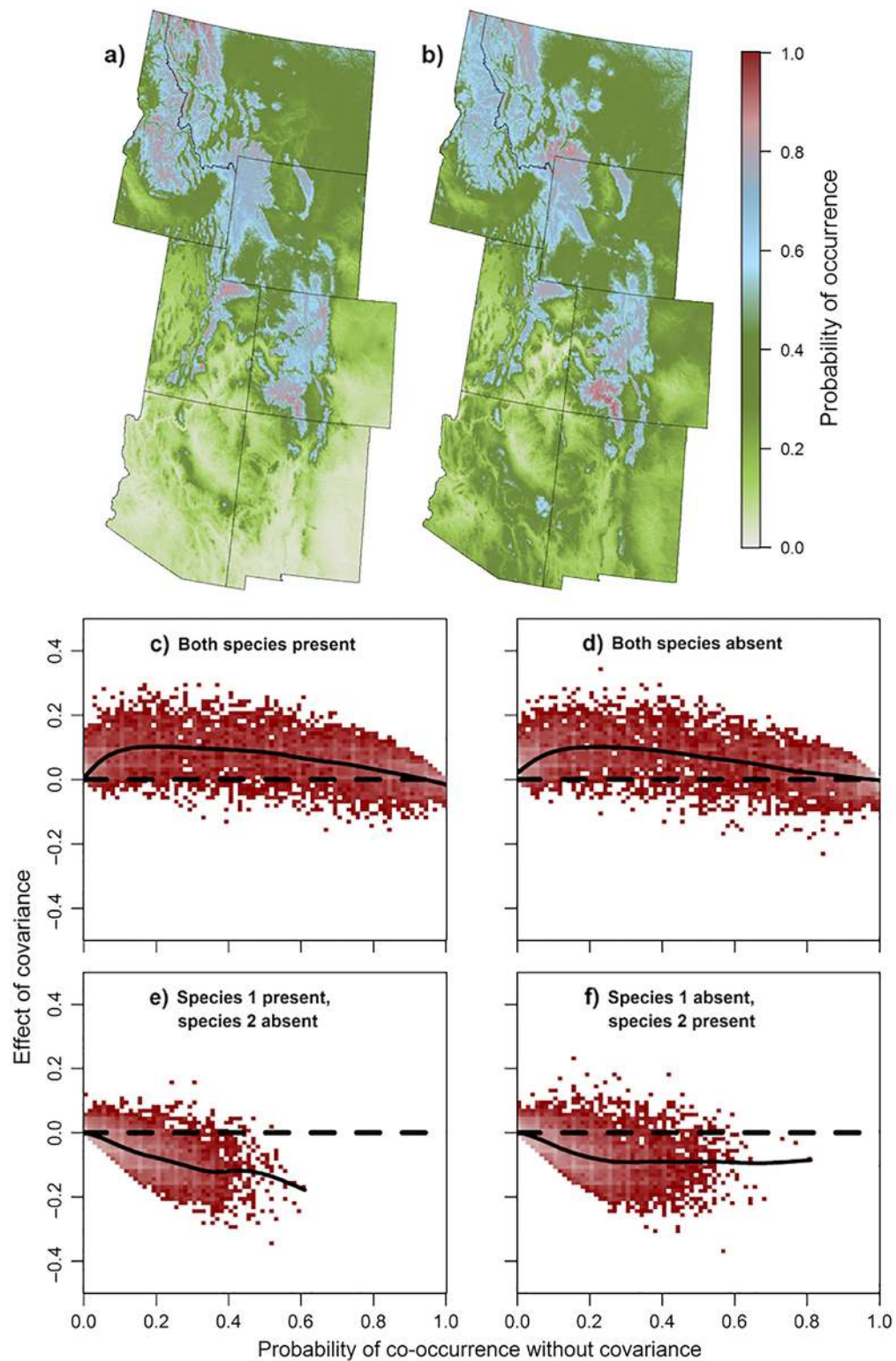


Fig. 4. Subalpine fir (a) and Engelmann spruce (b) distributions show significant overlap across their U.S. distributions in the states of Idaho, Montana, Wyoming, Utah, Colorado, Arizona, and New Mexico. When

(Fig. 4. Continued)

modeled using a Joint Species Distribution model (P. E. Copenhaver-Parry and Bell, *unpublished manuscript*), the predicted probability of occurrence for each species shows little difference when accounting for covariance between species and when excluding covariance (c–f). The dashed black line illustrates no difference between predicted probabilities of co-occurrence with and without covariance, while the solid black line characterizes the trend in the effect of covariance. For this species pair, which demonstrates a positive association, accounting for covariance among species slightly increases the probability that both species occur at a site (c) and that neither occur at a site (d), and slightly decreases the probability that one species will be present a site, while the other is absent (e, f).

patterns are overwhelmingly explained by climatic factors, even in studies that directly model the independent effects of local processes and regional climate (e.g., Gutiérrez et al. 2016). Biotic interactions have been shown to influence abundance patterns far more strongly than distributions in a variety of other plant systems and regions (Rouget et al. 2001, Boulangeat et al. 2012, Meier et al. 2010), and this may be a general pattern indicative of the averaging of weak, local interactions across the coarse spatial resolutions over which species distributions are analyzed (Pearson and Dawson 2003, Soberón and Nakamura 2009, Araújo and Rozenfeld 2014). For example, *Picea sitchensis* distributions are more accurately reproduced using regional bioclimatic variables than local parameters that account for biotic interactions, yet local parameters are necessary to accurately reproduce local species composition (Gutiérrez et al. 2016).

Climate has also been shown to have a significantly greater influence than competition on growth and performance at distribution limits, which play an important role in defining species distributions (Ettinger et al. 2011, Ettinger and HilleRisLambers 2013, Copenhaver-Parry and Cannon 2016). Specifically, tree performance at upper elevational edges is strongly related to cold temperatures and precipitation, while lower elevational limits may be determined by a combination of climate and regeneration failure, and competition fails to explain growth and performance declines in adult trees at both distributional limits (Ettinger et al. 2011, Ettinger and HilleRisLambers 2013, Copenhaver-Parry and Cannon 2016). Regeneration failure, however, could be influenced by the high sensitivity of seedlings to competition at lower distribution edges, which is consistent with evidence indicating that regeneration patterns of North American trees may be strongly influenced by biotic

interactions (Dobrowski et al. 2015, Godoy et al. 2015). Species distributions are typically only represented by the occurrence of adult individuals, and regeneration dynamics of North American trees across broad spatial scales have been little evaluated (but see Bell et al. 2013); these findings highlight the need for further investigation into the links between biotic interactions, regeneration dynamics, and distribution patterns and suggest that seedling distributions may reveal relationships between distributions and biotic interactions that may be masked when only adult individuals are considered (see *Life stage*).

Ultimately, existing empirical evidence indicates a minimal role for biotic interactions in generating the coarse spatial patterns that characterize species distributions. A variety of approaches have been used to mediate the complications associated with aggregation of local processes over coarse spatial resolutions (e.g., Gutiérrez et al. 2016), correlations between climate and biotic interactions (e.g., Pollock et al. 2014, Morueta-Holme et al. 2016), and variation in interactions across a species' distribution (e.g., Ettinger and HilleRisLambers 2013, Copenhaver-Parry and Cannon 2016), and climate has consistently emerged as the stronger driver of North American tree distributions. Recent climate-driven migrations of North American trees reveal that species range shifts do not appear to be impeded by the presence or absence of competitors, regardless of a species' competitive status (Boisvert-Marsh et al. 2014), indicating that shifts are driven largely by climate and not strongly influenced by competition. This is consistent with historical evidence indicating that past species responses to climate change were largely individualistic. Yet, accurately characterizing and predicting the impact of biotic interactions on future species distributions remains a difficult task and continues to represent a critical and

important challenge in ecology and biogeography. Overall, however, existing empirical evidence offers little evidence for a significant influence of biotic interactions on the contemporary distributions of North American trees.

### *Dispersal limitation*

Dispersal limitation has been accepted as a general constraint on plant distributions, particularly in the Northern Hemisphere (Svenning and Skov 2007, Gaston 2009, Hargreaves et al. 2014), yet surprisingly few direct empirical evaluations of its influence on North American tree distributions exist. Many North American tree species have relatively high fecundity, high seed release height, and dispersal syndromes that facilitate long-distance dispersal (Clark 1998, Fenner and Thompson 2004, Aitken et al. 2008), and all of these characteristics promote strong dispersal ability (Fenner and Thompson 2004). North American tree species are capable of dispersal over distances exceeding 200 m, particularly following disturbances (Turner et al. 1997, Romme et al. 2005, Wirth et al. 2008). Range shift studies of species in response to contemporary climate change have been the primary tool used to infer the role of dispersal, as dispersal distances are assumed to represent the dominant control on rates of plant movement (Corlett and Westcott 2013).

In general, range shifts of North American tree species are occurring at a pace that is slower than that of current climate velocity, yet comparable to post-glacial migration rates during the Holocene (Boisvert-Marsh et al. 2014). This is broadly indicated by limited seedling regeneration beyond current distribution edges. Seedling distributions in eastern U.S. forests indicate limited northward migration (Woodall et al. 2009), with little colonization beyond range margins (Murphy et al. 2010). Yet, many eastern North American species show strong signs of range contraction at both northern and southern boundaries (Woodall et al. 2009, Murphy et al. 2010, Zhu et al. 2012), which is inconsistent with the movement of suitable habitat under climate change and suggests that alternative processes beyond climate-driven migration lags may contribute to range shifts. Regeneration patterns in western U.S. forests also indicate range contraction, particularly along southern and western range margins, though regeneration failure has also been demonstrated

in core areas (Bell et al. 2013). Individual populations of western North American tree species have been shown to lag their 1961–1990 climatic niches by ~130 km in latitude or 60 m in elevation with particularly pronounced lags in the Rocky Mountains and boreal forests, indicating regeneration failure at both latitudinal and elevational distribution limits (Gray and Hamann 2013). While slow migration rates have often been interpreted as evidence of dispersal limitation, migration may be limited by alternative factors unrelated to dispersal such as limited seedling establishment (e.g., via seed production, seed predation, or abiotic conditions not conducive to establishment; Rooney et al. 2000, Bogdziewicz et al. 2016, Buechling et al. 2016, Larson and Funk 2016), and range shift studies rarely distinguish between these two processes (Clark et al. 1998). In fact, regeneration failure at range boundaries of eastern North American tree distributions was found to be unrelated to seed size and dispersal characteristics (Zhu et al. 2012), and dispersal ability has also failed to explain the range sizes of North American tree species (Morin and Chuine 2006).

Zhu et al. (2012) proposed that patterns among eastern North American tree species are likely related to human-caused habitat fragmentation. Habitat fragmentation has been shown to reduce species migration in both simulation (Kubisch et al. 2013) and empirical (Higgins et al. 2003) studies and is predicted to drastically reduce the rate of plant migration in response to contemporary climate change, particularly as landscapes become increasingly fragmented (Corlett and Westcott 2013, Lawler et al. 2013; see *Human land use*). While fragmented landscapes may present significant barriers to dispersal, North American tree species have historically demonstrated an ability to overcome even large dispersal barriers when given enough time (Jackson and Overpeck 2000, Gugger et al. 2008, Lesser and Jackson 2012). Another strong hypothesis for migration lags suggests that trees, which have particularly long generation times, are likely to exhibit episodic range shifts, with particularly long time lags in between migration episodes (Renwick and Rocca 2015). These episodes may be related to disturbances or periods of particularly suitable climatic conditions (Brown and Wu 2005, Boisvert-Marsh et al. 2014, Renwick and Rocca 2015), and may involve



establishment of disjunct colonizing populations, as has been observed for *Pinus ponderosa* in the western United States (Lesser and Jackson 2012).

Many North American tree species appear to occupy distributions that are completely ringed by unoccupied but climatically suitable areas (Fig. 3a; Boucher-Lalonde et al. 2012). The presence of suitable unoccupied habitat both north and south of current range margins indicates that failure to disperse northward (in the direction of current climate change) cannot fully explain disequilibrium of distributions with climate (Fig. 3c). This disequilibrium might indicate the presence of sink populations that lie outside of a species' climatic niche (i.e., the climatic space in which population growth is positive; Hutchinson 1957, Holt 2009), but to which propagules are capable of dispersing and establishing. Correlative niche models cannot properly exclude sink populations, and thus artificially expand a species' climatic niche by including sink populations (Boucher-Lalonde et al. 2012). Considering these methodological shortcomings, predicted unoccupied but suitable habitat may not reflect dispersal limitation, but may instead represent regions outside of a species' regeneration niche (Grubb 1977).

Transplant studies beyond species' ranges offer more direct evidence of whether distributions reflect niche limits or dispersal limitation (Gaston 2009, Hargreaves et al. 2014, Lee-Yaw et al. 2016). Jack pine (*Pinus banksiana*; Asselin et al. 2001), sugar maple (*Acer saccharum*; Kellman 2004), gambel oak (*Quercus gambelii*; Neilson and Wullstein 1983), paper birch (*Betula papyrifera*; Hobbie and Chapin 1998), and quaking aspen (*Populus tremuloides*; Hobbie and Chapin 1998) have all shown limited success when transplanted beyond their distributional limits, as evidenced by low germination success, low seedling survival, and/or failure to produce viable seed. These findings are consistent with the hypothesis that low germination and establishment success may limit the establishment of new populations more strongly than failure to disperse to new locations (Fenner and Thompson 2004), and indicate that distributional limits correspond with bioclimatic limits on growth and reproduction rather than dispersal limitation (Lee-Yaw et al. 2016).

However, some lines of evidence point to a more prominent role for dispersal limitation in shaping North American tree species distributions.

For example, low abundance of eastern North American trees near distribution edges corresponds with limited dispersal and low colonization probabilities beyond current distributions, indicating that low seed availability may contribute to distribution limits. Continued declines in abundance are projected to generate substantial and increasing migration lags over the next 100 yr (Iverson et al. 2004). Eastern tree species also appear to occupy broader climatic niches across elevational than latitudinal gradients, demonstrating a failure to reach potential latitudinal limits, and latitudinal and elevational limits have been directly correlated with dispersal mode and maximum height (Siefert et al. 2015). However, these findings could also be explained by the existence of high-elevation sink populations (Boucher-Lalonde et al. 2012), or a stronger influence of human land use at high latitudes relative to high elevations (see *Human land use*).

Overall, studies that directly evaluate the influence of dispersal limitation on North American tree species distributions are scarce; few studies have directly evaluated dispersal of propagules beyond distribution limits on a broad scale, and most available data conflate dispersal and establishment. Existing empirical evidence is not fully supportive of a general importance of dispersal limitation on distributions of North American trees. Yet, many species are currently failing to track movement in suitable habitat. These findings underscore the importance of further study into the mechanisms and causes of recruitment failure beyond distributional limits, which may clarify the role of dispersal limitation (see *Life stage*).

### Disturbance

Natural disturbance regimes are an important characteristic of North American forests and have undoubtedly played an important role in the evolutionary history of tree species (Hopper 2009, Mucina and Wardell-Johnson 2011, He et al. 2016). Disturbances such as fire, drought, insect outbreaks, and extreme weather events have large effects on North American forests (Dale et al. 2001), yet the impacts of such disturbances on species distributions remain unclear (Austin 2002, Le Roux et al. 2013). This may be because relatively few disturbances have sufficiently homogeneous effects across a large enough spatial extent

to be detectable at the spatial resolution of species distributions. For example, bark beetle outbreaks have decimated large areas of North American forests, but their effects are heterogeneous within a stand, with both live and dead trees remaining in affected areas (Meddens et al. 2012). Thus, while the impacts of such catastrophic outbreaks are large, they may only be detectable as changes in abundance, rather than changes in occurrence at the scale of the species distribution. In fact, many disturbances generate patchy landscape dynamics that are not detectable at the scale of species distributions (Liénard and Strigul 2016), with the notable exception of some fire regimes, which can remove species from large, continuous areas. Nevertheless, while the immediate effects of many disturbances may not always be large enough to impact species distributions, natural disturbances may provide opportunities for gradual changes in distribution patterns over time.

Specifically, disturbances may promote distribution shifts by reducing competition and providing favorable environmental conditions for previously excluded species to establish (Dale et al. 2001, Leithead et al. 2010). Abundant examples exist of species composition shifts on disturbed sites, yet the implications of altered establishment patterns for species distributions may not always be persistent. For example, the 1988 fires in Yellowstone National Park provided an opportunity for broad-scale establishment of aspen seedlings and an increase in aspen occurrence relative to pre-fire conditions (Turner et al. 2003, Romme et al. 2005). At the time, high aspen seedling densities were suggested to be indicative of a potential range expansion event, yet re-measurement of burned areas in subsequent years has shown that many aspen have been outcompeted by recovering lodgepole pine (Hansen et al. 2016), which has resumed its historical distribution in Yellowstone. Similarly, variable fire return intervals in California forests promote transient expansion of *Pinus coulteri* during long fire-free periods, yet a stable climatic regeneration niche, to which *P. coulteri* retreats following fire, is maintained under all fire return intervals (Franklin et al. 2005). While disturbance may interact with successional dynamics to drive temporal variation in species distributions, these effects may be mediated by the overriding impacts of climate over the longer temporal

scales and coarser spatial resolutions at which species distributions are typically characterized.

However, long-term stability may be disrupted when climate changes, and in such instances, disturbance may offer opportunities for distribution shifts to persist. For example, in the Sierra Nevada Mountains in California, low regeneration of subalpine and montane tree species following fire was simulated in response to a 2°C shift in temperature that made previously occupied locations unsuitable for germinating individuals (Loudermilk et al. 2013). Distribution shifts associated with disturbance have also been observed at the boreal–temperate forest ecotone in Canada, where treefall gaps in boreal species-dominated forests have provided opportunities for temperate tree species to establish and shift their distributions northward (Leithead et al. 2010). Nevertheless, in each of these cases, regeneration was still dependent upon climate. Disturbance may affect the timing of regeneration events, thereby shaping transient distribution dynamics, but the long-term persistence of regenerating species will still ultimately depend upon climatic suitability. In fact, disturbances such as fire and insect outbreaks are themselves highly correlated with and often controlled by climate, particularly when observed over broad spatiotemporal scales (Coops et al. 2005, Whitman et al. 2015). Fire in particular is synchronized across broad geographical regions by climate, and other underlying drivers including topography and fuels only appear to contribute to variation in fire frequency and severity at finer spatial scales (Westerling et al. 2006, Falk et al. 2007, Littell et al. 2010, Ireland et al. 2012).

There are, however, limited contexts in which disturbance frequency becomes decoupled from climatic controls on species distributions. Modeling studies have shown that climatic suitability of many North American angiosperm tree species extends into North American prairies, which are currently maintained as grasslands by frequent fires that exclude long-lived tree species (Bond et al. 2005). In the Black Hills of South Dakota, USA, fire maintains grasslands in regions that are climatically suitable for ponderosa pine, thus truncating the pine distribution relative to climatic equilibrium (King et al. 2013). Fire and grazing have also been shown to directly limit tree distributions at the mid-

continent prairie–forest boundary (Curtis 1959, Tilman et al. 2000, Bond et al. 2005) and at the lower treeline in the Rocky Mountains (Mast et al. 1997, 1998). Historic fire suppression by humans also appears to involve a threshold of non-climatic environmental change beyond which species distributions may shift in disequilibrium with climate. Fire suppression has led to expansion of closed-canopy forests dominated by oak and pine into previously open grasslands in the eastern United States (Nowacki and Abrams 2008, Rhemtulla et al. 2009), and encroachment of less fire-tolerant species, such as Douglas-fir (*Pseudotsuga menziesii*), hemlock (*T. heterophylla*), grand fir (*Abies grandis*), and white fir (*Abies concolor*) into historically pure ponderosa pine stands in the western United States (Coops et al. 2005). Fire suppression involves a drastic departure from natural disturbance regimes, and such strong human impacts may dissociate climate from other environmental factors influencing species distributions (see *Human land use*).

Many disturbance regimes may be insufficient to override long-term climatic controls on distributions of North American trees, yet it appears as though a threshold in disturbance frequency exists beyond which species distributions are maintained in long-term disequilibrium with climate, such as is observed at the prairie–forest boundary (Bond et al. 2005). These thresholds may become particularly important under continued climate change and associated increases in fire frequency and severity (Westerling et al. 2011). Colonization occurs slowly on sites experiencing large fires as propagules must disperse from adjacent unburned areas, with the exception of colonization by serotinous or sprouting species such as *P. contorta* (Turner et al. 1997, Harvey et al. 2016). Increasing fire frequency might prevent establishment on large burned patches if adjacent forests are burned before sufficient propagules can be supplied. These changes may interact with increased drought severity following fires to further limit recruitment as has been observed in burned forests in the Rocky Mountains (Harvey et al. 2016) and modeled in Sierra Nevada forests (Liang et al. 2016). Therefore, it is possible that the effects of disturbance on North American tree distributions may become increasingly important under

continued climate change. Overall, however, existing evidence indicates that disturbance generates temporal instability in tree species distributions, but may not override the effects of climate on distribution patterns except for in specific ecological contexts (Fig. 3d).

#### *Life stage*

While the majority of investigations seeking to understand the factors controlling tree distributions have considered primarily mature individuals, including those reviewed above, a growing body of evidence indicates that seedling characteristics may be more strongly related to distributional limits than adult characteristics (Jackson et al. 2009). The persistence and migration of tree species in a particular location depends upon successful regeneration (Clark et al. 2011, Bell et al. 2013, Máliš et al. 2016), which is likely to depend more on seedling establishment than on adult reproductive success. Seedlings generally show a greater sensitivity to climate and biotic factors than adult conspecifics, thus occupying much narrower niches (Cavender-Bares and Bazzaz 2000, Maher and Germino 2006, Jackson et al. 2009, Lenoir et al. 2009). In particular, seedlings are highly susceptible to periods of drought, owing to their poorly developed and shallow root systems (Fenner and Thompson 2004), and to competition, which is one of the most significant causes of tree seedling mortality (Lorimer et al. 1994, Fenner and Thompson 2004). The critical transition in environmental requirements and sensitivities in trees may occur between the seedling and sapling stage, thus implicating seedlings as particularly sensitive indicators of environmental controls on species distributions (HilleRisLambers et al. 2013, Máliš et al. 2016).

Several studies have documented a restricted climatic niche of western U.S. tree seedlings relative to adult conspecific niches, with the greatest differences occurring near distributional limits (Stohlgren et al. 1998, Bell et al. 2013, Dobrowski et al. 2015). In particular, seedling distributions are often most abundant in lower elevational regions of adult distributions (Stohlgren et al. 1998) and are constrained to sites beneath existing forest canopies where climate may be buffered (Dobrowski et al. 2015). Water availability appears to be the primary climatic constraint limiting seedling distributions, but biotic factors

may also play an important role (Dobrowski et al. 2015, McIntire et al. 2016). Specifically, aggregated regeneration patterns indicate that seedlings may rely on facilitation from parent plants and other adult conspecifics to escape exposure to unfavorable climate and competition (Fenner and Thompson 2004, Dobrowski et al. 2015, McIntire et al. 2016). Yet, these static spatial patterns of seedling and adult distributions mask long-term fluctuations in spatial patterns of seedling establishment that may also contribute to current distribution limits.

Due to broader niches and greater environmental tolerance, mature trees are capable of persisting under conditions that prevent continual establishment of seedlings (Johnstone et al. 2010). Short periods of favorable climate or reduced biotic pressure following disturbance may provide opportunities for regeneration pulses, during which seedlings are capable of establishing in otherwise sub-optimal habitats. Episodic recruitment appears to be the normal pattern of establishment for most tree species (Jackson et al. 2009). In tree species occurring in the Rocky Mountains, episodic recruitment events have been shown to maintain long-term distribution limits for high-elevation species (Stohlgren et al. 1998), to expand distributions to new, unoccupied locations (Lesser and Jackson 2012), and to alter species composition, shifting adjacent species distributions toward climatic equilibrium (Johnstone et al. 2010). While disturbances may provide opportunities for episodic recruitment events (Black and Bliss 1980), climate ultimately determines establishment success and persistence of seedlings following disturbance (Harvey et al. 2016). For example, recruitment pulses of fire-adapted ponderosa pine in the southwestern United States are strongly correlated with pluvial periods, which not only reduces climatic stresses on seedlings, but also reduces fire frequency, allowing sufficient time for successful establishment (Brown and Wu 2005). Serra-Diaz et al. (2015) identified a similar pattern of regeneration pulses in Mediterranean forests within the California Floristic Province, and suggest that such patterns may typically go undetected when analyzing species distributions against long-term average climate trends. The species in their study responded strongly to climatic fluctuations and were able to take advantage of very short windows of climatic

suitability to establish. These studies caution that while adult tree species distributions may not appear to occur in equilibrium with contemporary climate, climate may still be the dominant control on species distributions by determining when and where seedlings can establish. However, due to the episodic nature of seedling establishment, static evaluations of seedling distributions relative to adult distributions may also fail to reflect long-term climatic controls on tree species distributions.

Seedlings are also particularly sensitive to biotic interactions, and the influence of competition and facilitation on seedling establishment may contribute to explain North American tree species distributions. Shielding of wind and radiation by neighboring trees facilitates seedlings at treeline and appears to override the effects of temperature on seedling establishment and growth, thereby determining the upper elevational limits of tree distributions occurring at treeline (McIntire et al. 2016). While biotic interactions generally fail to explain elevational distribution limits of adult trees and saplings, seedlings may be particularly sensitive to competition at lower distributional limits, and this may explain elevational distribution patterns that do not appear to be determined by climate (HilleRisLambers et al. 2013).

In eastern North American forests, tree seedlings exhibit a trend of increasingly strong negative density dependence toward their southern distributional limits, and this trend is strongly correlated with recruitment potential (Godoy et al. 2015). Similarly, eastern North American seedlings exhibit strong positive density dependence at northern distributional limits, indicating that facilitation may be an important mechanism promoting seedling establishment in more stressful climates. Yet, while biotic interactions certainly appear to contribute to the distribution patterns of eastern North American tree seedlings, climate sensitivity, particularly to seasonal freezing temperatures, still appears to be the dominant factor explaining seedling recruitment patterns (Godoy et al. 2015). Furthermore, seedlings can show evidence of local adaptation to combinations of temperature and moisture availability (Eickmeier et al. 1975), which can enable new climatic conditions to be suitable to a given species generally but not to the extant



populations of seedlings in a given area. If so, disequilibrium could emerge in areas where the species should be present, but where suitable populations have not yet established (Davis and Shaw 2001, Etterson and Shaw 2001).

These findings suggest that climate may be the overriding control on seedling establishment, and thus distribution limits of North American tree species, and biotic interactions may exert a secondary effect. However, in a recent study of the distribution of regenerating trees in California forests, Serra-Diaz et al. (2015) found no evidence for a strong relationship between regeneration and climate. Management activities associated with human land use appeared to be more important in explaining regeneration patterns in this region, though this hypothesis has not been fully explored. In general, however, the available evidence indicates that the climatic sensitivity of seedlings may play a particularly important role in defining tree distributions, yet few studies have directly evaluated their specific role, likely owing to the difficulty of capturing recruitment trends that occur over broad spatial and temporal scales. We posit that by devoting a greater amount of research focus to the role of seedlings, many apparent and unexplained inconsistencies regarding current distribution patterns of North American trees may be resolved.

#### *Human land use*

Human land use has been suggested to underlie disequilibrium of North American tree distributions with climate (e.g., Van der Putten 2012, Zhu et al. 2012, Corlett and Westcott 2013), but few analyses have tested its influence explicitly. Clearly, forest clear cutting, agricultural conversion, or exurban expansion will remove trees from climatically suitable regions and truncate their distributions, yet the extent to which such practices have impacted distributions has seldom been explicitly quantified, making it difficult to generalize on the relative importance of human land use for contemporary tree distributions. Nevertheless, observations of range shifts under climate change are providing increasing opportunities to document the effects of human activities on tree species distributions.

For example, the slow migration rates of many tree species relative to the rate of climate change have been attributed to human-caused habitat

fragmentation in several studies (Honnay et al. 2002, Scheller and Mladenoff 2008, Serra-Diaz et al. 2015). Habitat fragmentation directly reduces seed dispersal distance and increases the probability that dispersed seeds land in unfavorable sites, thus preventing species from spreading into all climatically suitable regions (Honnay et al. 2002, Higgins et al. 2003, Van der Putten 2012). This effect has been modeled directly for North American tree species: In a simulation of migration patterns of 22 tree species in northern Wisconsin, USA, landscape fragmentation caused by human activities was shown to limit effective seed dispersal, prevent seedling establishment, and to prevent species from moving in equilibrium with climate (Scheller and Mladenoff 2008). Human land use may also promote upslope range shifts by providing microrefugial habitats that allow species to establish above natural distribution limits, such as has been observed along mountain roads (Lembrechts et al. 2016).

In other cases, cessation of human activities has allowed species with historically truncated distributions to slowly equilibrate with climate. These distribution expansions are often associated with less-intensive forest harvesting and reforestation of agricultural land, which represents the dominant land-cover change in the United States throughout the 19th and 20th centuries (Ramankutty and Foley 1999). Forest expansion onto abandoned agricultural sites has been documented across the United States, from western North America (Loudermilk et al. 2013), to the central United States (Rhemtulla et al. 2009), to eastern North America (Raup 1966, Cavallin and Vasseur 2009, Thompson et al. 2011). Colonization onto former agricultural land is limited by low germination success, resulting in relatively slow expansion (Cavallin and Vasseur 2009). Thus, many species whose distributions were historically affected by extensive agricultural practices are probably still not in equilibrium with climate, despite substantial land abandonment. In fact, recovery of forests following agricultural abandonment has produced strikingly different tree distributions at landscape to regional scales (Foster et al. 1998, Fuller et al. 1998).

Patterns of forest expansion following human land abandonment may occur particularly rapidly in mountainous regions, where short

dispersal distances allow for rapid movement. This phenomenon has been documented in European mountain ranges, where recent cessation of human activities at high elevations has allowed the treeline to expand upslope in many regions, and changes in treeline associated with land use have occurred far more rapidly than those associated with climate (Gehrig-Fasel et al. 2007, Palombo et al. 2013, Ameztegui et al. 2015). In North America, human activities are often concentrated at lower elevations (Van der Putten 2012). In the northeast United States, patterns of downslope shifts in boreal forests could reflect recovery of historic distributions following the cessation of decades of selective harvesting of red spruce at lower-elevation edges (Foster and D'Amato 2015).

Human alteration of natural disturbance regimes may also, in some cases, have drastic impacts on tree distributions. For example, most eastern North American tree distributions may be in disequilibrium with climate due to human fire management throughout the 19th century, and current distribution patterns have been proposed to reflect a history of fire suppression rather than climatic control (Nowacki and Abrams 2008). However, paleoecological datasets indicate increased rather than reduced burning after European settlement, making the disturbance history of eastern U.S. forests unclear (Parshall and Foster 2002, Parshall et al. 2003). As reviewed above, fire suppression may also allow for encroachment of forest species into grasslands, thus expanding tree distributions beyond their historical limits (Coops et al. 2005, Nowacki and Abrams 2008, Rhemtulla et al. 2009).

Aside from these few examples, the impacts of human land use on broad-scale species distributions have been little investigated, particularly in North American forests. Studies in European ecosystems, where human impacts are more prominent, have generally found that the effects of land use on species distributions are small relative to the effects of climate, but key land-use types such as agriculture may be important in predicting plant distributions (Pearson et al. 2004, Thuiller et al. 2004, Ay et al. 2016). Existing evidence indicates that human land use may also be an important factor limiting the distributions of North American tree distributions relative to climatic suitability. Additional research is needed

to determine the precise contexts in which human land use may play a significant role in constraining species distributions, and which distributions reflect these influences most strongly. Ultimately, improved efforts to incorporate metrics of human land use into species distribution models and range models are needed, which will help to clarify the factors controlling species distribution patterns.

## SYNTHESIS AND CONCLUSIONS

In this review, we demonstrate how ecological and evolutionary history provides a powerful context for understanding contemporary distribution patterns. The history of North American tree species distributions indicates that species traits have been shaped within an environment of extreme climate variability and rapidly shifting distributions. Species have responded to past climatic changes rapidly and individually, and past distribution patterns and shifts can be explained primarily by climate. This historical legacy would be expected to select for species and traits that continue to respond predominantly to climate. Our review of contemporary distribution patterns indicates that contemporary North American tree distributions are largely consistent with historical legacy in that biotic interactions, dispersal limitation, and disturbance only appear to exert secondary effects on species distribution, yet current distributions exhibit disequilibrium with climate. However, we acknowledge that evidence regarding these factors is incomplete and further research may reveal previously unidentified relationships. Specifically, few studies have evaluated the role of interactions across trophic levels (but see Moorcroft et al. 2006, Van der Putten et al. 2010, Katz and Ibáñez 2016) or have attempted to distinguish between dispersal limitation and failure to establish. The role of disturbance has received little attention at spatial scales relevant to species distributions, but available evidence suggests that climate may override the effects of disturbance with the exception of specific contexts where thresholds in disturbance frequencies are crossed. Human modification of habitat and disturbance regimes may contribute to the apparent disequilibrium of tree distributions with contemporary climate and generate new responses that

cannot be predicted from species' ecological and evolutionary history. Disequilibrium may also be explained by differential responses of seedlings to climate, disturbance, and biotic interactions relative to adult conspecifics.

While integration of historical and contemporary evidence can provide a reliable understanding of the factors currently influencing North American tree species distributions, climate change may generate new and unexpected responses in the future. Historical events have undoubtedly shaped the traits that determine current species responses, yet it is possible that future climate change will drive adaptation to new conditions and unexpected responses will emerge as a result (Aitken et al. 2008). North American trees possess particularly high within-population genetic diversity and high gene flow, which may facilitate rapid adaptation to new environmental conditions via natural selection (Rehfeldt et al. 1999, Aitken et al. 2008, Liepe et al. 2016). At the same time, North American tree species exhibit steep geographic clines that are associated with variable responses to extreme environmental conditions, such as drought and frost, across populations (Rehfeldt et al. 1999, Liepe et al. 2016, Montwé et al. 2016). Local adaptation of populations to unique, local climates may generate variable climate change responses across a species' range, and recent evidence suggests that locally adapted traits may not be tightly correlated with temperature gradients (Liepe et al. 2016), adding an additional element of uncertainty to expected species responses. We do not dedicate significant consideration to genetic adaptation in this review, as a thorough review of the issue is provided elsewhere (Aitken et al. 2008), yet it is important to recognize that future climate change responses may not be fully predictable from past selective pressures.

We also emphasize that this review sought to characterize general trends across broad spatiotemporal scales and a diverse group of species, and a variety of different responses may be observed when evaluating individual species at finer spatial or temporal scales. As noted earlier, climatic disequilibrium may be particularly apparent at finer temporal scales in response to disturbance or pulsed regeneration dynamics, and biotic interactions may affect abundance patterns observed at finer spatial scales. The precise

importance of each of these factors will also vary according to species life history and the particular ecological context, especially when the high genetic diversity of North American tree species is considered. Phylogeographic evidence indicates that genetic discontinuities have formed five distinct geographic regions among North American trees (eastern North America, Boreal North America, Pacific Northwest, California Floristic Province, North and Central Mexico; Jaramilla-Correa et al. 2009). Our review collated species across these regions in an attempt to identify general trends as consideration of each in isolation was beyond our scope, but studies emphasizing individual regions or species will also be important in providing a more robust understanding of the drivers of North American tree species distributions.

We conclude by arguing that a consistent conceptual framework of North American tree species distributions must not only consider historical legacy, but must also address the influences of differences in life stage along with the impacts of human land use. Future species distributions may well be shaped by the ability of tree seedlings to establish in human-modified habitat, which may drive marked disequilibrium of species distributions with climate. Such considerations are crucial, as our understanding of the factors and mechanisms underlying species distributions will determine our ability to accurately predict future changes in species distributions, and to recommend management and conservation strategies that will effectively protect biodiversity.

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## LITERATURE CITED

Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or

- extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1:95–111.
- Ameztegui, A., L. Coll, L. Brotons, and J. M. Ninot. 2015. Land-use legacies rather than climate change are driving the recent upward shift of the mountain tree line in the Pyrenees. *Global Ecology and Biogeography* 25:263–273.
- Araújo, M. B., R. G. Pearson, and C. Rahbek. 2005. Equilibrium of species' distributions with climate. *Ecography* 28:693–695.
- Araújo, M. B., and A. Rozenfeld. 2014. The geographic scaling of biotic interactions. *Ecography* 37:406–415.
- Araújo, M. B., A. Rozenfeld, C. Rahbek, and P. A. Marquet. 2011. Using species co-occurrence networks to assess the impacts of climate change. *Ecography* 34:897–908.
- Asselin, H., M.-J. Fortin, and Y. Bergeron. 2001. Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Quebec boreal forest. *Forest Ecology and Management* 140:29–37.
- Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. *Ecological Modelling* 157: 101–118.
- Ay, J.-S., J. Guillemot, N. Martin-StPaul, L. Doyen, and P. Leadley. 2016. The economics of land use reveals a selection bias in tree species distribution models. *Global Ecology and Biogeography* 26:65–77.
- Bartlein, P. J. 1997. Past environmental changes: characteristic features of Quaternary climate variations. Pages 11–29 in P. B. Huntley, P. W. Cramer, P. A. V. Morgan, P. H. C. Prentice, and D. J. R. M. Allen, editors. *Past and future rapid environmental changes*. NATO ASI Series 47. Springer, Berlin, Germany.
- Bartlein, P. J., and C. Whitlock. 1993. Paleoclimatic interpretation of the Elk Lake pollen record. *Geological Society of America Special Papers* 276: 275–294.
- Bell, D. M., J. B. Bradford, and W. K. Lauenroth. 2014. Early indicators of change: Divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography* 23:168–180.
- Bennett, K. D. 1990. Milankovitch cycles and their effects on species in ecological and evolutionary time. *Paleobiology* 16:11–21.
- Bennett, K. D. 2004. Continuing the debate on the role of Quaternary environmental change for macroevolution. *Philosophical Transactions of the Royal Society B* 359:295–303.
- Bennett, K. D., P. C. Tzedakis, and K. J. Willis. 1991. Quaternary refugia of north European trees. *Journal of Biogeography* 18:103–115.
- Berland, A., B. Shuman, and S. Manson. 2011. Simulated importance of dispersal, disturbance, and landscape history in long-term ecosystem change in the big woods of Minnesota. *Ecosystems* 14:398–414.
- Bialozyt, R., B. Ziegenhagen, and R. J. Petit. 2006. Contrasting effects of long distance seed dispersal on gene diversity during range expansion. *Journal of Evolutionary Biology* 19:12–20.
- Black, R. A., and L. C. Bliss. 1980. Reproductive ecology of *Picea Mariana* (Mill.) BSP., at tree line near Inuvik, Northwest Territories, Canada. *Ecological Monographs* 50:331–354.
- Blois, J. L., et al. 2014. A framework for evaluating the influence of climate, dispersal limitation, and biotic interactions using fossil pollen associations across the late Quaternary. *Ecography* 37:1095–1108.
- Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan. 2013. Climate change and the past, present, and future of biotic interactions. *Science* 341:499–504.
- Blonder, B., et al. 2015. Linking environmental filtering and disequilibrium to biogeography with a community climate framework. *Ecology* 96:972–985.
- Blonder, B., et al. 2017. Predictability in community dynamics. *Ecology Letters* 20:293–306.
- Bogdziewicz, M., E. Crone, M. A. Steele, and R. Zwolak. 2016. Effects of nitrogen deposition on reproduction in a masting tree: Benefits of higher seed production are trumped by negative biotic interactions. *Journal of Ecology* 105:310–320.
- Boisvert-Marsh, L., C. Périé, and S. De Blois. 2014. Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. *Ecosphere* 5:1–33.
- Bond, W. J., F. I. Woodward, and G. F. Migley. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165:525–538.
- Boucher-Lalonde, V., A. Morin, and D. J. Currie. 2012. How are tree species distributed in climatic space? A simple and general pattern. *Global Ecology and Biogeography* 21:1157–1166.
- Boulangeat, I., D. Gravel, and W. Thuiller. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters* 15:584–593.
- Braconnot, P., et al. 2007. Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum – Part 1: experiments and large-scale features. *Climate of the Past* 3:261–277.
- Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* 27:597–623.
- Brown, P. M., and R. Wu. 2005. Climate and disturbance forcing of episodic tree recruitment in a



- southwestern ponderosa pine landscape. *Ecology* 86:3030–3038.
- Buechling, A., P. H. Martin, C. D. Canham, W. D. Sheperd, and M. A. Battaglia. 2016. Climate drivers of seed production in *Picea engelmannii* and response to warming temperatures in the southern Rocky Mountains. *Journal of Ecology* 104:1051–1062.
- Case, T. J., R. D. Holt, M. A. McPeck, and T. H. Keitt. 2005. The community context of species' borders: ecological and evolutionary perspectives. *Oikos* 108:28–46.
- Cassini, M. H. 2011. Ecological principles of species distribution models: the habitat matching rule. *Journal of Ecology and Biogeography* 38:2057–2065.
- Cavallin, N., and L. Vasseur. 2009. Red spruce forest regeneration dynamics across a gradient from Acadian forest to old field in Greenwich, Prince Edward Island National Park, Canada. *Plant Ecology* 201:169–180.
- Cavender-Bares, J., and F. A. Bazzaz. 2000. Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia* 124:8–18.
- Chase, M., C. Bleskie, I. R. Walker, D. G. Gavin, and F. S. Hu. 2008. Midge-inferred Holocene summer temperatures in Southeastern British Columbia, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 257:244–259.
- Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist* 152:204–224.
- Clark, J. S., et al. 2001. Reid's paradox of rapid plant migration. *BioScience* 48:13–24.
- Clark, J. S., D. M. Bell, M. H. Hersh, and L. Nichols. 2011. Climate change vulnerability of forest biodiversity: climate and competition tracking of demographic rates. *Global Change Biology* 17:1834–1849.
- Clark, J. S., A. E. Gelfand, C. W. Woodall, and K. Zhu. 2014. More than the sum of the parts: forest climate response from joint species distribution models. *Ecological Applications* 24:990–999.
- Clark, J. S., M. Lewis, and L. Horvath. 2001*b*. Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist* 157:537–554.
- Clark, P. U., S. J. Marshall, G. K. C. Clarke, S. W. Hostetler, J. M. Licciardi, and J. T. Teller. 2001*a*. Freshwater forcing of abrupt climate change during the last glaciation. *Science* 293:283–287.
- Clark, P. U., et al. 2012. Global climate evolution during the last deglaciation. *Proceedings of the National Academy of Sciences USA* 109:E1134–E1142.
- Claussen, M. 2009. Late Quaternary vegetation-climate feedbacks. *Climate of the Past* 5:203–216.
- COHMAP Members. 1988. Climatic changes of the last 18,000 years: observations and model simulations. *Science* 24:1043–1052.
- Cook, E. R., C. A. Woodhouse, C. M. Eakin, D. M. Meko, and D. W. Stahle. 2004. Long-term aridity changes in the western United States. *Science* 306:1015–1018.
- Coops, N. C., R. H. Waring, and B. E. Law. 2005. Assessing the past and future distribution and productivity of ponderosa pine in the Pacific Northwest using a process model: 3-PG. *Ecological Modelling* 183:107–124.
- Copenhaver-Parry, P. E., S. E. Albeke, and D. B. Tinker. 2016. Do community-level models account for the effects of biotic interactions? A comparison of community-level and species distribution modeling of Rocky Mountain conifers. *Plant Ecology* 217:533–547.
- Copenhaver-Parry, P. E., and E. Cannon. 2016. The relative influences of climate and competition on tree growth along montane ecotones in the Rocky Mountains. *Oecologia* 182:13–25.
- Corlett, R. T., and D. A. Westcott. 2013. Will plant movements keep up with climate change? *Trends in Ecology and Evolution* 28:482–488.
- Curtis, J. T. 1959. The vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press, Madison, Wisconsin, USA.
- Cwynar, L. C., and G. M. MacDonald. 1987. Geographical variation of lodgepole pine in relation to population history. *American Naturalist* 129:463–469.
- Dale, V. H., et al. 2001. Climate change and forest disturbances. *BioScience* 51:723–734.
- Davis, M. B. 1969. Climatic changes in southern Connecticut recorded by pollen deposition at Rogers Lake. *Ecology* 50:409–422.
- Davis, M. B. 1984. Climatic instability, time lags, and community disequilibrium. Pages 269–284 in J. Diamond and T. J. Case, editors. *Community Ecology*. Harper and Row, New York, New York, USA.
- Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292:673–679.
- Davis, M. B., K. D. Woods, S. L. Webb, and R. P. Futyma. 1986. Dispersal versus climate: expansion of *Fagus* and *Tsuga* into the upper Great Lakes region. *Plant Ecology* 67:93–104.
- Dean, W. E., J. P. Bradbury, R. Y. Anderson, and C. W. Barnosky. 1984. The variability of Holocene climate change: evidence from varved lake sediments. *Science* 226:1191–1194.
- Dial, R. J., T. S. Smeltz, P. J. Sullivan, C. L. Rinas, K. Timm, J. E. Ceck, S. C. Tobin, T. S. Golden, and E. C. Berg. 2015. Shrub-line but not treeline advance matches climate velocity in montane ecosystems of south-central Alaska. *Global Change Biology* 22:1841–1856.

- Dobrowski, S. Z., A. K. Swanson, J. T. Abatzoglou, Z. A. Holden, H. D. Safford, M. K. Schwartz, and D. G. Gavin. 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species. *Global Ecology and Biogeography* 24:917–927.
- Eickmeier, W., M. Adams, and D. Lester. 1975. Two physiological races of *Tsuga canadensis* in Wisconsin. *Canadian Journal of Botany* 53:940–951.
- Etterson, J. R., and R. G. Shaw. 2001. Constraints to adaptive evolution in response to global warming. *Science* 294:151–154.
- Ettinger, A. K., K. R. Ford, and J. HilleRisLambers. 2011. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology* 92:1323–1331.
- Ettinger, A. K., and J. HilleRisLambers. 2013. Climate isn't everything: Competitive interactions and variation by life stage will also affect range shifts in a warming world. *American Journal of Botany* 100:134–1355.
- Falk, D. A., C. Miller, D. McKenzie, and A. E. Black. 2007. Cross-scale analysis of fire regimes. *Ecosystems* 10:809–823.
- Fastie, C. L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology* 76:1899–1916.
- Fenner, M., and K. Thompson. 2004. *The ecology of seeds*. Cambridge University Press, Cambridge, UK.
- Foster, J. R., and A. W. D'Amato. 2015. Montane forest ecotones moved downslope in northeastern US in spite of warming between 1984 and 2011. *Global Change Biology* 21:4497–4507.
- Foster, D., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems* 1:96–119.
- Franklin, J., A. D. Syphard, H. S. He, and D. J. Mladenoff. 2005. Altered fire regimes affect landscape patterns of plant succession in the foothills and mountains of southern California. *Ecosystems* 8:885–898.
- Fuller, J. L., D. R. Foster, J. S. McLachlan, and N. Drake. 1998. Impact of human activity on regional forest composition and dynamics in Central New England. *Ecosystems* 1:76–95.
- Gaston, K. J. 2009. Geographic range limits: achieving synthesis. *Proceedings of the Royal Society B* 276:1395–1406.
- Gavin, D. G., and F. S. Hu. 2006. Spatial variation of climatic and non-climatic controls on species distribution: the range limit of *Tsuga heterophylla*. *Journal of Biogeography* 33:1384–1396.
- Gehrig-Fasel, J., A. Guisan, and N. E. Zimmermann. 2007. Tree line shifts in the Swiss Alps: Climate change or land abandonment? *Journal of Vegetation Science* 18:571–582.
- Godoy, O., M. Rueda, and B. A. Hawkins. 2015. Functional determinants of forest recruitment over broad scales. *Global Ecology and Biogeography* 24:192–202.
- Godsoe, W., and L. J. Harmon. 2012. How do species interactions affect species distribution models? *Ecography* 35:811–820.
- Godsoe, W., R. Murray, and M. J. Plank. 2015. The effect of competition on species' distributions depends on coexistence, rather than scale alone. *Ecography* 38:001–009.
- Gonzales, L. M., and E. C. Grimm. 2009. Synchronization of late-glacial vegetation changes at Crystal Lake, Illinois, USA with the North Atlantic Event Stratigraphy. *Quaternary Research* 72:234–245.
- Graham, R. W., and E. C. Grimm. 1990. Effects of global climate change on the patterns of terrestrial biological communities. *Trends in Ecology and Evolution* 5:289–292.
- Gray, S. T., J. L. Betancourt, S. T. Jackson, and R. G. Eddy. 2006. Role of multidecadal climate variability in a range extension of pinyon pine. *Ecology* 87:1124–1130.
- Gray, L. K., and A. Hamann. 2013. Tracking suitable habitat for tree populations under climate change in western North America. *Climatic Change* 117:289–303.
- Grimm, E. C. 1984. Fire and other factors controlling the big woods vegetation of Minnesota in the mid-19th century. *Ecological Monographs* 54:291–311.
- Grimm, E. C., W. A. Watts, G. L. Jacobson Jr., B. C. S. Hansen, H. R. Almquist, and A. C. Dieffenbacher-Krall. 2006. Evidence for warm wet Heinrich events in Florida. *Quaternary Science Reviews* 25:2197–2211.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52:107–145.
- Gugger, P. F., J. S. McLachlan, P. S. Manos, and J. S. Clark. 2008. Inferring long-distance dispersal and topographic barriers during post-glacial colonization from the genetic structure of red maple (*Acer rubrum* L.) in New England. *Journal of Biogeography* 35:1665–1673.
- Gutiérrez, A. G., R. S. Snell, and H. Bugmann. 2016. Using a dynamic forest model to predict tree species distributions. *Global Ecology and Biogeography* 25:347–358.
- Hampe, A., and A. S. Jump. 2011. Climate relicts: past, present, future. *Annual Review of Ecology, Evolution, and Systematics* 42:313–333.
- Hansen, W. D., W. H. Romme, A. Ba, and M. G. Turner. 2016. Shifting ecological filters mediate

- postfire expansion of seedling aspen (*Populus tremuloides*) in Yellowstone. *Forest Ecology and Management* 362:218–230.
- Hargreaves, A. L., K. E. Samis, and C. G. Eckert. 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *American Naturalist* 183:157–173.
- Harrison, S. P., and M. F. S. Goñi. 2010. Global patterns of vegetation response to millennial-scale variability and climate change during the last glacial period. *Quaternary Science Reviews* 29:2957–2980.
- Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. *Global Ecology and Biogeography* 25:655–669.
- He, T., C. M. Belcher, B. B. Lamont, and S. L. Lim. 2016. A 350-million-year-legacy of fire adaptation among conifers. *Journal of Ecology* 104:352–363.
- Higgins, S. I., S. Lavorel, and E. Revilla. 2003. Estimating plant migration rates under habitat loss and fragmentation. *Oikos* 101:354–366.
- HilleRisLambers, J., M. A. Harsch, A. K. Ettinger, K. R. Ford, and E. J. Theobald. 2013. How will biotic interactions influence climate change-induced range shifts? *Annals of the New York Academy of Sciences* 1297:112–125.
- Hobbie, S. E., and F. S. Chapin III. 1998. An experimental test of limits to tree establishment in Arctic tundra. *Journal of Ecology* 86:449–461.
- Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences* 106:19659–19665.
- Honnay, O., K. Verheyen, J. Butay, H. Jacquemyn, B. Bossuyt, and M. Hermy. 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters* 5: 525–530.
- Hopper, S. D. 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant and Soil* 322:49–86.
- Huntley, B., P. J. Bartlein, and I. C. Prentice. 1989. Climatic control of the distribution and abundance of beech (*Fagus*) in Europe and North America. *Journal of Biogeography* 16:551–560.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology* 22:415–427.
- Ibrahim, K. M., R. A. Nichols, and G. M. Hewitt. 1996. Spatial patterns of genetic variations generated by different forms of dispersal during range expansion. *Heredity* 77:282–291.
- Ireland, K. B., A. B. Stan, and P. Z. Fulé. 2012. Bottom-up control of a northern Arizona ponderosa pine forest regime in a fragmented landscape. *Landscape Ecology* 27:983–997.
- Iverson, L. R., M. W. Schwartz, and A. M. Prasad. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography* 13:209–219.
- Jackson, S. T., J. L. Betancourt, R. K. Booth, and S. T. Gray. 2009. Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences* 106:19658–19692.
- Jackson, S. T., and J. T. Overpeck. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* 26:194–220.
- Jacobson, G. L. 1979. The paleoecology of white pine (*Pinus strobus*) in Minnesota. *Journal of Ecology* 67:697–726.
- Jacobson, G. L., and E. C. Grimm. 1986. A numerical analysis of Holocene forest and prairie vegetation in central Minnesota. *Ecology* 67:958–966.
- Jacobson, G. L., T. Webb III, and E. C. Grimm. 1987. Patterns and rates of vegetation change during the deglaciation of eastern North America. Pages 277–288 in W. F. Ruddiman, editor. *North America and adjacent oceans during the last deglaciation: the geology of North America*. Geological Society of America, Boulder, Colorado, USA.
- Jaramilla-Correa, J. P., J. Beaulieu, D. P. Khasa, and J. Bousquet. 2009. Inferring the past from the present phylogeographic structure of North American forest trees: seeing the forest for the genes. *Canadian Journal of Forest Research* 39:286–307.
- Jiménez-Moreno, G., R. S. Anderson, S. Desprat, L. D. Grigg, E. C. Grimm, L. E. Heusser, B. F. Jacobs, C. López-Martínez, C. L. Whitlock, and D. A. Willard. 2010. Millennial-scale variability during the last glacial in vegetation records from North America. *Quaternary Science Reviews* 29:2865–2881.
- Johnstone, J. F., E. J. B. McIntire, E. J. Pederson, G. King, and M. J. Pisaric. 2010. A sensitive slope: estimating landscape patterns of forest resilience in a changing climate. *Ecosphere* 1:1–21.
- Katz, D. S. W., and I. Ibáñez. 2016. Differences in biotic interactions across range edges have only minor effects on plant performance. *Journal of Ecology* 105:321–331.
- Kellman, M. 2004. Sugar maple (*Acer saccharum* Marsh.) establishment in boreal forest: results of a transplantation experiment. *Journal of Biogeography* 31:1515–1522.
- King, D. A., D. M. Bachelet, and A. J. Symstad. 2013. Climate change and fire effects on a prairie-

- woodland ecotone: projecting species range shifts with a dynamic global vegetation model. *Ecology and Evolution* 3:5076–5097.
- Kubisch, A., T. Degan, T. Hovestadt, and H. J. Poethke. 2013. Predicting range shifts under global change: the balance between local adaptation and dispersal. *Ecography* 36:873–882.
- Lankau, R. A., K. Zhuk, and A. Ordóñez. 2015. Mycorrhizal strategies of tree species correlate with trailing range edge responses to current and past climate change. *Ecology* 96:1451–1458.
- Larson, J. E., and J. L. Funk. 2016. Regeneration: an overlooked aspect of trait-based plant community assembly models. *Journal of Ecology* 104:1284–1298.
- Lavergne, S., N. Mouquet, W. Thuiller, and O. Ronce. 2010. Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution and Systematics* 41:321–350.
- Lawler, J. J., A. S. Ruesch, J. D. Olden, and B. H. McRae. 2013. Projected climate-driven faunal movement routes. *Ecology Letters* 16:1014–1022.
- Le Roux, P. C., R. Virtanen, and M. Luoto. 2013. Geomorphological disturbance is necessary for predicting fine-scale species distributions. *Ecography* 36:800–808.
- Lee-Yaw, J. A., H. M. Kharouba, M. Bontrager, C. Mahony, A. M. Csörgő, A. M. E. Noreen, Q. Li, R. Schuster, and A. L. Angert. 2016. A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecology Letters* 19:710–722.
- Leithhead, M. D., M. Anand, and L. C. R. Silva. 2010. Northward migrating trees establish in treefall gaps at the northern limit of the temperate-boreal ecotone, Ontario, Canada. *Oecologia* 164:1095–1106.
- Lembrechts, J. J., et al. 2016. Mountain roads shift native and non-native plant species ranges. *Ecography* 40:353–364.
- Lenoir, J., J.-C. Gégout, A. Guisan, P. Vittoz, T. Wohlgemuth, N. E. Zimmermann, S. Dullinger, H. Pauli, W. Willner, and J.-C. Svenning. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33:295–303.
- Lenoir, J., J.-C. Gégout, J.-C. Pierrat, J.-D. Bontemps, and J. F. Dhôte. 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). *Ecography* 32:765–777.
- Lesser, M. R., and S. T. Jackson. 2012. Making a stand: five centuries of population growth in colonizing populations of *Pinus ponderosa*. *Ecology* 93:1071–1081.
- Levesque, A. J., L. C. Cwynar, and I. R. Walker. 1997. Exceptionally steep north-south gradients in lake temperatures during the last deglaciation. *Nature* 385:423–426.
- Liang, S., M. D. Hurteau, and A. L. Westerling. 2016. Response of Sierra Nevada forests to projected climate-wildfire interactions. *Global Change Biology* 23:2016–2030.
- Liénard, J. F., and N. S. Strigul. 2016. Modeling of hardwood forest in Quebec under dynamic disturbance regimes: a time-inhomogeneous Markov chain approach. *Journal of Ecology* 104:806–816.
- Liepe, K. J., A. Hamann, P. Smets, C. R. Fitzpatrick, and S. N. Aitken. 2016. Adaptation of lodgepole pine and interior spruce to climate: implications for reforestation in a warming world. *Evolutionary Applications* 9:409–419.
- Lindbladh, M., W. W. Oswald, D. R. Foster, E. K. Faison, J. Hou, and Y. Huang. 2007. A late-glacial transition from *Picea glauca* to *Picea mariana* in southern New England. *Quaternary Research* 67:502–508.
- Littell, J. S., E. E. Oneil, D. McKenzie, J. A. Hicke, J. A. Lutz, R. A. Norheim, and M. M. Elsner. 2010. Forest ecosystems, disturbance, and climatic change in Washington State, USA. *Climatic Change* 102:129–158.
- Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. *Nature* 462:1052–1055.
- Lorimer, C. G., J. W. Chapman, and W. D. Lambert. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. *Journal of Ecology* 82:227–237.
- Loudermilk, E. L., R. M. Scheller, P. J. Weisberg, J. Yang, T. E. Dilts, S. L. Karam, and C. Skinner. 2013. Carbon dynamics in the future forest: the importance of long-term successional legacy and climate-fire interactions. *Global Change Biology* 19:3502–3515.
- Lyford, M. E., S. T. Jackson, J. L. Betancourt, and S. T. Gray. 2003. Influence of landscape structure and climate variability on a late Holocene plant migration. *Ecological Monographs* 73:567–583.
- Maher, E. L., and M. J. Germino. 2006. Microsite differentiation among conifer species during seedling establishment at alpine treeline. *Ecoscience* 13:334–341.
- Malcolm, J. R., A. Markham, R. P. Neilson, and M. Garaci. 2002. Estimated migration rates under scenarios of global climate change. *Journal of Biogeography* 29:835–849.
- Máliš, F., M. Kopecký, P. Petřík, J. Vladovič, J. Meranič, and T. Vida. 2016. Life-stage, not climate



- change, explains observed tree range shifts. *Global Change Biology* 22:1904–1914.
- Manchester, S. R. 1999. Biogeographical relationships of North American Tertiary floras. *Annals of the Missouri Botanical Garden* 86:472–522.
- Mann, M. E., Z. Zhang, S. Rutherford, R. S. Bradley, M. K. Hughes, D. Shindell, C. Ammann, G. Faluvegi, and F. Ni. 2009. Global signatures and dynamical origins of the little ice age and medieval climate anomaly. *Science* 326:1256–1260.
- Marsicek, J. P., B. Shuman, S. Brewer, D. R. Foster, and W. W. Oswald. 2013. Moisture and temperature changes associated with the mid-Holocene *Tsuga* decline in the northeastern United States. *Quaternary Science Reviews* 80:129–142.
- Martinsen, G. D., T. G. Whitham, R. J. Turek, and P. Keim. 2001. Hybrid populations selectively filter gene introgressions between species. *Evolution* 55:1325–1335.
- Massot, M., J. Clobert, and R. Ferrier. 2008. Climate warming, dispersal inhibition and extinction risk. *Global Change Biology* 14:461–469.
- Mast, J. N., T. T. Veblen, and M. E. Hodgson. 1997. Tree invasion within a pine/grassland ecotone: an approach with historic aerial photography and GIS modeling. *Forest Ecology and Management* 93:181–194.
- Mast, J. N., T. T. Veblen, and Y. B. Linhart. 1998. Disturbance and climatic influences on age structure of ponderosa pine at the pine/grassland ecotone, Colorado Front Range. *Journal of Biogeography* 25:743–755.
- McAndrews, J. H. 1968. Pollen evidence for the protohistoric development of the “Big Woods” in Minnesota (U.S.A.). *Review of Palaeobotany and Palynology* 7:201–211.
- McGill, B. J. 2010. Matters of scale. *Science* 328:575–576.
- McIntire, E. J. B., F. I. Piper, and A. Fajardo. 2016. Wind and light exposure, more than elevation-related temperature, limit treeline seedling abundance on three continents. *Journal of Ecology* 104:1379–1390.
- McLachlan, J. S., J. S. Clark, and P. S. Manos. 2005. Molecular indicators of tree migration capacity under rapid climate change. *Ecology* 86:2088–2098.
- Meddens, A. J. H., J. A. Hicke, and C. A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecological Applications* 22:1876–1891.
- Meier, E. S., F. Kienast, P. B. Pearman, J.-C. Svenning, W. Thuiller, M. B. Araújo, A. Guisan, and N. E. Zimmermann. 2010. Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography* 33:1038–1048.
- Meier, E. S., H. Lischke, D. R. Schmatz, and N. E. Zimmermann. 2012. Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography* 21:164–178.
- Minckley, T., R. K. Shriver, and B. Shuman. 2012. Resilience and regime change in a southern Rocky Mountain ecosystem during the past 17000 years. *Ecological Monographs* 82:49–68.
- Montwé, D., M. Isaac-Renton, A. Hamann, and H. Spiecker. 2016. Drought tolerance and growth in populations of a wide-ranging tree species indicate climate change risks for the boreal north. *Global Change Biology* 22:806–815.
- Moorcroft, P. R., S. W. Pacala, and M. A. Lewis. 2006. Potential role of natural enemies during tree range expansions following climate change. *Journal of Theoretical Biology* 241:601–616.
- Morin, X., C. Augspurger, and I. Chuine. 2007. Process-based modeling of species’ distributions: What limits temperate tree species’ range boundaries? *Ecology* 88:2280–2291.
- Morin, X., and I. Chuine. 2006. Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. *Ecology Letters* 9:185–195.
- Morueta-Holme, N., B. Blonder, B. Sandel, B. J. McGill, R. K. Peet, J. E. Ott, C. Viole, B. J. Enquist, P. M. Jørgensen, and J.-C. Svenning. 2016. A network approach for inferring species associations from co-occurrence data. *Ecography* 39:1139–1150.
- Mucina, L., and G. W. Wardell-Johnson. 2011. Landscape age and soil fertility, climatic stability, and fire regime predictability: beyond the OCBIL framework. *Plant and Soil* 341:1–23.
- Murphy, H. T., J. VanDerWal, and J. Lovett-Doust. 2010. Signatures of range expansion and erosion in eastern North American trees. *Ecology Letters* 13:1233–1244.
- Neilson, R. P., and L. H. Wullstein. 1983. Biogeography of two southwest American oaks in relation to atmospheric dynamics. *Journal of Biogeography* 10:275–297.
- Nelson, D. M., and F. S. Hu. 2008. Patterns and drivers of Holocene vegetational change near the prairie-forest ecotone in Minnesota: revisiting McAndrews’ transect. *New Phytologist* 179:449–459.
- Nelson, D. M., F. S. Hu, E. C. Grimm, B. B. Curry, and J. E. Slate. 2006. The influence of aridity and fire on Holocene prairie communities in the eastern prairie peninsula. *Ecology* 87:2523–2536.
- Newton, A. C., T. R. Allnutt, A. C. M. Gillies, A. J. Lowe, and R. A. Ennos. 1999. Molecular phylogeography, intraspecific variation and the

- conservation of tree species. *Trends in Ecology and Evolution* 14:140–145.
- Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and “mesophication” of forests in the eastern United States. *BioScience* 58:123–138.
- Ordóñez, A., and J.-C. Svenning. 2016. Functional diversity of North American broad-leaved trees is codetermined by past and current environmental factors. *Ecosphere* 7:e01237.
- Ordóñez, A., and J. W. Williams. 2013. Climatic and biotic velocities for woody taxa distributions over the last 16,000 years in eastern North America. *Ecology Letters* 16:773–781.
- Oswald, W. W., E. K. Faison, D. R. Foster, E. D. Doughty, B. R. Hall, and B. C. S. Hansen. 2007. Post-glacial changes in spatial patterns of vegetation across southern New England. *Journal of Biogeography* 34:900–913.
- Palombo, C., G. Chirici, M. Marchetti, and R. Tognetti. 2013. Is land abandonment affecting forest dynamics at high elevation in Mediterranean mountains more than climate change? *Plant Biosystems* 147:1–11.
- Parshall, T., and D. R. Foster. 2002. Fire on the New England landscape: regional and temporal variation, cultural and environmental controls. *Journal of Biogeography* 29:1305–1317.
- Parshall, T., D. Foster, E. Faison, D. MacDonald, and B. C. S. Hansen. 2003. Long-term history of vegetation and fire in pitch pine-oak forests on Cape Cod, Massachusetts. *Ecology* 84:736–748.
- Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography* 12:361–371.
- Pearson, R. G., T. P. Dawson, and C. Liu. 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography* 27:285–298.
- Petit, R. J., E. Pineau, B. Demesure, R. Bacillieri, A. Ducouso, and A. Kremer. 1997. Chloroplast DNA footprints and postglacial recolonization by oaks. *Proceedings of the National Academy of Sciences USA* 94:9996–10001.
- Pither, J. 2003. Climate tolerance and interspecific variation in geographic range size. *Proceedings of the Royal Society of London B* 270:475–481.
- Pollock, L. J., R. Tingley, W. K. Morrow, N. Golding, R. B. O’Hara, K. M. Parris, P. A. Vesk, and M. A. McCarthy. 2014. Understanding co-occurrence by modelling species simultaneously with a joint species distribution model (JSDM). *Methods in Ecology and Evolution* 5:397–406.
- Prentice, I. C., P. J. Bartlein, and T. Webb III. 1991. Vegetation and climate change in eastern North America since the last glacial maximum: a response to continuous climatic forcing. *Ecology* 72:2038–2056.
- Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecology Letters* 3:349–361.
- Qian, H., J. J. Wiens, J. Zhang, and Y. Zhang. 2015. Evolutionary and ecological causes of species richness patterns in North American angiosperm trees. *Ecography* 38:241–250.
- Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in global land cover: croplands from 1700 to 1992. *Global Biogeochemical Cycles* 13:997–1027.
- Raup, H. M. 1966. The view from John Sanderson’s farm: a perspective for the use of the land. *Forest History* 10:2–11.
- Rehfeldt, G. E., N. L. Crookston, W. V. Warwell, and J. Evans. 2006. Empirical analyses of plant-climate relationships for the western United States. *International Journal of Plant Sciences* 167:1123–1150.
- Rehfeldt, G. E., C. C. Ying, D. L. Spittlehouse, and D. A. Hamilton Jr. 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecological Monographs* 69:375–407.
- Renwick, K. M., and M. E. Rocca. 2015. Temporal context affects the observed rate of climate-driven range shifts in tree species. *Global Ecology and Biogeography* 24:44–51.
- Rhemtulla, J. M., D. J. Mladenoff, and M. K. Clayton. 2009. Historical forest baselines reveal potential for continued carbon sequestration. *Proceedings of the National Academy of Sciences* 106:6082–6087.
- Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* 7:1–5.
- Romme, W. H., M. G. Turner, G. A. Tuskan, and R. A. Reed. 2005. Establishment, persistence, and growth of aspen (*Populus tremuloides*) seedlings in Yellowstone National Park. *Ecology* 86:404–418.
- Rooney, T. P., R. J. McCormick, S. L. Solheim, and D. M. Waller. 2000. Regional variation in recruitment of hemlock seedlings and saplings in the Upper Great Lakes, USA. *Ecological Applications* 10:1119–1132.
- Rouget, M., D. M. Richardson, S. Lavorel, J. Vayreda, C. Gracia, and S. J. Milton. 2001. Determinants of distribution of six *Pinus* species in Catalonia, Spain. *Journal of Vegetation Science* 12:491–502.
- Sandel, B. 2015. Towards a taxonomy of spatial scale-dependence. *Ecography* 38:358–369.
- Scheller, R. M., and D. J. Mladenoff. 2008. Simulated effects of climate change, fragmentation, and interspecific competition on tree species migration in northern Wisconsin, USA. *Climate Research* 36:191–202.

- Serra-Diaz, J. M., et al. 2015. Averaged 30 year climate change projections mask opportunities for species to establish. *Ecography* 39:844–845.
- Shakun, J. D., P. U. Clark, F. He, S. A. Marcott, A. C. Mix, Z. Liu, B. Otto-Bliesner, A. Schmittner, and E. Bard. 2012. Global warming preceded by increasing carbon dioxide concentrations during the last deglaciation. *Nature* 484:49–54.
- Shuman, B., P. Bartlein, N. Logar, P. Newby, and T. Webb. 2002a. Parallel climate and vegetation responses to the early-Holocene collapse of the Laurentide Ice Sheet. *Quaternary Science Reviews* 21:1793–1805.
- Shuman, B. N., A. K. Henderson, C. Plank, I. Stefanova, and S. S. Ziegler. 2009a. Woodland-to-forest transition during prolonged drought in Minnesota after ca. AD 1300. *Ecology* 90:2792–2807.
- Shuman, B. N., and J. P. Marsicek. 2016. The structure of Holocene climate change in mid-latitude North America. *Quaternary Science Reviews* 141:38–51.
- Shuman, B. N., P. Newby, and J. P. Donnelly. 2009b. Abrupt climate change as an important agent of ecological change in the Northeast U.S. throughout the past 15,000 years. *Quaternary Science Reviews* 28:1693–1709.
- Shuman, B., P. Newby, Y. Huang, and T. Webb III. 2004. Evidence for the close climatic control of New England vegetation history. *Ecology* 85:1297–1310.
- Shuman, B., T. Webb III, P. Bartlein, and J. W. Williams. 2002b. The anatomy of a climatic oscillation: vegetation change in eastern North America during the Younger Dryas chronozone. *Quaternary Science Reviews* 21:1777–1791.
- Siefert, A., M. R. Lesser, and J. D. Fridley. 2015. How do climate and dispersal traits limit ranges of tree species along latitudinal and elevational gradients. *Global Ecology and Biogeography* 24:581–593.
- Soberón, J., and M. Nakamura. 2009. Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Science* 106:19644–19650.
- Stohlgren, T. J., R. R. Bachand, Y. Onami, and D. Binkley. 1998. Species-environment relationships and vegetation patterns: effects of spatial scale and tree life-stage. *Plant Ecology* 135:215–228.
- Svenning, J.-C., W. L. Eiserhardt, S. Normand, A. Ordoñez, and B. Sandel. 2015. The influence of paleoclimate on present-day patterns in biodiversity and ecosystems. *Annual Review of Ecology, Evolution and Systematics* 46:551–572.
- Svenning, J.-C., and B. Sandel. 2013. Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany* 100:1266–1286.
- Svenning, J.-C., and F. Skov. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters* 10:453–460.
- Svenning, J.-C., et al. 2014. The influence of interspecific interactions on species range expansion rates. *Ecography* 37:001–012.
- Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simons, and Z. G. Davies. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* 411:577–581.
- Thompson, J. N. 2005. *The geographic mosaic of coevolution*. The University of Chicago Press, Chicago, Illinois, USA.
- Thompson, J. R., D. R. Foster, R. Scheller, and D. Kittridge. 2011. The influence of land use and climate change on forest biomass and composition in Massachusetts, USA. *Ecological Applications* 21:2425–2444.
- Thuiller, W., M. B. Araújo, and S. Lavorel. 2004. Do we need land-cover data to model species distributions in Europe? *Journal of Biogeography* 31:353–361.
- Tilman, D., P. Reich, H. Phillips, M. Menton, A. Patel, E. Vos, D. Peterson, and J. Knops. 2000. Fire suppression and ecosystem carbon storage. *Ecology* 81:2680–2685.
- Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67:411–433.
- Turner, M. G., W. H. Romme, R. A. Reed, and G. A. Tuskan. 2003. Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. *Landscape Ecology* 18:127–140.
- Umbanhowar, C. E. 2004. Interaction of fire, climate and vegetation change at a large landscape scale in the Big Woods of Minnesota, USA. *Holocene* 14:661–676.
- Van der Putten, W. H. 2012. Climate change, above-ground-belowground interactions, and species' range shifts. *Annual Review of Ecology, Evolution and Systematics* 43:365–383.
- Van der Putten, W. H., M. Macel, and M. E. Visser. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B* 365:2025–2034.
- Veloz, S. D., J. W. Williams, J. L. Blois, F. He, B. Otto-Bliesner, and Z. Liu. 2012. No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. *Global Change Biology* 18:1698–1713.

- Walter, R., and B. K. Epperson. 2001. Geographic pattern of genetic variation in *Pinus resinosa*: area of greatest diversity is not the origin of postglacial populations. *Molecular Ecology* 10:103–111.
- Webb III, T. 1986. Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio* 67:75–91.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313:940–943.
- Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. H. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences* 108:13165–13170.
- Whitlock, C., P. Bartlein, and W. A. Watts. 1993. Vegetation history of Elk Lake. Pages 251–274 in J. P. Bradbury and W. Dean, editors. Elk Lake, Minnesota: evidence for rapid climate change in the north central United States. Special Paper 276. Geological Society of America, Boulder, Colorado, USA.
- Whitman, E., E. Batllori, M.-A. Parisien, C. Miller, J. D. Coop, M. A. Krawchuk, G. W. Chong, and S. L. Haire. 2015. The climate space of fire regimes in north-western North America. *Journal of Biogeography* 42:1736–1749.
- Whittaker, R. J., K. J. Willis, and R. Field. 2001. Scale and species richness: towards a general hierarchical theory of species diversity. *Journal of Biogeography* 28:453–470.
- Wiens, J. J. 2011. The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society B* 366:2336–2350.
- Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5: 475–482.
- Williams, J. W., D. M. Post, L. C. Cwynar, A. F. Lotter, and A. J. Levesque. 2002. Rapid and widespread vegetation responses to past climate change in the North Atlantic region. *Geology* 30:971–974.
- Williams, J. W., B. N. Shuman, T. Webb III, P. J. Bartlein, and P. L. Leduc. 2004. Late-Quaternary vegetation dynamics in North America: scaling from taxa to biomes. *Ecological Monographs* 74:309–334.
- Williams, J. W., et al. 2006. An atlas of pollen-vegetation-climate relationships for the United States and Canada. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas, USA.
- Willis, K. J., R. M. Bailey, S. A. Bhagwat, and H. J. B. Birks. 2000. Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using paleoecological data. *Trends in Ecology and Evolution* 25:583–591.
- Wirth, C., J. W. Lichstein, J. Dushoff, A. Chen, and F. S. Chapin. 2008. White spruce meets black spruce: dispersal, postfire establishment, and growth in a warming climate. *Ecological Monographs* 78:489–505.
- Wisn, M. S., et al. 2013. The role of biotic interactions in shaping distributions and realized assemblages of species: implications for species distribution modeling. *Biological Reviews* 88:15–30.
- Woodall, C. W., C. M. Oswalt, J. A. Westfall, C. H. Perry, M. D. Nelson, and A. O. Finley. 2009. An indicator of tree migration in forests of the eastern United States. *Forest Ecology and Management* 257:1434–1444.
- Woodward, F. I. 1987. *Climate and plant distribution*. Cambridge University Press, Cambridge, UK.
- Worth, J. R. P., G. J. Williamson, S. Sakaguchi, P. G. Nevill, and G. J. Jordan. 2014. Environmental niche modelling fails to predict last glacial maximum refugia: Niche shifts, microrefugia or incorrect paleoclimate estimates? *Global Ecology and Biogeography* 23:1186–1197.
- Xiang, Q.-Y., W. H. Zhang, R. E. Ricklefs, H. Qian, Z. D. Chen, J. Wen, and J. H. Li. 2004. Regional differences in rates of plant speciation and molecular evolution: a comparison between eastern Asia and eastern North America. *Evolution* 58:2175–2184.
- Yu, Z. 2007. Rapid response of forested vegetation to multiple climatic oscillations during the last deglaciation in the northeastern United States. *Quaternary Research* 67:297–303.
- Zhu, K., C. W. Woodall, and J. S. Clark. 2012. Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology* 18:1042–1052.