

## DISEQUILIBRIUM VEGETATION DYNAMICS UNDER FUTURE CLIMATE CHANGE<sup>1</sup>

JENS-CHRISTIAN SVENNING<sup>2</sup> AND BRODY SANDEL

Ecoinformatics & Biodiversity Group, Department of Bioscience, Aarhus University, Ny Munkegade 114,  
DK-8000 Aarhus C, Denmark

- *Premise of the study:* Near-future climate changes are likely to elicit major vegetation changes. Disequilibrium dynamics, which occur when vegetation comes out of equilibrium with climate, are potentially a key facet of these. Understanding these dynamics is crucial for making accurate predictions, informing conservation planning, and understanding likely changes in ecosystem function on time scales relevant to society. However, many predictive studies have instead focused on equilibrium end-points with little consideration of the transient trajectories.
- *Methods:* We review what we should expect in terms of disequilibrium vegetation dynamics over the next 50–200 yr, covering a broad range of research fields including paleoecology, macroecology, landscape ecology, vegetation science, plant ecology, invasion biology, global change biology, and ecosystem ecology.
- *Key results:* The expected climate changes are likely to induce marked vegetation disequilibrium with climate at both leading and trailing edges, with leading-edge disequilibrium dynamics due to lags in migration at continental to landscape scales, in local population build-up and succession, in local evolutionary responses, and in ecosystem development, and trailing-edge disequilibrium dynamics involving delayed local extinctions and slow losses of ecosystem structural components. Interactions with habitat loss and invasive pests and pathogens are likely to further contribute to disequilibrium dynamics. Predictive modeling and climate-change experiments are increasingly representing disequilibrium dynamics, but with scope for improvement.
- *Conclusions:* The likely pervasiveness and complexity of vegetation disequilibrium is a major challenge for forecasting ecological dynamics and, combined with the high ecological importance of vegetation, also constitutes a major challenge for future nature conservation.

**Key words:** climate change; dispersal limitation; global change; plant migration; plant population dynamics; predictive modeling; range shift; succession; time lags; transient dynamics.

Since von Humboldt's seminal work on plant geography (von Humboldt and Bonpland, 1807), climate has been recognized to play a central role for the distribution of vegetation and plant species. Strong changes in climate are predicted for the next decades and centuries (IPCC, 2007), and much work has focused on estimating the impacts of climate change on vegetation, with respect to ancient changes (Delcourt et al., 1982; Williams et al., 2001; Svenning, 2003; Giesecke et al., 2006; Willis et al., 2007; Beer and Tinner, 2008; Birks and Birks, 2008; Ehrlich et al., 2008; Pearman et al., 2008; Correa-Metrio et al., 2012), recent changes within the last 200 yr (Lenoir et al., 2008, 2010a; Parolo and Rossi, 2008; Bertrand et al., 2011; Gottfried et al., 2012), and projected future anthropogenic climate change (Thuiller et al., 2005; Bomhard et al., 2005; Normand et al., 2007; Rickebusch et al., 2008; Randin et al., 2009; Scheiter and Higgins, 2009; Araújo et al., 2011).

In magnitude, the near-future climate changes approach those seen at the last glacial–interglacial transition and are thus likely to elicit major vegetation changes (Delcourt et al., 1982;

Williams et al., 2001; Bush et al., 2004). Mean annual temperatures are projected to rise between 1.8–4.0°C by 2090–2099 relative to 1980–1999 depending on how greenhouse gas emissions develop, with an increase of up to 6.4°C within the likely range at high emissions (IPCC, 2007). Warming will be strongest at high northern latitudes, with increases of 5.0–8.0°C under the A1B scenario, which predicts a global average increase of 2.8°C (IPCC, 2007). Spatial climate shifts will occur at a global mean velocity of 0.42 km·yr<sup>-1</sup> for mean annual temperature under the A1B scenario with low velocities in mountainous biomes (biome means as low as 0.08 km·yr<sup>-1</sup>) and high velocities in lowland biomes (biome means up to 1.26 km·yr<sup>-1</sup>; Loarie et al., 2009). A number of associated changes are also predicted: snow cover will contract, thaw depth will increase in most permafrost areas, heat and precipitation extremes are likely to increase, tropical cyclone intensity is likely to increase, extratropical storm tracks will shift poleward, and precipitation is likely to increase at high latitudes and likely to decrease at subtropical latitudes (IPCC, 2007). Directly linked to these climate changes are strong changes in atmospheric CO<sub>2</sub> concentration as well as sea level rises. All of these changes are likely to impact plant populations via direct and indirect climate effects (e.g., Lenoir et al., 2008; Lenoir et al., 2010b) as well as direct CO<sub>2</sub> effects on plant productivity and water-use efficiency (e.g., Körner, 2003; Rickebusch et al., 2008; Bond and Midgley, 2012; Higgins and Scheiter, 2012) and localized coastal inland migration of habitats (Moeslund et al., 2011). Under most scenarios all of these changes in climate and

<sup>1</sup>Manuscript received 7 October 2012; revision accepted 11 February 2013.

This article is a contribution of the ERC Starting Grant 310886-HISTFUNC project and the Center for Informatics Research on Complexity in Ecology (CIRCE), funded by the Aarhus University Research Foundation under the AU Ideas program (both to J.C.S.).

<sup>2</sup>Author for correspondence (e-mail: svenning@biology.au.dk)

associated factors are predicted to continue into the following centuries (IPCC, 2007).

Predicting changes in vegetation under climate change is complicated by the fact that there may be time lags in vegetation's response to climate (e.g., Davis, 1986), potentially causing highly complex dynamics. Understanding these lags is crucial for (1) making accurate predictions in the near- to midterm (50–200 yr), (2) informing conservation planning, and (3) understanding likely changes in ecosystem function under climate change on time scales relevant to society. Lags in vegetation responses affect more than simply those species involved in the lag because plants are often key components of ecosystems and may act as ecosystem engineers (Jones et al., 1994). Disequilibrium vegetation dynamics thus may also have consequences for ecosystem structure and functioning such as productivity, carbon sequestration, soil conditions, and the buildup of vegetation-defined habitats for other organisms, i.e., due to the latter's dependence on e.g., plant species composition, physical structure of the living plants and vegetation, or coarse woody debris. However, many predictive studies ignore lags, instead focusing on equilibrium end-points with little consideration of the trajectory of change leading to that end-point or how long it will take to arrive at that point. Proper consideration of these dynamics may be particularly challenging because plant ecology and vegetation science developed during the 19th and 20th centuries, under much more stable conditions than are expected for the next 50–200 yr. Thus, fully embracing dynamic, disequilibrium vegetation dynamics may require a change of perspective.

In this review, we assess how prevalent vegetation disequilibrium with climate is likely to be over the next 50–200 yr. We begin by defining disequilibrium and addressing potential causes of disequilibrium, while distinguishing dynamics at the leading and trailing edges of species ranges and vegetation zones. We then look into the empirical evidence for different causes of vegetation disequilibrium at the leading edge, including slow migration, slow population buildup and community dynamics, the loss and slow recovery of local adaptations and slow development of ecosystem structure (such as soil properties). We then turn to disequilibrium at the trailing edge, focusing on slow dieback of populations, evolutionary response, and slow losses of ecosystem structural components. We next discuss how interactions with other global change factors may exacerbate these disequilibrium dynamics, and the representation of disequilibrium dynamics in two key methods for studying vegetation responses to climate change (predictive modeling and experiments). Finally, we synthesize the evidence relevant for assessing the likely magnitude of future vegetation disequilibrium with climate and outline a research agenda to improve our understanding of this crucial issue.

A broad range of research fields provides insights on these issues including paleoecology, macroecology, landscape ecology, vegetation science, plant ecology, invasion biology, global change biology, and ecosystem ecology. Due to the magnitude of these fields, we have not attempted an exhaustive literature coverage of most themes, but rather synthesize what we consider key findings in the literature and present illustrative examples. For select specific topics, we have done systematic literature searches to provide quantitative results.

## DEFINING EQUILIBRIUM

Vegetation equilibrium and disequilibrium require careful definition. Delcourt and Delcourt (1983) considered vegetation disequilibrium to be major compositional changes in species

due to continual changes in extrinsic forcing factors such as climate. This broad definition includes the ongoing marked shifts in vegetation predicted directly from the expected future climate as species track their suitable conditions. Webb (1986) more strictly defined disequilibrium with climate as occurring when plant communities in a given climate do not contain all the species for which that climate is suitable. Equilibrium here requires that the vegetation responses to climate be fast relative to the climate dynamics themselves (Prentice, 1986). Under island biogeographic and neutral theory, plant communities are assembled via stochastic dispersal and population dynamics and are arguably never in equilibrium in terms of species composition (MacArthur and Wilson, 1967; Hubbell, 2001). Further, vegetation may in many cases consist of successional mosaics driven by relatively small-scale disturbances (Pickett and White, 1985).

Acknowledging a role for such stochastic and disturbance processes, we define vegetation to be in equilibrium with climate when no climate-driven directional changes would occur in species composition and richness, vegetation structure (e.g., biomass, individual size structure) or other aspects of vegetation-controlled ecosystem structure (e.g., amount of coarse woody debris) in the absence of further climate change. We include the purely structural aspects as these are crucial determinants of ecosystem function; for example, trees must reach a certain size to provide nesting cavities. We include dynamics driven by direct CO<sub>2</sub> effects on plant productivity and water use efficiency as well as sea-level rise effects in this definition, as these together with climate effects are all linked to anthropogenic atmospheric change (IPCC, 2007) and all involve similar and intertwined vegetation dynamics (cf. e.g., Rickebusch et al., 2008; Higgins and Scheiter, 2012). We note that it may be challenging to assess whether a given patch of vegetation is in disequilibrium with climate at any given point in time. This, however, does not prevent the concept from being important, nor disequilibrium dynamics from potentially being real and important.

## POTENTIAL CAUSES OF DISEQUILIBRIUM

Several mechanisms may cause vegetation to be out of equilibrium with climate under climate change (Fig. 1). On one hand, climate changes that increase suitability for a species or vegetation type can lead to one type of disequilibrium whereby it is not as abundant or widely distributed as expected given its current climatic requirements, other ecological characteristics, and the newly improved conditions. We refer to this situation as leading-edge disequilibrium, as it will often occur at expanding range margins. On the other hand, a species or vegetation type may persist at higher-than-expected abundance in the landscape after climate conditions have worsened. We refer to this contrasting situation as trailing-edge disequilibrium as it will typically occur at contracting range margins. Particularly for small-range species, leading- or trailing-edge disequilibrium dynamics may characterize the whole range of a species. For example, *Torreya taxifolia* Arn. has experienced, range-wide decline, which may be due to lagged responses to climate change (Barlow and Martin, 2005).

Causes of leading-edge disequilibrium include delayed arrival of a species into a newly suitable area (migration lag) and subsequent slow growth toward the population carrying capacity (establishment lag). These lags may involve or even be driven by interactions with other species, such as migrational lags due to weakly dispersing mutualists (Wilkinson, 1998) or slow establishment due to competition (Moorcroft et al., 2006). Lags in

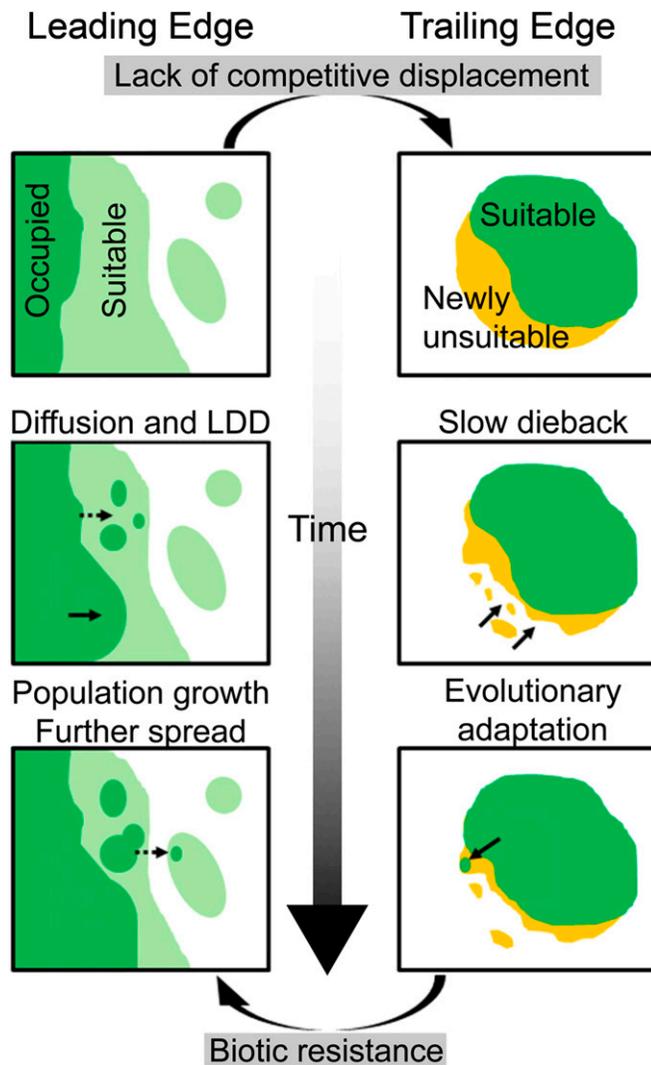


Fig. 1. Conceptual diagram of leading-edge disequilibrium (left column) and trailing-edge disequilibrium (right column) species range dynamics under climate change. In the left column, a species does not occupy (dark green) the full area of suitable conditions (light green) available on the landscape. Over time, by slow, diffusive spread and rare long-distance dispersal (LDD) events, the species expands into the unoccupied portion. The rate of spread is expected to depend on species traits (dispersal vectors, seed traits, population growth rates) and on the landscape context (connectivity, wind speed and direction). As more time passes, further jumps are possible, and the population “fills in” between LDD loci. This rate of spread is dependent on generation time and local ecological interactions (notably, competition from already-established species). In the right column, a species continues to occupy unsuitable habitat (orange). Its population growth rate may be negative, yet the population could persist for quite some time. Extirpation of the population could require particular disturbance events (e.g., drought or fire). Furthermore, over sufficient time, the remnant population could perhaps adapt to the changed local conditions, rendering the habitat again suitable for the species. Trailing-edge disequilibrium remnant populations may enforce leading-edge disequilibrium, by continuing to occupy habitat and resisting the invasion of new species (arrow: biotic resistance). On the other hand, the delayed arrival of new competitors may slow the extirpation of a resident species from unsuitable habitat (arrow: lack of competitive replacement; Urban et al., 2012), such that leading-edge disequilibrium may enforce trailing-edge disequilibrium as well.

local evolutionary responses (Davis et al., 2005) and edaphic lags (Webb III, 1986) may also contribute to leading-edge disequilibrium. Vegetation structure or other vegetation-controlled aspects of ecosystem structure may analogously be subject to leading-edge disequilibrium dynamics due to dependence on time-dependent and cumulative processes (e.g., Luysaert et al., 2008).

Trailing-edge disequilibrium refers to the continued presence of a species or vegetation type at a site at higher-than-expected abundance following a worsening of conditions. This may occur because populations contain long-lived individuals or clonal genets that persist for years or decades even though they no longer reproduce. Such remnant populations may compete against new arrivals in a community, slowing the growth of immigrant species and contributing to leading-edge disequilibrium in these species (Fig. 1). Strong trailing-edge disequilibrium in species composition may also cause ecosystem disequilibrium. For example, long-lived remnant tree populations may continue to provide habitat for a variety of forest species, leaf litter and coarse woody debris even after the climate conditions at a site should no longer support trees. The latter may even persist after all trees have died.

#### CLIMATE-DRIVEN PROCESSES CAUSING LEADING-EDGE DISEQUILIBRIUM

What is the empirical evidence for the different processes that may be driving disequilibrium dynamics at the leading edge? To answer this question, we consider the following processes: migration at continental to landscape scales, local population and community dynamics, evolutionary adaptation, and ecosystem development.

**Migration**—When climates shift, migration rates are a key factor determining the degree to which plant communities and vegetation will be in equilibrium with climate. These rates are influenced by both species characteristics (e.g., seed morphology, dispersal adaptations, and plant height (Matlack, 1994, 2005; Honnay et al., 2002; Normand et al., 2011; Thomson et al., 2011) (Fig. 2; Appendix S1, see Supplemental Data with the online version of this article), biotic interactions (e.g., with competition slowing migration rates: Urban et al., 2012) and environmental characteristics (e.g., habitat continuity, wind speeds, and dispersal barriers). For example, landscapes with continuous habitat and steep but continuous climate gradients will increase migration, while landscapes with fragmented habitats and flat or discontinuous climate gradients will decrease it (e.g., Collingham and Huntley, 2000; Honnay et al., 2002; Levey et al., 2005; Soons et al., 2005; Bertrand et al., 2011).

Future climate change expected under the A1B and A2 scenarios entails major expansions (and synchronous losses) of potential habitat for many plants species. For example, a study of 26 European plant species found that the 2100 centroid for their climatically suitable area was located up to 1230 km from any part of their currently realized range, with an average migration rate of 3.9 km/yr needed for them to reach this centroid from their current range (Skov and Svenning, 2004). Empirical evidence suggests that such migration rates will only rarely be achieved, as short-distance, slow migration is what is most frequently seen in empirical plant studies (Fig. 2). Strong immigration lags would both cause species to fail to occupy larger suitable areas at any given point in time and fail to track optimum or even suitable climatic conditions. This has several implications.

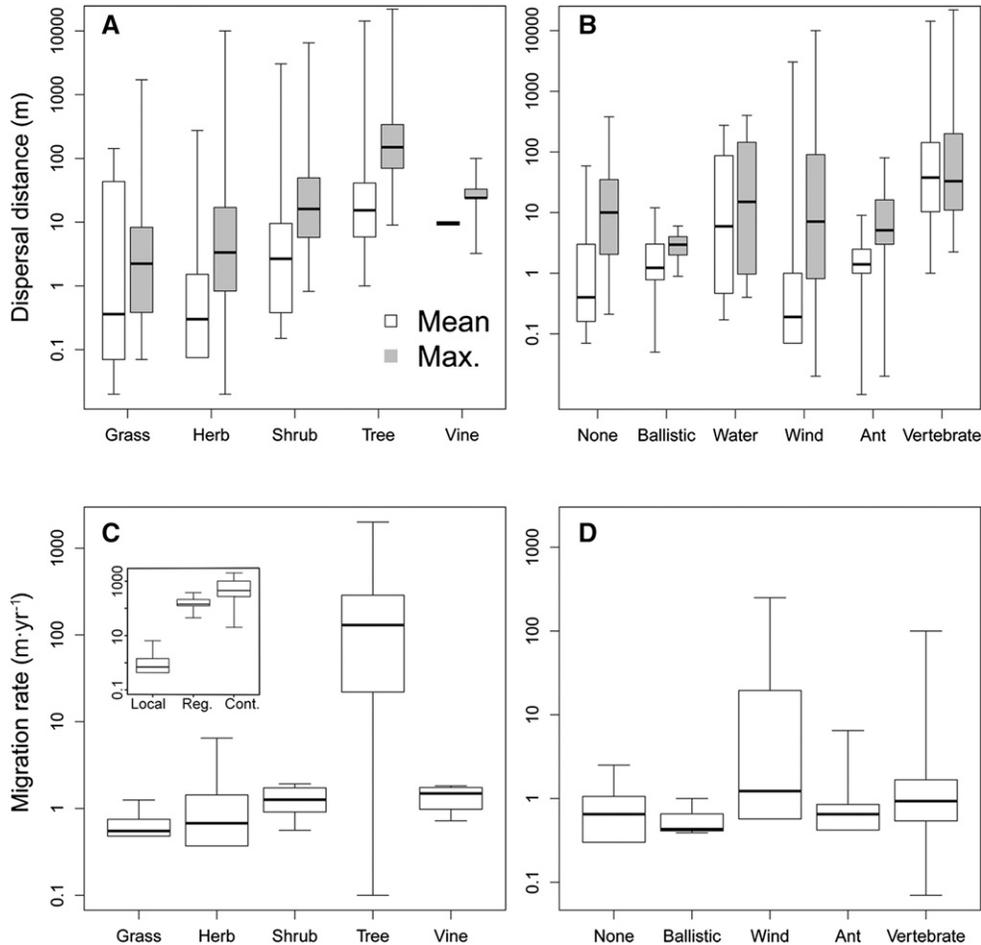


Fig. 2. Estimates of dispersal capabilities of plant species. Panels A and B show single-event seed dispersal distances, with 612 distinct estimates across 517 species assembled from the literature. Each estimate included information on the central tendency (either mean or median, denoted “Mean”) and/or extreme (maximum observed or 99th percentile, denoted “Max.”) of the seed dispersal distribution. Panels C and D show population spread rates, with 175 estimates across 157 species. Each box shows the interquartile range, with the central bar representing the median. The whiskers indicate the range of the values. Plants differ strongly in dispersal distances and migration rates across growth forms (A, C) and dispersal modes (B, D), but short-distance, slow migration is the general rule. Further, the estimated population spread rate depends strongly on the spatial scale of measurement (C, inset, local, regional or continental), suggesting that long-distance dispersal to new landscapes and local expansion within landscapes can be considered as distinct processes. We note that large-scale migration rate estimates from palynological studies of postglacial range expansions probably have been over-estimated due to overlooked cryptic northern glacial refugia (McLachlan et al., 2005). The data are provided in Appendix S1 (see Supplemental Data with the online version of this article).

First, it may threaten the existence of the species concerned. Furthermore, ranges will still be continuously shifting even after the climate stabilizes, if this is achieved. Immigration lags will cause communities to not be composed of the full set of species the climate would allow and, perhaps to some extent, instead of species suboptimally adapted to the current climatic conditions. As a result, communities would be open to immigration of climatically adapted species whenever these arrive; as many fail to arrive, the way may be paved for the increasing success of those that do arrive, e.g., human-dispersed potentially native or truly exotic invasive species.

Here, by considering multiple instructive perspectives, we comprehensively assess how often establishment of a species at a newly suitable site will be limited by immigration at time scales of 50–200 yr. Specifically, we address the following questions: To what extent have postglacial range expansions allowed vegetation to achieve broad-scale equilibrium with climate? How closely have recent vegetation shifts in response to

contemporary climate change tracked climate? What are the upper bounds on broad-scale plant range expansions, as indicated by recent invasions by exotic plant species? How fast do plant migrations within landscapes allow smaller-scale range filling? What do theoretical migration simulations tell us about likely plant migration rates in response to future climate change?

*To what extent have postglacial range expansions allowed vegetation to achieve broad-scale equilibrium with climate?*—Postglacial migrational lags have been extensively discussed in the paleobotanical literature (e.g., Smith, 1965; Davis, 1976, 1986; Delcourt and Delcourt, 1983), with many authors arguing against strong postglacial migration lags (e.g., Silvertown, 1985; Webb, 1986; Pennington, 1986; Prentice et al., 1991; Giesecke et al., 2007; Giesecke et al., 2011). This view may reflect the fact that paleobotanical studies generally have focused on the more widely distributed species (i.e., those most likely to have ranges relatively close to climatic equilibrium),

while strongly dispersal-limited, small-range species would not be sufficiently represented in the paleorecord to be analyzed. Nevertheless, the general message from the paleobotanical literature is still one of at least multicentury migration lags in large-scale expansions following strong warming. For example, regarding continental-scale distribution patterns for the main dominant plant groups across eastern North America, Prentice et al. (1991, p. 2054) concluded, “Both our results and those of Davis and co-workers are consistent with lags no greater than 1500 yr during the entire period since the last glacial maximum.” Similarly, estimated spread rates were no more than 20–90 m·yr<sup>-1</sup> (2–9 km per century) under ideal growing conditions for three *Fagus* species on three continents (Bradshaw et al., 2010).

European beech (*Fagus sylvatica* L.) is a much-discussed case and is interesting as an often dominant component of temperate forest ecosystems. Its distribution—at least where fairly abundant—was restricted to central and southeastern parts of Europe during the mid-Holocene 6000 yr BP, while its modern distribution covers most of temperate Europe (Giesecke et al., 2007). Several macroecological studies in conjunction with the species’ widespread naturalization north of its native range in Europe suggest that the expansion of beech has been and still is strongly dispersal limited, with multimillennial migration lags (Fig. 3; e.g., Svenning and Skov, 2004; Fang and Lechowicz, 2006; Svenning et al., 2008). Hind-casting of a physiological bioclimatic model suggests that it should have been as widespread 6000 yr ago as now given the past climate, which is also suggestive of millennial-scale migration lags, though the authors

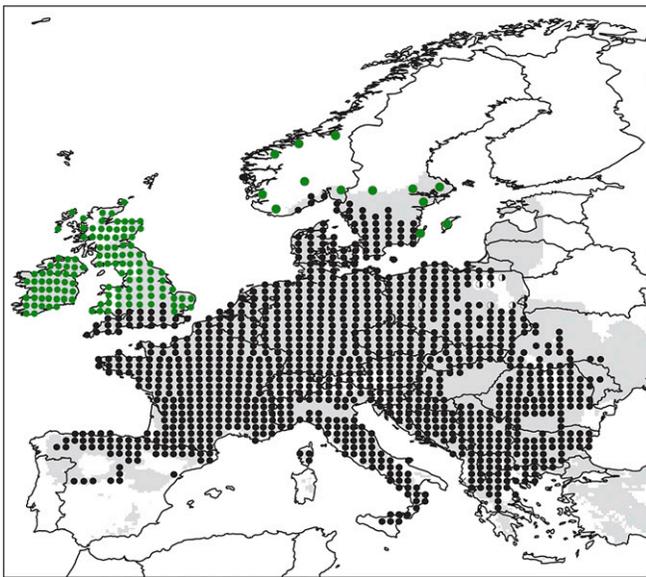


Fig. 3. Postglacial migrational lag in a forest dominant, the European beech (*Fagus sylvatica* L.). The native distribution of the species (black dots indicate native occurrences at ~50-km grain; black/white dots indicate occurrences of uncertain native status) does not fully occupy the climatically suitable (gray) areas (estimated by a bioclimatic envelope model) for the species in northern and northwestern parts of Europe. The species has become fully naturalized in many of these areas after human introduction, as indicated by the green dots (small dots ~50-km grain, large dots indicates a coarser regional grain), confirming migrational lag as the explanation for its absence as a native species here. In contrast, absences in northeastern Europe probably reflect climatic limitations that were not accounted for by envelope model. Figure adapted from Svenning and Skov (2004), with additional information from Packham et al. (2012).

attribute this to complex climate explanations and competitive interactions delaying the expansion of beech (Giesecke et al., 2007). Other studies have also concluded in favor of broad-scale equilibrium with climate for this species (Huntley et al., 1989; Tinner and Lotter, 2006). Even so, in their review of the species’ Holocene history in Central Europe, Tinner and Lotter (2006) concluded that migration over 100 km would require 250–1000 yr (except when increased by rare long-distance dispersal events) and (see next section) that expansions in response to climate change have lasted for several centuries probably due to fairly low intrinsic population growth rates and inter-specific competition.

While many authors have argued that paleobotanical evidence supports general equilibrium between climate and plant distributions, even following those interpretations this is typically not achieved without lags lasting several centuries. This is consistent with an important role for disequilibrium dynamics in shaping vegetation responses to anthropogenic climate changes over the next 50–200 yr.

Macroecological approaches (ecological studies across broad spatial scales) offer an alternative approach to elucidate the influence of past climate changes on modern plant distributions, enabling inferences about the role of migration limitation. In contrast to the paleobotanical literature, recent macroecological studies suggest that many European plant species (including a majority of trees) have, since the end of the last ice age, remained more or less constrained to their southern refuge locations, having only expanded to fill a small proportion of the area with suitable climate conditions (Svenning and Skov, 2004; Svenning et al., 2008; Normand et al., 2011). For example, distance to the nearest glacial refuge area is the strongest predictor of species richness in beech-forest understories (Willner et al., 2009). Similar postglacial migrational lags are also seen at smaller scales within the Alps (Essl et al., 2011). These spatial immigration constraints are particularly strong for small-range species (potentially explaining the discrepancy with the paleobotanical interpretations, see earlier) and weaker for species with multiple long-distance dispersal vectors and dispersal by small wind-dispersed spores (Normand et al., 2011).

Postglacial migrational lags in plants have received the most attention in Europe, which was also particularly strongly affected by the Pleistocene glaciations. Thus, the general importance of postglacial (or deeper-time) migrational lags is uncertain. There are, however, studies from northwestern North America suggesting disequilibrium there, with strong postglacial migrational lags in many taxa including ecosystem dominant trees such as *Tsuga* spp. in formerly glaciated areas (Gavin and Hu, 2006; Gavin, 2009). In addition, there are also studies from other regions including tropical lowlands that suggest postglacial migration lags (e.g., Stropp et al., 2009; Kristiansen et al., 2011; Rakotoarinivo et al., 2013). On a global scale, palms (Arecaceae) are less likely to be present and, where they are present, less species-rich where the temperature shift between the Last Glacial Maximum (LGM, 21 000 yr ago) and the present has been strongest, controlling for modern environment (Kissling et al., 2012). Further, within Africa, some palm species are limited to the vicinity of recognized glacial rain-forest refugia despite climatically suitable areas being much more widely available (Blach-Overgaard et al., 2010). Thus, there is emerging evidence that many plant species across a wide range of systems have not yet achieved equilibrium with climate following the onset of the current interglacial.

Numerous cases of species naturalizing beyond their native range (but within a given biogeographic region) provide semi-experimental verification of these macroecological findings, showing that plants are commonly capable of persisting and expanding beyond their current distributional limits (e.g., Skov and Svenning, 2004; Svenning and Skov, 2004; Figs. 3, 4). Transplant experiments further reinforce this idea. A 5-yr seedling-transplant experiment involving 17 tree species and two sites (southern Appalachians and the North Carolina Piedmont) failed to find growth differences between residents and potential immigrants (Ibañez et al., 2009). When the forest herb *Hyacinthoides non-scripta* (L.) Chouard was transplanted 60 km beyond its range limit, 41% of 27 experimental populations still survived after

45 yr and are apparently undergoing slow expansion (Van der Veken et al., 2007). Another study involving four forest herb species found 13–100% survival after 7 yr for the three species transplanted 50–200 km beyond their range edges, while a species transplanted 500 km beyond its range limit went extinct (Van der Veken et al., 2012).

*How closely has climate been tracked by recent vegetation shifts in response to contemporary climate change?*—Many organisms including plants shift their ranges in response to the recent and ongoing warming and associated climate changes, although often 20–50% of the species investigated either did not respond or even shifted in the opposite direction of that



Fig. 4. Many plants have failed to fully track postglacial climatic conditions and thrive in sometimes broad areas beyond their native range, but within their biogeographic region, after human introduction (Svenning and Skov, 2004). There are, for example, many species native to central and southern Europe, which after introduction have naturalized across more or less wide parts of northern and northwestern Europe: naturalized populations of (A) *Quercus cerris* L., (B) *Pentaglottis sempervirens* (L.) Tausch ex L. H. Bailey, and (C) evergreen *Prunus laurocerasus* L. observed in England and (D) *Acer pseudo-platanus* L., (E) *Telekia speciosa* Baumg., and (F) *Myrrhis odorata* Scop. observed in Denmark. (Photos: Jens-Christian Svenning.)

expected from warming (Parmesan and Yohe, 2003; Lenoir et al., 2010b). Several studies have reported plant range shifts along elevation gradients that lag relative to the realized climate changes. In a study of 171 forest plant species across France mainly during the late 20th century, species shifted upward at a rate of 29 m per decade, much lower than the ~75 m per decade expected from the realized warming and elevation lapse rates (Lenoir et al., 2008). Further, elevational range shifts were much lower in woody plants (~10 m per decade) than in herbaceous plants (~40 m per decade), suggesting that the generally longer times to maturation and higher longevity cause stronger range shift lags in woody species at this time scale. A study of forest plant species distribution dynamics in the Jura Mountains during 1989–2007 found no upward shift despite a 1°C warming, but instead local increases in abundance and, for some, extinctions at the lower edge (Lenoir et al., 2010a). Studies from other regions including the Italian Alps (Parolo and Rossi, 2008) and the Subantarctic Islands (Le Roux and McGeoch, 2008) have documented similar lags. In contrast, Kelly and Goulden (2008) reported range shifts among both woody and herbaceous plants of the same magnitude as the realized warming in southern California between 1977 and 2006–2007 (also see Klanderud and Birks, 2003). Lags are expected to be strongest in lowland areas due to the generally greater climate-change velocity there (Loarie et al., 2009). In support of this, a large study of the dynamics in French forest herb assemblages from 1965 to 2008 found that assemblages in highlands responded to climatic warming by lagged expansions of thermophilic species, while assemblages in lowlands did not exhibit significant compositional responses (Bertrand et al., 2011). Slower migration due to greater habitat fragmentation in lowland areas and greater thermal tolerance of the lowland species may contribute to these differing responses (Bertrand et al., 2011).

Studies at the northern and southern range limits of plant species complement studies on elevational gradients and, consistent with Bertrand et al. (2011)'s findings, suggest little or highly localized climate change responses. A massive study (43 334 plots) of the relative latitudinal limits of seedlings and adults of 92 tree species across eastern United States largely failed to find evidence for ongoing warming-driven migrations, with only 21% of species exhibiting northward shifts and 59% contracting at both northern and southern limits (Zhu et al., 2012). A survey of forest stands near and at the northern limit for lodgepole pine (*Pinus contorta* Douglas ex Loudon) showed rapid local postfire population expansion at the limit, with no indication of strong climatic limitation (Johnstone and Chapin, 2003). Similarly, within lowlands, there are documented warming-driven expansions of thermophilic plant species into natural areas from planted individuals and stands in gardens and parks, e.g., invasion of evergreen exotics such as the palm *Trachycarpus fortunei* (Hook.) H. Wendl. into southern Swiss broad-leaved, deciduous forest (Walther, 2000). However, despite strong local expansions, migration rates have been 100–125 m per decade or less, leading to a moving front of evergreens with a strong concentration of the invasion in the immediate vicinity of the planted seed sources (Walther, 2000). Similarly, while the evergreen *Ilex aquifolium* L. has expanded in northern Europe—probably in large part from garden plantings—in response to the warming from 1931 to 1960 and 1981 to 2000, the newly suitable range remains only locally occupied (Walther et al., 2005).

Tree-line advances into herbaceous and shrub vegetation constitute a particular type of range expansion that has received

much attention. Arctic and alpine tree-line advances in response to the warming since the Little Ice Age (~1350–1850) have been highly variable, with sometimes slow or negligible advances, for example, in northern Eurasia during the 20th century (Macdonald et al., 2008; as discussed in, e.g., Dullinger et al., 2004; Danby and Hik, 2007)). This slowness at least partly reflects dispersal limitation, but may also involve edaphic lags (Payette, 2007; Macdonald et al., 2008; also see Dullinger et al., 2004). The likelihood of expansion appears to depend on the form of the treeline and the underlying mechanisms maintaining it (Holtmeier and Broll, 2005, Harsch and Bader, 2011), and in some cases, lags are only a few decades (Harsch et al., 2009). Infilling where sparse trees already exist can be rapid (Macdonald et al., 2008), but may still involve dynamics up to ~150 yr (Macdonald et al., 1993). These empirical observations are consistent with vegetation simulations by Chapin and Starfield (1997), estimating 150–250-yr lags (at 2°–5°C warming per century) for even initial (5%) forest establishment in Alaskan tundra and 250–375-yr lags for 80% conversion of tundra into forest. The latter lags were reduced to 50 yr when seed input unrealistically was set to values typical of forest rather than tree line (Chapin and Starfield, 1997). Arctic tree-line expansions in the early Holocene have typically similarly lagged warming on a centennial scale (Macdonald et al., 2008). For example, in western Norway the typical phases are a pioneer phase of open vegetation lasting 50–250 yr, followed by an intermediate phase dominated by dwarf shrubs (*Empetrum*, *Vaccinium*), with the final phase of *Betula pubescens* Ehrh.-dominated woodlands developing after 200–300 yr (Birks and Birks, 2008). At the start of the Holocene, the final phase took even longer (~700 yr) to develop, with stronger migrational lag due to greater distances to source areas during this period as one potential explanation (Birks and Birks, 2008; Fig. 5). Indicating even longer lags, dendrochronological evidence suggest that *Picea glauca* (Moench) Voss is still undergoing dispersal-limited postglacial expansion northward and upward into tundra areas in coastal northern Labrador, perhaps due to the complex topography of this region (Payette, 2007). Summarizing tree-line advance studies, Macdonald et al. (2008) concluded that there is potential for decadal to centennial scale lags in tree-line advances, but with important regional variation.

*What are the upper bounds on broad-scale plant range expansions, as indicated by recent invasions by exotic plant species?*—Invasive exotic plant species have sometimes expanded rapidly across large areas and probably represent the upper bound on what can be expected for future plant species migration rates under climatic warming. As one of the most dramatic cases, the annual cheatgrass (*Bromus tectorum* L.), now the most widespread exotic plant species in the intermountain West of North America, reached its present distribution within 32–39 yr after entering the region in the late 19th century. Its fast expansion probably was assisted by anthropogenic dispersal with the newly established railroad system (Mack, 1981). Another of the worst invasive plants in North America is the perennial wetland plant purple loosestrife (*Lythrum salicaria* L.); this species was introduced into eastern United States as early as 1814 and has since expanded to much of North America, remaining in strong disequilibrium with climate for the first 100 yr and only reaching its climatic limits in parts of the continent after 150 yr, with climatically suitable areas still remaining unoccupied at both small and large scales in other areas (Welk, 2004; also cf. Thompson et al., 1987). Numerous

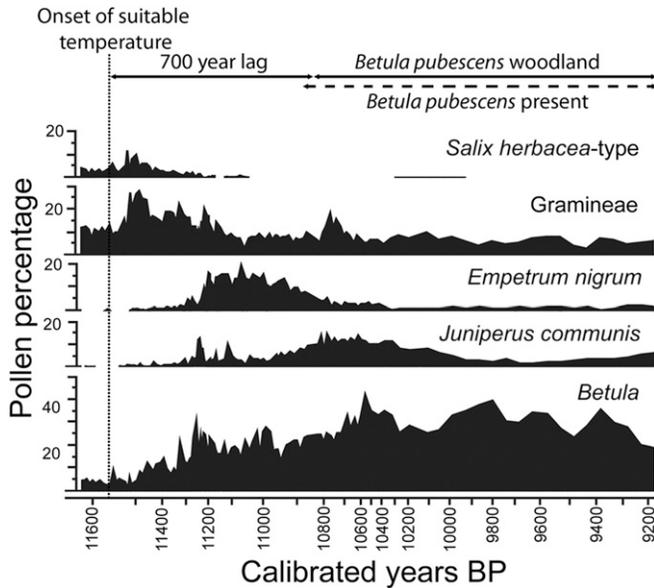


Fig. 5. Pollen records for a lake in western Norway, showing a successional sequence and slow expansion of tree birch (*Betula pubescens*) in the community after the climate became suitable for it at the Younger Dryas-Holocene boundary (dotted line). The local presence of *Betula pubescens* according to the macrofossil record is indicated. This succession lasted about 400 yr longer than typically observed today, with migrational lag due to greater distances to source areas as one potential explanation. Figure adapted from Birks and Birks (2008).

other invasive plant species are obviously still under expansion and hence in climatic disequilibrium despite having been introduced to a region 50–200 yr ago (e.g., Delisle et al., 2003; Wangen and Webster, 2006; Figs. 6, 7).

*How fast do plant migrations within landscapes allow smaller-scale range filling?*—Numerous studies have focused on plant species migration within landscapes, on smaller scales than the continental and regional scales discussed already. Migration rates in such landscapes vary among plant species and groups, with some groups showing very slow rates (e.g., Matlack, 1994; Honnay et al., 2002). A number of studies show poor to very poor recolonization of spatially isolated young forest patches on 25-yr to >100-yr time scales by forest herbs within landscapes where source populations are available, with recolonization success declining with increasing fragmentation (Peterken and Game, 1984; Matlack, 1994; Honnay et al., 2002). In some cases, species require at least 400 yr and probably more for complete recolonization (Peterken and Game, 1984). Further, even in the absence of isolation, >100-yr lags are also seen for recolonization into young forest patches adjacent to old source forest areas (Peterken and Game, 1984; Svenning et al., 2004, 2009; Chai and Tanner, 2010). Migration rates in these studies can often be linked to dispersal mode, with dispersal by ants and gravity conferring slow rates and dispersal by endo- and ectozoochory conferring relatively fast rates (e.g., Matlack, 1994; Honnay et al., 2002). Importantly, migration rates estimated in such local studies are much lower than those estimated at regional or continental scales (Fig. 2; but cf. Zhu et al., 2012).

*What do migration simulations tell us about likely plant migration rates in response to future climate change?*—Migration

modeling studies provide theory-based insights into plant species migration rates across spatial scales. A decade and half ago, the possibility for very fast migration was highlighted in models involving fat-tailed dispersal kernels, where the vast majority of propagules are dispersed short distances, while a few are dispersed very far (e.g., Pitelka and Plant Migration Workshop Group, 1997). Improved modeling since then, which avoids artifacts inherent to the earlier models, have generally suggested much slower migration rates: using life history data for trees, Clark et al. (2001) estimated migration rates of  $\sim 300$  m·yr<sup>-1</sup> for boreal spruce, 20–80 m·yr<sup>-1</sup> for wind-dispersed temperate species, and only 0.1–1 m·yr<sup>-1</sup> for animal-dispersed temperate species, with even slower rates if variable reproduction is included. Allowing for variable long-distance dispersal, Clark et al. (2003) estimated rates of 44 m·yr<sup>-1</sup> for wind-dispersed *Acer rubrum* L. and 0.6 m·yr<sup>-1</sup> for animal-dispersed *Carya glabra* (Mill.) Sweet, given moderate population increase (net reproductive rate = 2). Several other models of noninvasive tree migration also estimate low migration rates (e.g., Dullinger et al., 2004; Iverson et al., 2004). Notably, modeling of tree species migration in eastern North America taking species abundance and forest cover into account found highly limited migration over 100 yr following climatic release, with relatively high probability of colonization within 10–20 km of the current boundary, but a small probability of colonization further away (Iverson et al., 2004; Fig. 8). Migration models for three invasive tree species in South Africa estimate migration rates as  $\sim 700$  m·yr<sup>-1</sup>,  $\sim 100$  m·yr<sup>-1</sup>, and  $\sim 25$  m·yr<sup>-1</sup> for the three species, albeit with high parameter uncertainty (Higgins et al., 2003a). Models that incorporate habitat fragmentation show that the fragmented nature of many landscapes is likely to cause dramatic drops in migration rates for nonmatrix species: a simulation model for small-leaved lime *Tilia cordata* Mill. showed a sharp drop from 25% habitat availability toward lower habitat availability (Collingham and Huntley, 2000). In another study, migration models that describe barrier effects on seed-dispersal distances estimate realized vs. potential (no barrier) migration rates of 83 vs. 216 m·yr<sup>-1</sup> for the wind-dispersed (tumbleseeds) shrub *Leucadendron rubrum* Burm. f. in the Cape and 968 and 2186 m·yr<sup>-1</sup> for the ectozoochorous lynx-dispersed weed *Xanthium strumarium* L. in Spain (Higgins et al., 2003b).

The estimated global mean spatial shift (climate-change velocity) in mean temperature under the A1B scenario is 42 km per 100 yr, but with velocities of 100–1000 km per 100 yr in many regions (Loarie et al., 2009). While there remains significant uncertainty about how fast plant species can migrate, all lines of evidence suggest that a large proportion of plant species will be unable to make range expansions across many 10s of kilometers over the next 50–200 yr, with many—perhaps a majority—restricted to much smaller range expansions. Thus, range shifts can be expected to strongly lag behind the climate changes predicted by most scenarios on this time scale.

*Local population and community dynamics*—Immigration is not enough to achieve equilibrium with climate; populations also need to expand to the carrying capacity and equilibrium age and size structure set by the local ecosystem and climate conditions. Although it is not possible to make a perfectly unambiguous distinction, we separately consider large-scale migration into new regions and landscapes (covered above) from local population growth, which may include increased local filling of the range area. Two perspectives are important here, the intrinsic capacity of plant populations to increase and community-driven successional dynamics.

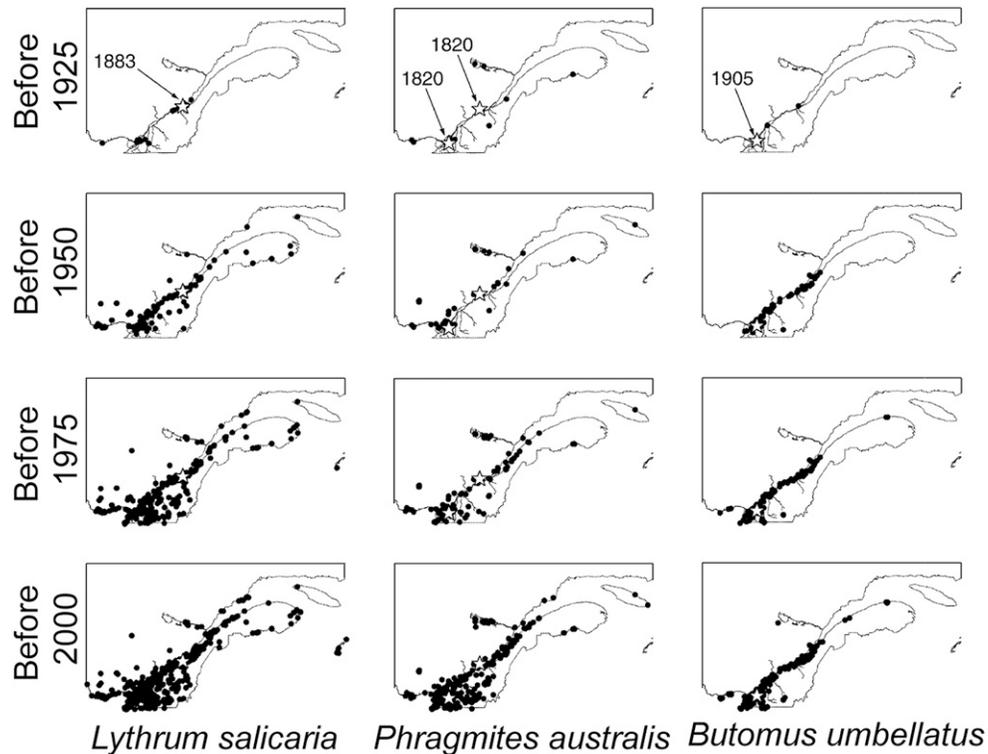


Fig. 6. Protracted spread of three invasive wetland plants along the St. Lawrence River in southern Quebec, assessed using herbarium records. The sites of first collection are marked with a star and dated. The expansion of each species has continued across >100 yr after it was first detected on the landscape. Figure adapted from Delisle et al. (2003).

*Over what time scales do local populations build up?*—Over the short time frame of 50–200 yr, the life cycle length of plants will impose simple lags in local population build up. While some plants are annual and biennial, the majority are perennial, with many requiring one or more decades to reach maturity even under ideal growing conditions. Under typical field conditions, time to maturity may often be considerably extended due to abiotic stresses, herbivory, and competitive suppression. Exemplifying this, the time required to reach the canopy for six nonpioneer tropical trees was estimated to be 34–59 yr at maximum growth rates, but 177–462 yr at median growth rates (Clark and Clark, 2001). Northern conifers typically reach reproductive maturity in 15–40 yr, making lags in both migration and establishment inevitable (Macdonald et al., 2008).

In situ dynamics may involve both expansions of recently arrived species and abundance changes among species long present. Concerning the former, there is evidence for sometimes long lag times between arrival and expansion, with expansion sometimes depending on disturbance of the already established vegetation. Pronounced lags, lasting multiple decades, between initial colonization and the onset of rapid population growth and range expansion are often seen in invasive exotic species (Sakai et al., 2001). These lags also occur locally. For example, *Acer platanoides* L. arrived in a ~800 ha forest area in the northern United States in 1938, and experienced only slow population expansion until 1965, after which it expanded more rapidly, but nevertheless still only occupied ~200 ha in 2002, >60 yr after arrival (Wangen and Webster, 2006; Fig. 7). Such lags are also seen under natural invasions, although their duration varies. In southern Scandinavia, local expansion of northward-migrating *Fagus sylvatica* was delayed for up to 1000 yr after

arrival and only happened after disturbance (Björkman and Bradshaw, 1996; Cowling et al., 2001; Bradshaw and Lindbladh, 2005), despite the fact that *Fagus sylvatica* is a shade-tolerant, late-successional dominant under the regional climate. In other cases, later dominants rapidly invade locally without any disturbance, as has been the case with the other main shade-tolerant, late-successional dominant in southern Scandinavia, *Picea abies* (Björkman and Bradshaw, 1996; Bradshaw and Lindbladh, 2005). Nevertheless, despite rapid expansion of this species within the first generation after arrival 175 yr ago, local expansion has continued since then (Björkman and Bradshaw, 1996). For Central Europe, Tinner and Lotter (2006) likewise concluded that local expansions of *Fagus sylvatica* in response to climate change lasted for several centuries, probably due to fairly low intrinsic population growth rates and competition. Such time scales for local expansions are probably typical at least in the cases of long-lived species. In forest herbs, it is common for species to show extremely slow rates of local population expansions, often just a few meters or less per year. For example, in a study of the migration of herb-layer plants from ancient woodlands into adjacent recent stands, 49 woodland plant species exhibited maximum expansion rates over 30–75 yr of 0.00–1.25 m·yr<sup>-1</sup>, with a median of just 0.53 m·yr<sup>-1</sup> (Brunet and von Oheimb, 1998). Populations of the forest herb *Hyacinthoides nonscripta* established 60 km beyond the range limit exhibited expansion rates of just 0.006–0.06 m·yr<sup>-1</sup> over 45 yr (Van der Veken et al., 2007).

*How much time does secondary succession require?*—Even in the absence of immigrating new species, the expected climate changes are likely to elicit strong successional dynamics

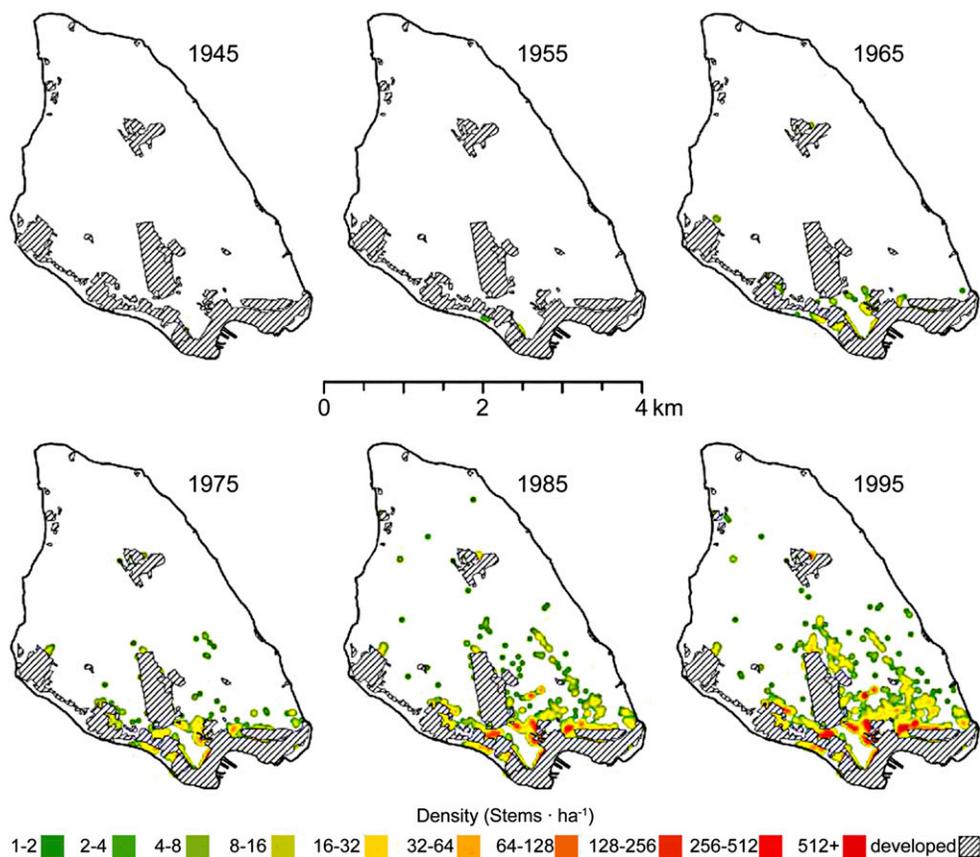


Fig. 7. Spread of *Acer platanoides* L. on the small, forested Mackinac Island in Lake Huron, USA. Despite the island being largely covered by suitable habitat, the spread of this invasive tree species has been very limited, even 50 yr after introduction. Figure adapted from Wangen and Webster (2006).

within established vegetation due to losses of sensitive species and changing competitive status. In his review of vegetation–climate equilibrium, Webb (1986) suggested that such purely *in situ* dynamics (without the involvement of range extensions and soil development) require 50–80 yr to proceed roughly 2/3 toward completion. Mechanistic forest tree community simulation models also suggest that *in situ* successional dynamics may occur over protracted time periods. A model of oak–northern hardwoods forests in northeastern North America simulates successional trajectories lasting 500–1500 yr depending on the initial abundances of the various tree species (Pacala et al., 1996) (Fig. 9). The authors conclude that “the implication here is that second growth stands will be dominated by initial conditions for periods exceeding the age of most forest stands in northeastern North America” (p. 23).

Linking such forest simulation models to paleoclimatic simulations also provides insights into the time scales for successional dynamics within established vegetation in response to past climatic fluctuations. During the present and earlier interglacials, there are several cases of short-term cooling events that elicited strong vegetation responses. Campbell and McAndrews (1993) assessed the response of a mixed northern temperate forest in southern Canada to the Little Ice Age cooling (2°C from 1200 to 1850), comparing the pollen record to the results of a forest simulator. They found the cooling to result in the near-loss of two of the three initially dominant species [*Fagus grandifolia* Ehrh. and *Tsuga canadensis* (L.) Carrière] and the resulting release of multiple other species (notably *Acer*

*saccharum* Marshall and *Pinus strobus* L.). Furthermore, they found that the successional dynamics in the simulation continued until the end of the simulation in 2000, indicating disequilibrium dynamics continuing at least 150 yr after the cooling has stopped.

Disturbances may, however, also drive fast shifts in composition in some cases. At the northern limit for lodgepole pine (*Pinus contorta*), local postfire population expansion is so rapid that many stands appear to be switching from spruce to pine dominance after a single fire event (Johnstone and Chapin, 2003). Such fast shifts will of course only occur for species adapted to exploit such severe disturbances and will be as stochastic in space and time as the disturbances themselves.

**Evolutionary adaptation**—Many species of plants show great within-species variation, with particular populations showing adaptation to local conditions (Linhart and Grant, 1996; Joshi et al., 2001; Davis et al., 2005; Giménez-Benavides et al., 2007; De Frenne et al., 2011). With future fast climate change, such adaptations may become obsolete, causing less fit individuals and more poorly performing local populations than expected from the species’ overall climatic niche and general ecological characteristics. This has been demonstrated in transplant experiments across climate gradients (e.g., Davis et al., 2005; Giménez-Benavides et al., 2007; De Frenne et al., 2011), sometimes with differing effects among populations across the species’ range (Reich and Oleksyn, 2008). Evolutionary responses to the new conditions may occur, involving selection

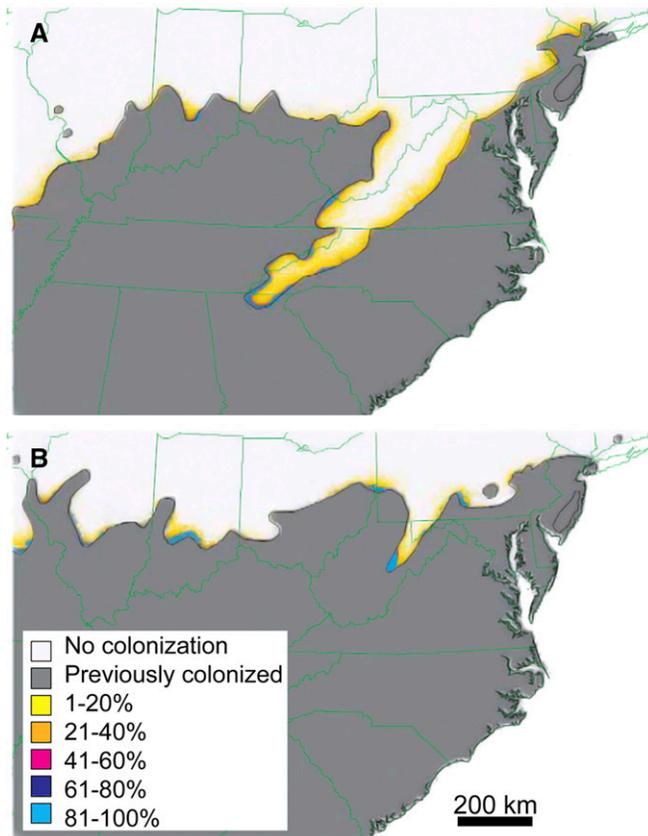


Fig. 8. Slow, large-scale migration rates in trees. Estimated probability of colonization outside the current range of the eastern North American trees (A) *Liquidambar styraciflua* L. and (B) *Diospyros virginiana* L. 100 yr after release from climatic limitation. The model only considers dispersal and habitat availability (forest cover). Overall expansions of the species are expected to be quite restricted. Figure modified from Iverson et al. (2004).

for particular trait states or for trait plasticity, thereby allowing performance to recover. Such evolutionary responses are likely to lag strongly in organisms with long generation times (Aitken et al., 2008). Davis et al. (2005) concluded that local adaptations evolve at time-scales of decades to within a century in herbs, but over 100s or 1000s of years in trees; hence, at least for the latter, evolutionary lags will be strong. Maladapted stressed local populations might simply not tolerate the novel climate conditions as well as populations that have had sufficient time to adapt, leading to reduced performance or even local extinction under conditions the species would otherwise have tolerated. In addition, such stressed populations are likely to become less competitive relative to other species and more susceptible to attacks by pests and pathogens, as perhaps evidenced by recent drought- and warming-induced insect outbreaks in many forests (Allen et al., 2010).

**Ecosystem development**—Leading-edge disequilibrium may not only arise in terms of species distributions and composition, but also in terms of ecosystem structure and functioning. We consider the likelihood of disequilibrium dynamics in three key aspects of ecosystem development: soils, productivity and carbon sequestration, and vegetation-defined habitat structure.

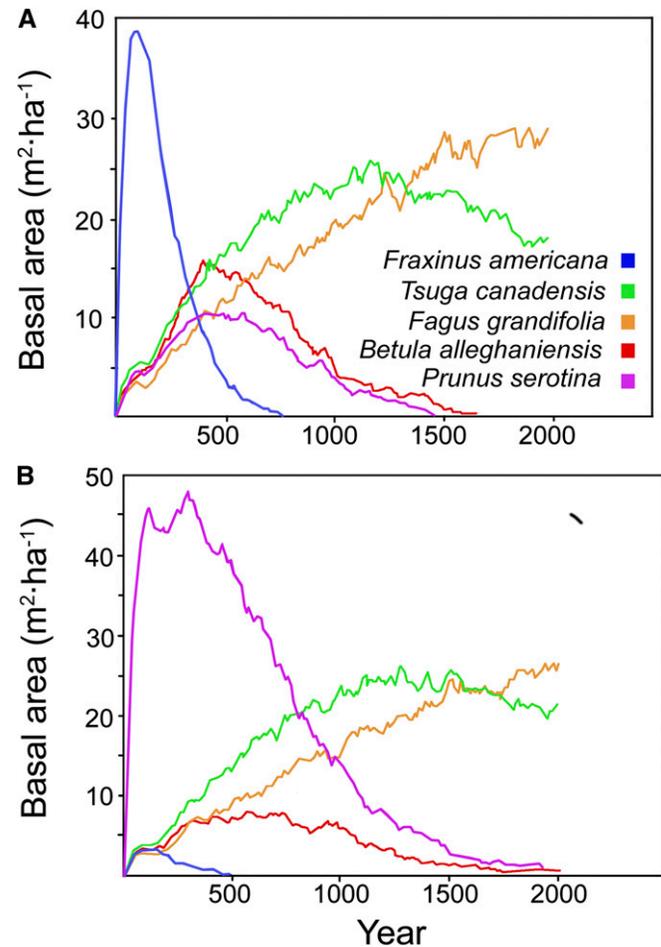


Fig. 9. Slow successional dynamics in forest composition in eastern North American temperate forest predicted by the SORTIE model, given different initial conditions. In (A), all species started with low (25 m<sup>2</sup>·ha<sup>-1</sup>) basal areas, except *Fraxinus americana* L., which had an area of 250 m<sup>2</sup>·ha<sup>-1</sup>. In (B), only *Prunus serotina* Ehrh. started with higher abundance. Community composition remains sensitive to initial conditions for at least 1000 yr. Figure adapted from Pacala et al. (1996).

*What is the time required for soil development?*—Soils are a key component of ecosystems, and their development is often ultimately controlled by climate (Birkeland, 1999) but proximately controlled by vegetation. Thus, vegetation change may induce soil change (e.g., Miles, 1985), with potentially strong consequences for ecosystem properties such as vegetation structure, litter accumulation, carbon sequestration, and nutrient cycling. For example, it is well known that many conifers may induce podsolization, as may certain broadleaved trees such as *Fagus sylvatica*. Such edaphic change has been implicated in sometimes driving vegetation dynamics during previous interglacials as well as during the Holocene (e.g., Andersen, 1966; Kuneš et al., 2011). Conversely, invasion by other broadleaved trees may cause such conifer-generated podzolic soils to develop into brown-earth soils, as observed in Hungary in the early Holocene, with strong impacts not just on land, but also on local lake chemistry (Willis et al., 1997). Importantly, vegetation-induced soil changes may require centuries or more for completion. Development of mature podzol soils requires at least 1000 yr, with early stages developing within 100–150 yr

(Miles, 1985), while the early Holocene podzol-to-brown-earth shift in Hungary took ~1000 yr (Willis et al., 1997). As vegetation-induced soil change may induce shifts in vegetation, if conditions become unsuitable for resident species or change to suitable for potential immigrant species, lagged vegetation-induced soil change may strongly add to disequilibrium conditions at the 50–200 yr time scale of future climate change.

A number of studies provide empirical evidence that lags in soil development may contribute to multicentury delays in vegetation response to warming. For example, much of northern Eurasia has thick climate-dependent organic soils, which may impede a warming-driven advance of trees such as *Betula* spp. and *Pinus sylvestris* L. because these have very poor recruitment on such soils (Macdonald et al., 2008).

A special type of dynamic that involves edaphic lags is succession on surfaces previously devoid of vegetation or primary succession. Near-future climate change will induce primary succession in areas undergoing deglaciation. Contemporary studies show that primary succession after deglaciation typically requires at least several centuries to proceed to the late-successional phase, with 200–300 yr required for soils to mature enough to allow trees to establish even in the absence of dispersal limitation (Pennington, 1986). In the High Arctic, vascular plants may constitute only a minor component of the ground cover for the first 100 yr (Hodkinson et al., 2003). The paleorecord points to similar partially edaphic lags under past deglaciations. One plausible case is the development of birch (*Betula pubescens*) forests in northwestern Europe after warming in the early late-glacial (Paus, 1995). Here, edaphic lags have been implicated as a strong contributor to the 500–1000-yr lags between warming and birch forest development (Pennington, 1986; Paus, 1995; also see Birks and Birks, 2008 and earlier discussion in migration section). Edaphic lags may sometimes last for thousands of years. A recent study shows that postglacial development of soils (soil depth) may explain 3000–6000-yr lags in spruce expansion [*Picea abies* (L.) H. Karst.] at high altitudes in central and western Switzerland after temperatures became suitable (Henne et al., 2011).

*Are productivity and carbon sequestration subject to disequilibrium dynamics?*—An important ecosystem function is carbon sequestration, with potential consequences for the atmosphere and the global climate system. Lags in vegetation development may cause lags in carbon build-up in vegetation. Notably, a global analysis of temperate and boreal forests between 15 and 800 yr in age found that net ecosystem productivity (net carbon balance including soils) is usually positive, demonstrating that old-growth forest continue to accumulate carbon for centuries (Luyssaert et al., 2008; Fig. 10). Hence, cumulative carbon sequestration in forests may increase for 500 yr or more, implying strong lags where climate change causes forest successions to start or restart. Dieback of established trees due to climate change may cause strong reductions in biomass and thus carbon storage. These may be of disequilibrium nature if succession will eventually restore biomass via abundance increases in species that are better adapted to the new climate. Simulating the effect of the Little Ice Age cooling on a northern temperate forest, Campbell and McAndrews (1993) found the cooling to result in disequilibrium species composition and a 30% loss of biomass primarily due to deaths of mature *Fagus grandifolia* trees, the precooling dominant. In some cases, complex shifts in productivity and carbon sequestration may occur, with lags at least as long as the species compositional

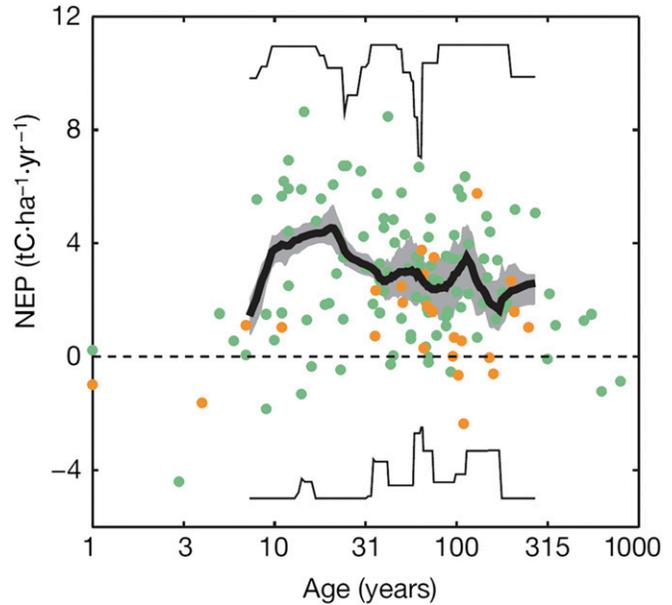


Fig. 10. Carbon accumulation in forests continues for hundreds of years. Net ecosystem productivity of temperate (green) and tropical (orange) forests is shown, with positive values indicating forests that are carbon sinks, and negative values indicating carbon sources. The black line is a weighted mean within 15-observation moving windows, with the 95% confidence interval of this mean shown as a gray area. The thin black lines show the 95% confidence interval of individual observations. Figure modified from Luyssaert et al. (2008)

shifts involved. For example, local expansion of lodgepole pine (*Pinus contorta*) at its northern range limit at the expense of spruce (*Picea* spp.) is likely to lead to more frequent fires, greater stand productivity, and lower soil carbon (Johnstone and Chapin, 2003).

*Is vegetation-defined habitat structure subject to disequilibrium dynamics?*—Many aspects of vegetation contribute habitat for codependent species. Some species are associated with disturbance and early succession habitats (Brawn et al., 2001), which may be expected to develop with relatively minor lags. In contrast, more species are associated with late successional vegetation (e.g., Tyrrell and Crow, 1994). Many groups of organisms include numerous old-growth dependent species. High-profile examples include the northern spotted owl (Carey et al., 1992) and the giant panda (Zhang et al., 2011). Further, many species of insects and fungi are associated with old trees of particular species and thus depend on structures that may take 200 yr or more to develop (e.g., Ranius and Jansson, 2000). In addition, many herbivorous insects and mycorrhizal fungi are associated with specific species or small sets of species and thus require their presence; hence, lags in the dynamics of their hosts will also induce lags in the dynamics of these species even if they themselves have adequate dispersal ability, generation time etc. to track climate (e.g., Araújo and Luoto, 2007; Schweiger et al., 2008; Preston et al., 2008). A key component of habitat structure in woody vegetation is coarse woody debris. Woody vegetation causes the build-up of woody debris, with coarse woody debris being of high importance for the large deadwood-inhabiting component of biodiversity such as many beetles, fungi, and bryophytes (Grove, 2002; Ódor et al., 2006).

Build-up of coarse woody debris is decidedly time-lagged where woody vegetation is newly established (e.g., Tyrrell and Crow, 1994; Dewalt et al., 2003).

#### CLIMATE-DRIVEN PROCESSES CAUSING TRAILING-EDGE DISEQUILIBRIUM

What is the empirical evidence for the different processes that may be driving disequilibrium dynamics at the trailing edge? To answer this question, we consider two factors that may delay local extinction: longevity and clonality, and evolutionary adaptation, as well as the potential for delayed losses of ecosystem structural components.

**Longevity and clonality**—Many plant species have very long-lived individuals. Numerous tree species and other woody plants commonly attain ages of several hundred years, and many even attain ages of a 1000 yr or more (e.g., Larson et al., 1999; Lanner, 2002; Laurance et al., 2004). Individuals of some herbaceous species live for decades or even >100 yr (e.g., Inghé and Tamm, 1985; García et al., 2008). Further, many herbaceous as well as woody plants are clonal, allowing genets to persist essentially indefinitely. Genetic evidence shows that saw palmetto [*Serenoa repens* (W. Bartram) Small]—an important shrub-layer plant in southeastern North American ecosystems—predominantly propagates clonally and that 10000-yr-old genets may be common (Takahashi et al., 2011). Further, genetic and paleobotanical evidence suggests that the clonal Tasmanian shrub *Lomatia tasmanica* W. M. Curtis is a single genet that has persisted for >40000 yr (Lynch et al., 1998). As a result, many long-lived plants and especially those with clonal propagation are able to build so-called remnant populations, i.e., populations that only decline very slowly over decades, centuries, or even longer after conditions have become unfavorable for recruitment (Eriksson, 1996).

A number of temperate plant species in the Mediterranean have population structures that are dominated by adults and senescent individuals, with poor seedling recruitment due to drought stress, and are apparently remnant populations from more-humid, past periods (e.g., García et al., 1999; Mejías et al., 2002). More generally, several studies have shown that longevity buffers plant species against extinction due to temporal fluctuations in population size, such as those induced by climate (García et al., 2008; Morris et al., 2008). Hence, longevity and clonality will most likely cause strong lags in vegetation adjustment to climate change over the next 50–200 yr via slow local extinction, by allowing some species to persist despite conditions having become so unfavorable that the species cannot complete its life cycle anymore. Remnant populations thus may increase community and ecosystem resilience to climate change by delaying extinction of the species concerned as well as by providing a persistent habitat for codependent species, enhancing colonization of other species dependent on established vegetation, and reducing variation in biogeochemical cycling (Eriksson, 2000), e.g., including carbon storage. However, remnant populations might also reduce colonization of potential immigrant species via competition (Urban et al., 2012), thereby contributing to leading-edge disequilibrium dynamics in other species (Fig. 1).

Such long lags will not buffer all species at all localities against rapid local extinctions. Thresholds may be passed where even established individuals quickly die off, as exemplified by

recent drought-induced, massive mortality of various tree populations around the world, including *Pinus edulis* Engelm. in the American Southwest (e.g., Allen et al., 2010; Mueller et al., 2005). Likewise, decadal-scale local extinction at the lower altitudinal limit of the long-lived alpine herb *Silene ciliata* Pourr. has been predicted due to drought-induced demographic impacts including reduced longevity (Giménez-Benavides et al., 2011). The paleoecological record also provides insights on the time scales for climatically induced diebacks although resolution often does not allow assessment of the timing of complete extinction. Numerous paleobotanical studies provide evidence of sometimes rapid declines in response to climate variability, e.g., within the Holocene, but often total local extinction is not indicated (e.g., McGlone et al., 2000; Beer and Tinner, 2008; Koutsodendrís et al., 2012).

**Evolutionary adaptation**—While evolutionary lags may cause leading-edge disequilibrium, they can also lead to trailing-edge disequilibrium when species are able to persist at a site longer than expected given shifting climatic conditions (Fig. 1). Predictions for future species distributions typically assume that future distributions will be constrained by the same climatic conditions as currently limit the species (Pearson and Dawson, 2003). Alternatively, species may remain fixed in space while adapting to changing conditions, which may delay extinctions perhaps until superior competitors under the new climate immigrate. In such a case, expectations based on a species' original climate tolerances will give a misleading indication of its transient responses to changing climate. Though such adaptive responses are theoretically expected, empirical evidence for them is relatively scarce, especially evidence that unequivocally attributes changes to adaptation rather than acclimation (Gienapp et al., 2008). Importantly, there is clearly also much conservatism in climatic tolerances and thus species distributions in many cases, even among drosophilids, despite their short generation times and high population sizes (Kellermann et al., 2012a, b). Still, evidence is accumulating for both animals (Bradshaw and Holzapfel, 2006) and plants (Woodward, 1990; Franks et al., 2007) that local evolutionary responses to climate change can be important in some cases.

**Delayed losses of ecosystem structural components**—As already discussed, remnant populations may delay losses of structural components, e.g., carbon losses. In addition, it is conceivable that structural features such as soils or coarse woody debris that have developed under certain vegetation conditions may remain for some time after this vegetation has disappeared. To our knowledge, such lags in structural losses, e.g., after climate-driven forest losses, have received little attention.

#### DISEQUILIBRIUM DYNAMICS DRIVEN BY OTHER GLOBAL-CHANGE FACTORS

Are nonclimatic global-change factors likely to interact with climate change to exacerbate future disequilibrium dynamics? Much evidence suggest that the answer is yes, with several global-change factors likely to contribute to vegetation disequilibrium under future climate change, either by interaction with climate change or independently. These include biological invasions (notably the arrival of novel competitors, pests, and pathogens), habitat loss and fragmentation effects, as well as changes in disturbance regimes, nitrogen deposition, and other

pollution. Given the predicted global and regional increases in human population densities and resource use, all of these effects are likely to increase over the next century (e.g., Sala et al., 2000). These effects represent disequilibrium dynamics by causing directional species declines despite a suitable climate and may directly affect or even elicit climate-driven disequilibrium dynamics.

Globalized trade and travel has led to increasing problems with exotic pests and pathogens, sometimes causing massive declines in certain native tree species such as the classical case of the American chestnut [*Castanea dentata* (Marshall) Borkh.] and the recent hemlock (*Tsuga canadensis*) decline (Fig. 11), both of which have important effects on community structure (Castello and Leopold, 1995; Orwig, 2002; Stadler et al., 2005). These dynamics may involve shifts in the realized climate niche (e.g., Paradis et al., 2008; Dukes et al., 2009; Fig. 11) as well as complex ecological and evolutionary interactions between hosts and pests and pathogens (e.g., Brasier, 2001). Invasive plants may cause similar disequilibrium dynamics on their own, given their dispersal-limited spread, which often last decades or centuries even for successful invasives, and via their interaction with resident species (cf. earlier discussion). These migration dynamics will themselves be influenced by future climate change (e.g., Walther, 2000; Paradis et al., 2008; Dukes et al., 2009; Fig. 11).

The growing human population and the associated increases in land-use intensity and habitat loss and fragmentation are also likely to drive disequilibrium dynamics. Notably, fragmentation may strongly slow migration rates for many species (Collingham and Huntley, 2000; Honnay et al., 2002; McInerny et al., 2007), which may increase lags in climate responses (see earlier discussion). Furthermore, successional dynamics after disturbance may affect species distributions and vegetation structure on landscape scales for hundreds of years (e.g., as has been found

in various tropical rain forest areas; Chazdon, 2003; Svenning et al., 2004) and are likely to strongly affect transient vegetation responses to climate change, retarding or accelerating responses depending on timing.

#### REPRESENTATION OF DISEQUILIBRIUM DYNAMICS IN CLIMATE-CHANGE IMPACT MODELING

Disequilibrium dynamics present a challenge for predictive modeling, which must be addressed by improved modeling approaches. In this section, we discuss several modeling approaches that hold promise for representing disequilibrium. Static, physiology-based, vegetation-type models (e.g., Prentice et al., 1992) as well as the commonly used statistical correlative models of species distributions (e.g., Dormann et al., 2012) do not generally represent transient dynamics, but rather forecast equilibrium conditions. The most common way to represent disequilibrium dynamics in forecasts based on statistical, correlative models is to implement so-called full- and no-dispersal scenarios (e.g., Skov and Svenning, 2004; Thuiller et al., 2005), in which full-dispersal scenarios assume that species can spread at unlimited rates to all suitable sites at a given time (obtain full equilibrium with climate instantaneously) and no-dispersal scenarios assume such strong dispersal limitation that the species will not spread beyond currently occupied sites. It is, of course, also possible to implement intermediate assumptions about potential spreading distances, and this offers a simple and promising approach to better represent disequilibrium dynamics in such modeling.

There are a number of forecasting models that represent population and community dynamics and/or dispersal to various extents (Dormann et al., 2012). These include dynamic

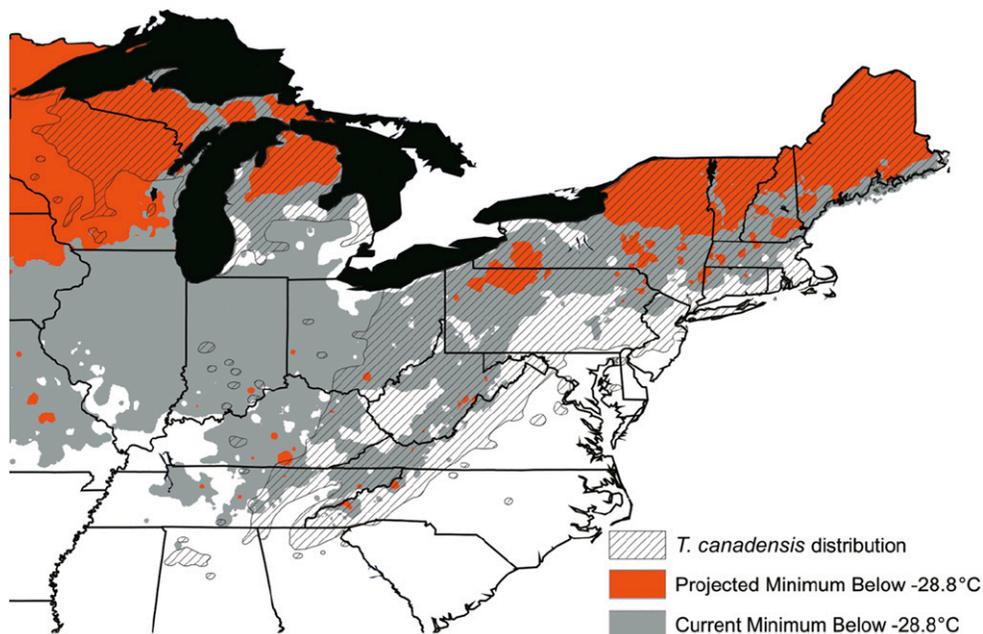


Fig. 11. The distribution of eastern hemlock (*Tsuga canadensis*, hatched area) and temperature tolerances of the invasive pest insect, the hemlock woolly adelgid (*Adelges tsugae*). Currently, the hemlock woolly adelgid is limited to areas with a minimum winter temperature above  $-28.8^{\circ}\text{C}$  (white), where it has been expanding since the late 1960s, driving massive declines in hemlock that may eventually lead to its extinction in these areas. Under the A2 emissions scenario, the  $-28.8^{\circ}\text{C}$  minimum temperature isocline is expected to advance substantially northward by 2070 (gray region), likely leading to hemlock declines across this region as well. Figure modified from Dukes et al. (2009).

global vegetation models (DGVMs), which extend equilibrium biome models to include dynamic physiological and population processes, thus more directly representing transient dynamics including disturbance and succession (e.g., Woodward and Beerling, 1997; Foley et al., 2000; Cramer et al., 2001). There are also forest simulation models that represent tree population dynamics and gap-phase dynamics (Botkin et al., 1972; Pacala et al., 1996), which are typically developed for specific local forest systems, but are now also developed as more generalized models by combination with DGVM methodology (Hickler et al., 2004). These are generally parameter-rich simulation models calibrated for small sets of species and represent successional dynamics especially well, but often do not include dispersal beyond local communities. Hybrid species distribution models, where statistical estimation of habitat suitability is combined with mechanistic modeling of population dynamic and/or dispersal processes (Dormann et al., 2012), allow the representation of transient dynamics. As these models are often less parameter-rich (beyond those estimated statistically from distribution data), they are more easily applied to large numbers of species and less-studied species and ecosystems. Exemplifying this, a recent such hybrid model forecast range dynamics of 150 high-mountain plant species across the European Alps from 2010 to 2100 under a standard warming scenario, simulating both demography and seed dispersal (Dullinger et al., 2012). This model predicts that across all species an average of 40% of the occupied range in year 2100 will have become climatically unsuitable, creating an extinction lag in which populations deterministically will decline to extinction during the subsequent decades or for some populations several centuries (Dullinger et al., 2012). At the same time, the model simulates strong dispersal limitation with an average across species of 20–40% of suitable sites being unoccupied by year 2100 (Dullinger et al., 2012).

Lags in vegetation responses have only to a limited extent been integrated into predictive modeling of other species, despite the ecological importance of plants, e.g., as ecosystem engineers (Jones et al., 1994). Exemplifying the potential impact of vegetation lags on codependent species, Kissling et al. (2010) forecast statistical models of bird species richness across Kenya as a function of climate, topography, and woody-plant species richness under a range of climate-change scenarios, modeling either instantaneous climate-tracking in woody-plant species richness or no tracking. Bird species richness is predicted to increase in most areas when the woody plant response is instantaneous, but to decline across the country when the response is strongly lagged (Kissling et al., 2010).

Currently, there is a strong trend toward better representation of processes and dynamics in forecasting models (e.g., Dormann et al., 2012), and so disequilibrium dynamics can be expected to be increasingly represented. However, this will often come at a cost of increasing model complexity and hence will invoke the classical trade-off between complexity and robustness. Many complex and interacting processes may be involved in disequilibrium dynamics, which may make them hard to predict, especially as some factors such as the introduction of novel exotic pests may be essentially stochastic. Hence, accurate spatiotemporal predictions may be hard to achieve. Nevertheless, better representation of disequilibrium dynamics will increase general ecological realism and thereby provide an improved basis for conservation planning, if interpreted with the uncertainties in mind. Schwartz (2012) argues that statistical species distribution models tend to overestimate extinction risks and should mainly be used for forecasting new areas of suitable

habitat. Similar issues need to be considered when forecasting disequilibrium dynamics. One of the more robust results might be lower limits on the time required for various dynamics, e.g., from immigration of a species to when it has reached its carrying capacity at a site.

#### REPRESENTATION OF DISEQUILIBRIUM DYNAMICS IN EXPERIMENTAL CLIMATE CHANGE MANIPULATIONS

Another key method for improving our understanding of vegetation responses to climate change is via experiments. While not generally a focus of experimental studies, these often suggest disequilibrium dynamics as the likely outcome of climate change, with time lags and transient effects evident in the responses of plant communities and ecosystems to experimental climate change and atmospheric CO<sub>2</sub> manipulations (e.g., Chapin et al., 1995; Arft et al., 1999; Shaver et al., 2000; Rustad, 2006; Souza et al., 2010; Norby and Zak, 2011). Following experimental warming, for example, transient increases or decreases in net ecosystem uptake of carbon are common, with some systems switching from carbon sinks to carbon sources as treatment effects develop (Shaver et al., 2000). Shifts in the magnitude and sign of responses occur because the different mechanisms of change take different amounts of time to act—for example, changes driven by a direct effect of temperature on decomposition rates can be quite rapid, while changes due to turnover in species composition are likely to be much slower (Fig. 12). Critically, different mechanisms do not necessarily drive ecosystem responses in the same directions, potentially resulting in complex transient dynamics (Shaver et al., 2000). For example, changes in tundra community composition following experimental warming showed short-term (up to 3 yr) dynamics that matched neither dynamics after 9 yr, nor vegetation change along natural gradients (Chapin et al., 1995). These complexities not only pertain to warming, but also to other changes in climate and in atmospheric CO<sub>2</sub>. Results from free-air CO<sub>2</sub> enrichment (FACE) experiments indicate that CO<sub>2</sub> enrichment may induce long-term changes in vegetation dynamics and community composition (Norby and Zak, 2011), e.g., an ongoing increase in forest understory woody plant biomass that may eventually affect future overstory species composition (Souza et al., 2010). Further, plant community composition shows strongly lagged responses to experimental precipitation increases (Sandel et al., 2010). Experimentally watered communities shifted toward compositions of species with high leaf nitrogen concentration, small seeds, and short-lived leaves. These changes in composition are opposite to that observed along natural precipitation gradients. Further, there is evidence for transient responses of vegetation to natural variation in precipitation that are opposite to the expected long-term effect (Sandel et al., 2010). Even 15 yr of precipitation manipulation were not enough to reverse these transient changes in community composition, which likely reflect rapid responses of weedy species to high resource availability, but very slow conversion of the community from grassland to woody vegetation, as is expected over the long term. Another example from a watering study comes from Suttle et al. (2007), who showed that initial responses of the plant community (first 2 yr) were driven by responses of each species to greater water availability, while modified interactions among species and an altered food web dominated changes in the next 3 yr, overturning initial community responses.

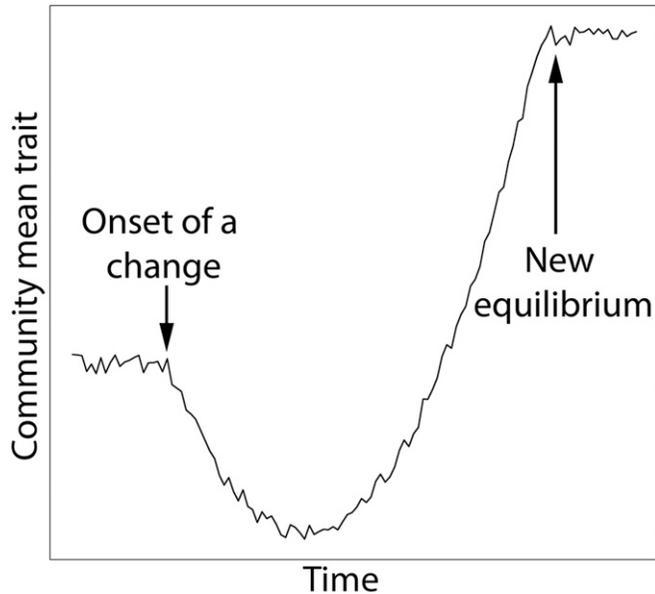


Fig. 12. The functioning of a plant community may be summarized by the mean value of a functional trait across all species in that community. A hypothetical community shows fluctuation in this value through time around some equilibrium, until a climate change disturbs the community away from this equilibrium. While the long-term consequence of this disturbance is an increase in the trait mean, the initial response of the community may be toward lower trait means. This can occur if the community change occurs in two phases, the first of which is driven by in situ changes in relative abundance, and the second of which is driven by time-lagged immigration of new species. Experimental studies of community response to climate change have suggested that these two phases may sometimes show differing and even opposite responses.

Together, experimental results provide an important line of evidence for disequilibrium responses of plant communities to climate change, over time scales of at least decades. Furthermore, compositional shifts and other vegetation changes within sites are often not simple and monotonic through time, but reflect complex transient dynamics. Climate-change manipulation experiments could be designed to better shed light on short- as well as long-term outcomes by taking disequilibrium dynamics and the underlying mechanism into account (cf. Fig. 12), e.g., with seed introductions (Turnbull et al., 2000) to simulate expected longer-term immigration of warmth- or drought adapted species.

#### SYNTHESIS AND OUTLOOK

Ecology and conservation biology are increasingly emphasizing disequilibrium concepts and perspectives (e.g., Hubbell, 2001; Gillson and Willis, 2004; Mori, 2011), notably recognizing a key role for disturbances in ecosystems (Pickett and White, 1985; Mori, 2011). Still, disturbances are often seen as periodic factors that contribute to maintaining steady state (Mori, 2011). Our review underscores the need for more radically embracing disequilibrium perspectives when considering vegetation dynamics over the next 50–200 yr. At this time scale, lagged vegetation responses to the expected strong climate shifts (IPCC, 2007) will cause ecosystems to behave as nonequilibrating dynamic systems even more than they would otherwise have done due to postglacial migrational lags (Svenning

and Skov, 2004; Payette, 2007; Normand et al., 2011), neutral dynamics (Hubbell, 2001), stochastic large disturbance events (Pickett and White, 1985; Peterken, 1996; Mori, 2011), and natural decadal- to millennial-scale climate variability (Campbell and McAndrews, 1993). In his well-cited contribution to the debate over vegetation equilibrium with climate in the paleoecological literature, Webb (1986) concluded that changes in vegetation would occur rapidly enough to maintain equilibrium with climate. Webb (1986) based his conclusion on time scales of 1000 yr or more and noted that response processes would generally be too slow to allow vegetation to equilibrate with climate on a 100-yr time scale, the relevant time-scale when considering vegetation responses to the expected climate changes over the next 50–200 yr. Our review confirms the latter point, indicating that the strong climate changes expected over this time period are likely to induce marked disequilibrium with climate in many aspects of vegetation conditions and at both leading and trailing edges, with leading-edge disequilibrium dynamics due to migrational lags at continental to landscape scales, and lags in local population build-up and succession, in local evolutionary responses, and in ecosystem development, and trailing-edge disequilibrium dynamics involving delayed extinctions due to longevity, clonality, and evolutionary adaptation, and delayed ecosystem structural losses. Interactions with other global change factors such as habitat loss and fragmentation as well as invasive pests and pathogens will further exacerbate these disequilibrium dynamics. While all of these disequilibrium dynamics are likely to become of wide importance over the next 50–200 yr, the evidence base is particularly broad and strong for lags in migration, local population build-up and succession, and ecosystem development.

The likely pervasiveness and complexity of vegetation disequilibrium with climate is a major challenge for forecasting future ecological dynamics and conditions and combined with the high ecological importance of vegetation also constitutes a major challenge for future nature conservation. This broad issue is well encapsulated in the assisted migration debate (Barlow and Martin, 2005; McLachlan et al., 2007; Hoegh-Guldberg et al., 2008). On one hand, assisted migration may strongly reduce migrational lags, helping to avoid extinction and genetic diversity losses in assisted species, and may benefit other species and ecosystem functioning by reducing lags in the establishment of foundation species, e.g., white-bark pine (*Pinus albicaulis* Engelm.; McLane and Aitken, 2012). On the other hand, it may in some cases also hasten local extinction of resident species maladapted to the changed climate, even if these otherwise might be able to adapt to the new conditions given time (cf. Ackerly, 2003). A better understanding of transient vegetation dynamics in response to climate change will be needed for optimizing management responses to the increasing climate-change induced dynamics and disequilibrium conditions expected for the next 50–200 yr and beyond.

A research agenda on vegetation disequilibrium dynamics under climate change should include more research outside of North America and Europe. These areas are well studied, so that our world view is shaped mainly by processes there. Because they were also strongly subject to Pleistocene glaciations, their biota may respond to climate change differently from biota in more stable regions (Dynesius and Jansson, 2000; Sandel et al., 2011). In addition, they hold only a small fraction of the world's plant species and do not represent all of the world's vegetation types. In particular, we need more insight into tropical responses (Svenning and Condit, 2008). We also need a better understanding

of trailing- and leading-edge disequilibrium dynamics due to adaptive evolutionary responses and lags therein, as the scope and time-scales for such responses are poorly understood. A crucial aspect that needs much more focus is how important vegetation disequilibrium dynamics are for ecosystem structure and processes, e.g., for key aspects such as carbon sequestration and vegetation as habitat structure for other organisms. Predictive vegetation modeling needs to further improve the representation of disequilibrium dynamics and the factors that may cause it. Predictive modeling of the response of other organism groups to climate change furthermore often focuses purely on climate, but should represent or at least consider vegetation and its dynamics in the many cases where species depend on vegetation-related habitat structure. At the same time, modeling development should also keep focus on the trade-off between model complexity and model robustness and also carefully consider where stochasticity and ecological complexity may fundamentally limit what can be predicted (e.g., Dukes et al., 2009), e.g., for how fine spatial and temporal grains are robust predictions possible? We emphasize again that one of the more solid results from modeling is probably the estimate of the minimum time required for various dynamics, e.g., from the time that the species immigrated to when it reaches its carrying capacity at a site.

#### LITERATURE CITED

- ACKERLY, D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences* 164 (S3): S165–S184.
- 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.
- ALLEN, C. D., A. K. MACALADY, H. CHENCHOUNI, D. BACHELET, N. McDOWELL, M. VENNETIER, T. KITZBERGER, ET AL. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259: 660–684.
- ANDERSEN, S. T. 1966. Interglacial vegetational succession and lake development in Denmark. *Palaeobotanist* 15: 117–127.
- ARAÚJO, M. B., D. ALAGADOR, M. CABEZA, D. NOGUÉS-BRAVO, AND W. THUILLER. 2011. Climate change threatens European conservation areas. *Ecology Letters* 14: 484–492.
- ARAÚJO, M. B., AND M. LUOTO. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography* 16: 743–753.
- ARFT, A. M., M. D. WALKER, J. GUREVITCH, J. M. ALATALO, M. S. BRETHARTE, M. DALE, M. DIEMER, ET AL. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological Monographs* 69: 491–511.
- BARLOW, C., AND P. S. MARTIN. 2005. Bring *Torreya taxifolia* north now. *Wild Earth* 1: 52–55.
- BEER, R., AND W. TINNER. 2008. Four thousand years of vegetation and fire history in the spruce forests of northern Kyrgyzstan (Kungey Alatau, Central Asia). *Vegetation History and Archaeobotany* 17: 629–638.
- BERTRAND, R., J. LENOIR, C. PIEDALLU, G. RIOFRIO-DILLON, P. DE RUFFRAY, C. VIDAL, J.-C. PIERRAT, AND J.-C. GÉGOUT. 2011. Changes in plant community composition lag behind climate warming in lowland forests. *Nature* 479: 517–520.
- BIRKELAND, P. W. 1999. Soils and geomorphology. Oxford University Press, New York, New York, USA.
- BIRKS, H. J. B., AND H. H. BIRKS. 2008. Biological responses to rapid climate change at the Younger Dryas–Holocene transition at Kråkenes, western Norway. *Holocene* 18: 19–30.
- BJÖRKMAN, L., AND R. BRADSHAW. 1996. The immigration of *Fagus sylvatica* L. and *Picea abies* (L.) Karst. into a natural forest stand in southern Sweden during the last 2000 years. *Journal of Biogeography* 23: 235–244.
- BLACH-OVERGAARD, A., J.-C. SVENNING, J. DRANSFIELD, M. GREVE, AND H. BALSLEV. 2010. Determinants of palm species distributions across Africa: The relative roles of climate, non-climatic environmental factors, and spatial constraints. *Ecography* 33: 380–391.
- BOMHARD, B., D. M. RICHARDSON, J. S. DONALDSON, G. O. HUGHES, G. F. MIDGLEY, D. C. RAIMONDO, A. G. REBELO, ET AL. 2005. Potential impacts of future land use and climate change on the Red List status of the Proteaceae in the Cape Floristic Region, South Africa. *Global Change Biology* 11: 1452–1468.
- BOND, W. J., AND G. F. MIDGLEY. 2012. Carbon dioxide and the uneasy interactions of trees and savannah grasses. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 367: 601–612.
- BOTKIN, D. B., J. F. JANAK, AND J. R. WALLIS. 1972. Some ecological consequences of a computer model of forest growth. *Journal of Ecology* 60: 849–872.
- BRADSHAW, R. H. W., N. KITO, AND T. GIESECKE. 2010. Factors influencing the Holocene history of *Fagus*. *Forest Ecology and Management* 259: 2204–2212.
- BRADSHAW, R. H. W., AND M. LINDBLADH. 2005. Regional spread and stand-scale establishment of *Fagus sylvatica* and *Picea abies* in Scandinavia. *Ecology* 86: 1679–1686.
- BRADSHAW, W. E., AND C. M. HOLZAPFEL. 2006. Evolutionary response to rapid climate change. *Science* 312: 1477–1478.
- BRASIER, C. M. 2001. Rapid evolution of introduced plant pathogens via interspecific hybridization. *Bioscience* 51: 123–133.
- BRAWN, J. D., S. K. ROBINSON, AND F. R. THOMPSON III. 2001. The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics* 32: 251–276.
- BRUNET, J., AND G. VON OHEIMB. 1998. Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology* 86: 429–438.
- BUSH, M. B., M. R. SILMAN, AND D. H. URREGO. 2004. 48,000 years of climate and forest change in a biodiversity hot spot. *Science* 303: 827–829.
- CAMPBELL, I. D., AND J. H. MCANDREWS. 1993. Forest disequilibrium caused by rapid Little Ice Age cooling. *Nature* 366: 336–338.
- CAREY, A. B., S. P. HORTON, AND B. L. BISWELL. 1992. Northern spotted owls—Influence of prey base and landscape character. *Ecological Monographs* 62: 223–250.
- CASTELLO, J. D., AND D. J. LEOPOLD. 1995. Pathogens, patterns, and processes in forest ecosystems. *BioScience* 45: 16–24.
- CHAI, S. L., AND E. V. J. TANNER. 2010. 150-year legacy of land use on tree species composition in old-secondary forests of Jamaica. *Journal of Ecology* 99: 113–121.
- CHAPIN, F. S., III, G. R. SHAVER, A. E. GIBLIN, K. J. NADELHOFFER, AND J. A. LAUNDRE. 1995. Responses of Arctic tundra to experimental and observed changes in climate. *Ecology* 76: 694–711.
- CHAPIN, F. S., III, AND A. M. STARFIELD. 1997. Time lags and novel ecosystems in response to transient climate change in Arctic Alaska. *Climatic Change* 35: 449–461.
- CHAZDON, R. L. 2003. Tropical forest recovery: Legacies of human impact and natural disturbance. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 51–71.
- CLARK, D. A., AND D. B. CLARK. 2001. Getting to the canopy: Tree height growth in a neotropical rain forest. *Ecology* 82: 1460–1472.
- CLARK, J. S., M. LEWIS, AND L. HORVATH. 2001. Invasion by extremes: Population spread with variation in dispersal and reproduction. *American Naturalist* 157: 537–554.
- CLARK, J. S., M. LEWIS, J. S. MCLACHLAN, AND J. HILLERISLAMBERS. 2003. Estimating population spread: What can we forecast and how well? *Ecology* 84: 1979–1988.
- COLLINGHAM, Y. C., AND B. HUNTLEY. 2000. Impacts of habitat fragmentation and patch size upon migration rates. *Ecological Applications* 10: 131–144.
- CORREA-METRIO, A., M. B. BUSH, K. R. CABRERA, S. SULLY, M. BRENNER, D. A. HODELL, J. ESCOBAR, AND T. GUILDNER. 2012. Rapid climate change and no-analog vegetation in lowland Central America during the last 86,000 years. *Quaternary Science Reviews* 38: 63–75.
- COWLING, S. A., M. T. SYKES, AND R. H. W. BRADSHAW. 2001. Palaeovegetation-model comparisons, climate change and tree succession

- in Scandinavia over the past 1500 years. *Journal of Ecology* 89: 227–236.
- CRAMER, W., A. BONDEAU, F. I. WOODWARD, I. C. PRENTICE, R. A. BETTS, V. BROVKIN, P. M. COX, ET AL. 2001. Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: Results from six dynamic global vegetation models. *Global Change Biology* 7: 357–373.
- DANBY, R. K., AND D. S. HIK. 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology* 95: 352–363.
- DAVIS, M. B. 1976. Pleistocene biogeography of temperate deciduous forests. *Geoscience and Man* 13: 13–26.
- DAVIS, M. B. 1986. Climatic instability, time lags, and community disequilibrium. In J. Diamond and T. J. Case [eds.], *Community ecology* 269–284. Harper & Row, New York, New York, USA.
- DAVIS, M. B., R. G. SHAW, AND J. R. ETTERTSON. 2005. Evolutionary responses to changing climate. *Ecology* 86: 1704–1714.
- DE FRENNE, P., J. BRUNET, A. SHEVTSOVA, A. KOLB, B. J. GRAAE, O. CHABRERIE, S. A. O. COUSINS, ET AL. 2011. Temperature effects on forest herbs assessed by warming and transplant experiments along a latitudinal gradient. *Global Change Biology* 17: 3240–3253.
- DELCOURT, P. A., AND H. R. DELCOURT. 1983. Late-Quaternary vegetational dynamics and community stability reconsidered. *Quaternary Research* 19: 265–271.
- DELCOURT, H. R., P. A. DELCOURT, AND T. WEBB III. 1982. Dynamic plant ecology: The spectrum of vegetational change in space and time. *Quaternary Science Reviews* 1: 153–175.
- DELISLE, F., C. LAVOIE, M. JEAN, AND D. LACHANCE. 2003. Reconstructing the spread of invasive plants: Taking into account biases associated with herbarium specimens. *Journal of Biogeography* 30: 1033–1042.
- DEWALT, S. J., S. K. MALIAKAL, AND J. S. DENSLow. 2003. Changes in vegetation structure and composition along a tropical forest chronosequence: Implications for wildlife. *Forest Ecology and Management* 182: 139–151.
- DORMANN, C. F., S. J. SCHYMANSKI, J. CABRAL, I. CHUINE, C. GRAHAM, F. HARTIG, M. KEARNEY, ET AL. 2012. Correlation and process in species distribution models: Bridging a dichotomy. *Journal of Biogeography* 39: 2119–2131.
- DUKES, J. S., J. PONTIUS, D. ORWIG, J. R. GARNAS, V. L. RODGERS, N. BRAZEE, B. COOKE, ET AL. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? *Canadian Journal of Forest Research* 39: 231–248.
- DULLINGER, S., T. DIRNBÖCK, AND G. GRABHERR. 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. *Journal of Ecology* 92: 241–252.
- DULLINGER, S., A. GATTRINGER, W. THULLER, D. MOSER, N. E. ZIMMERMANN, A. GUISAN, W. WILLNER, ET AL. 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change* 2: 619–622.
- DYNESIUS, M., AND R. JANSSON. 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences USA* 97: 9115–9120.
- EHRICH, D., I. G. ALSOS, AND C. BROCHMANN. 2008. Where did the northern peatland species survive the dry glacials: Cloudberry (*Rubus chamaemorus*) as an example. *Journal of Biogeography* 35: 801–814.
- ERIKSSON, O. 1996. Regional dynamics of plants: A review of evidence for remnant, source–sink and metapopulations. *Oikos* 77: 248–258.
- ERIKSSON, O. 2000. Functional roles of remnant plant populations in communities and ecosystems. *Global Ecology and Biogeography* 9: 443–449.
- ESSL, F., S. DULLINGER, C. PLUTZAR, W. WILLNER, AND W. RABITSCH. 2011. Imprints of glacial history and current environment on correlations between endemic plant and invertebrate species richness. *Journal of Biogeography* 38: 604–614.
- FANG, J., AND M. J. LECHOWICZ. 2006. Climatic limits for the present distribution of beech (*Fagus L.*) species in the world. *Journal of Biogeography* 33: 1804–1819.
- FOLEY, J. A., S. LEVIS, M. H. COSTA, W. CRAMER, AND D. POLLARD. 2000. Incorporating dynamic vegetation cover within global climate models. *Ecological Applications* 10: 1620–1632.
- FRANKS, S. J., S. SIM, AND A. E. WEIS. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences USA* 104: 1278–1282.
- GARCÍA, M. B., F. X. PICÓ, AND J. EHRLÉN. 2008. Life span correlates with population dynamics in perennial herbaceous plants. *American Journal of Botany* 95: 258–262.
- GARCÍA, D., R. ZAMORA, J. A. HÓDAR, AND J. M. GÓMEZ. 1999. Age structure of *Juniperus communis* L. in the Iberian peninsula: Conservation of remnant populations in Mediterranean mountains. *Biological Conservation* 87: 215–220.
- GAVIN, D. G. 2009. The coastal-disjunct mesic flora in the inland Pacific Northwest of USA and Canada: Refugia, dispersal and disequilibrium. *Diversity & Distributions* 15: 972–982.
- 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.
- GIENAPP, P., C. TEPLITSKY, J. S. ALHO, J. A. MILLS, AND J. MERILÄ. 2008. Climate change and evolution: Disentangling environmental and genetic responses. *Molecular Ecology* 17: 167–178.
- GIESECKE, T., K. D. BENNETT, H. J. BIRKS, A. E. BJUNE, E. BOZILOVA, A. FEURDEAN, W. FINSINGER, ET AL. 2011. The pace of Holocene vegetation change—Testing for synchronous developments. *Quaternary Science Reviews* 30: 2805–2814.
- GIESECKE, T., T. HICKLER, T. KUNKEL, M. T. SYKES, AND R. H. W. BRADSHAW. 2006. Towards an understanding of the Holocene distribution of *Fagus sylvatica* L. *Journal of Biogeography* 34: 118–131.
- GIESECKE, T., T. HICKLER, T. KUNKEL, M. T. SYKES, AND R. H. W. BRADSHAW. 2007. Towards an understanding of the Holocene distribution of *Fagus sylvatica* L. *Journal of Biogeography* 34: 118–131.
- GILLSON, L., AND K. J. WILLIS. 2004. 'As Earth's testimonies tell': Wilderness conservation in a changing world. *Ecology Letters* 7: 990–998.
- GIMÉNEZ-BENAVIDES, L., M. J. ALBERT, J. M. IRIONDO, AND A. ESCUDERO. 2011. Demographic processes of upward range contraction in a long-lived Mediterranean high mountain plant. *Ecography* 34: 85–93.
- GIMÉNEZ-BENAVIDES, L., A. ESCUDERO, AND J. M. IRIONDO. 2007. Local adaptation enhances seedling recruitment along an altitudinal gradient in a high mountain Mediterranean plant. *Annals of Botany* 99: 723–734.
- GOTTFRIED, M., H. PAULI, A. FUTSCHIK, M. AKHALKATSI, P. BARANOK, J. L. BENITO ALONSO, G. COLDEA, ET AL. 2012. Continent-wide response of mountain vegetation to climate change. *Nature Climate Change* 2: 111–115.
- GROVE, S. J. 2002. Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics* 33: 1–23.
- HARSCH, M. A., AND M. Y. BADER. 2011. Treeline form—A potential key to understanding treeline dynamics. *Global Ecology and Biogeography* 20: 582–596.
- HARSCH, M. A., P. E. HULME, M. S. MCGLONE, AND R. P. DUNCAN. 2009. Are treelines advancing? A global meta-analysis of treeline responses to climate warming. *Ecology Letters* 12: 1040–1049.
- HENNE, P. D., C. M. ELKIN, B. REINEKING, H. BUGMANN, AND W. TINNER. 2011. Did soil development limit spruce (*Picea abies*) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model. *Journal of Biogeography* 38: 933–949.
- HICKLER, T., B. SMITH, M. T. SYKES, M. B. DAVIS, S. SUGITA, AND K. WALKER. 2004. Using a generalized vegetation model to simulate vegetation dynamics in northeastern USA. *Ecology* 85: 519–530.
- HIGGINS, S. I., J. S. CLARK, R. NATHAN, T. HOVESTADT, F. SCHURR, M. V. FRAGOSO, M. R. AGUIAR, E. RIBBENS, AND S. LAVOREL. 2003a. Forecasting plant migration rates: Managing uncertainty for risk assessment. *Journal of Ecology* 91: 341–347.
- HIGGINS, S. I., S. LAVOREL, AND E. REVILLA. 2003b. Estimating plant migration rates under habitat loss and fragmentation. *Oikos* 101: 354–366.
- HIGGINS, S. I., AND S. SCHEITER. 2012. Atmospheric CO<sub>2</sub> forces abrupt vegetation shifts locally, but not globally. *Nature* 488: 209–212.

- HODKINSON, I. D., S. J. COULSON, AND N. R. WEBB. 2003. Community assembly along proglacial chronosequences in the high Arctic: Vegetation and soil development in north-west Svalbard. *Journal of Ecology* 91: 651–663.
- HOEGH-GULDBERG, O., L. HUGHES, S. MCINTYRE, D. B. LINDENMAYER, C. PARMESAN, H. P. POSSINGHAM, AND C. D. THOMAS. 2008. Assisted colonization and rapid climate change. *Science* 321: 345–346.
- HOLTMEIER, F.-K., AND G. BROLL. 2005. Sensitivity and response of the Northern Hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography* 14: 395–410.
- HONNAY, O., K. VERHEYEN, J. BUTAYE, 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.
- HUBBELL, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.
- HUNTLEY, B., P. J. BARTLEIN, AND I. C. PRENTICE. 1989. Climatic control of the distribution and abundance of beech (*Fagus L.*) in Europe and North America. *Journal of Biogeography* 16: 551–560.
- IBÁÑEZ, I., J. S. CLARK, AND M. C. DIETZE. 2009. Estimating colonization potential of migrant tree species. *Global Change Biology* 15: 1173–1188.
- INGHE, O., AND C. O. TAMM. 1985. Survival and flowering of perennial herbs. IV. The behaviour of *Hepatica nobilis* and *Sanicula europaea* on permanent plots during 1943–81. *Oikos* 45: 400–420.
- IPCC. 2007. Climate Change 2007: Synthesis report. Contribution of Working Groups I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.
- 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.
- JOHNSTONE, J. F., AND F. S. CHAPIN. 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biology* 9: 1401–1409.
- JONES, C. G., J. H. LAWTON, AND M. SHACHAK. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373–386.
- JOSHI, J., B. SCHMID, M. C. CALDEIRA, P. G. DIMITRAKOPOULOS, J. GOOD, R. HARRIS, A. HECTOR, ET AL. 2001. Local adaptation enhances performance of common plant species. *Ecology Letters* 4: 536–544.
- KELLERMANN, V., V. LOESCHKE, A. A. HOFFMANN, T. N. KRISTENSEN, C. FLØJGAARD, J. R. DAVID, J.-C. SVENNING, AND J. OVERGAARD. 2012b. Phylogenetic constraints in key functional traits behind species' climate niches: Patterns of desiccation and cold resistance across 95 *Drosophila* species. *Evolution* 66: 3377–3389.
- KELLERMANN, V., J. OVERGAARD, A. A. HOFFMANN, C. FLØJGAARD, J.-C. SVENNING, AND V. LOESCHKE. 2012a. Upper thermal limits of *Drosophila* are linked to species distributions and strongly constrained phylogenetically. *Proceedings of the National Academy of Sciences USA* 109: 16228–16233.
- KELLY, A. E., AND M. L. GOULDEN. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences USA* 105: 11823–11826.
- KISSLING, W. D., W. J. BAKER, H. BALSLEV, A. S. BARFOD, F. BORCHSENIUS, J. DRANSFIELD, R. GOVAERTS, AND J.-C. SVENNING. 2012. Quaternary and pre-Quaternary historical legacies in the global distribution of a major tropical plant lineage. *Global Ecology and Biogeography* 21: 909–921.
- KISSLING, W. D., R. FIELD, H. KORNTHEUER, U. HEYDER, AND K. BÖHNING-GAESE. 2010. Woody plants and the prediction of climate-change impacts on bird diversity. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 365: 2035–2045.
- KLANDERUD, K., AND H. J. B. BIRKS. 2003. Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene* 13: 1–6.
- KÖRNER, C. 2003. Ecological impacts of atmospheric CO<sub>2</sub> enrichment on terrestrial ecosystems. *Philosophical Transactions of the Royal Society, A, Mathematical, Physical and Engineering Sciences* 361: 2023–2041.
- KOUTSODENDRIS, A., J. PROSS, U. C. MÜLLER, A. BRAUER, W. J. FLETCHER, N. KÜHL, E. KIRILOVA, ET AL. 2012. A short-term climate oscillation during the Holsteinian interglacial (MIS 11c): An analogy to the 8.2 ka climatic event? *Global and Planetary Change* 92–93: 224–235.
- KRISTIANSEN, T., J.-C. SVENNING, D. PEDERSEN, W. L. EISERHARDT, C. GRÁNDEZ, AND H. BALSLEV. 2011. Local and regional palm (Arecaceae) species richness patterns and their cross-scale determinants in the western Amazon. *Journal of Ecology* 99: 1001–1015.
- KUNEŠ, P., B. V. ODGAARD, AND M.-J. GAILLARD. 2011. Soil phosphorus as a control of productivity and openness in temperate interglacial forest ecosystems. *Journal of Biogeography* 38: 2150–2164.
- LANNER, R. M. 2002. Why do trees live so long? *Ageing Research Reviews* 1: 653–671.
- LARSON, D. W., U. MATTHES, J. A. GERRATH, J. M. GERRATH, J. C. NEKOLA, G. L. WALKER, S. POREMBSKI, A. CHARLTON, AND N. W. K. LARSON. 1999. Ancient stunted trees on cliffs. *Nature* 398: 382–383.
- LAURANCE, W. F., H. E. M. NASCIMENTO, S. G. LAURANCE, R. CONDIT, S. D'ANGELO, AND A. ANDRADE. 2004. Inferred longevity of Amazonian rainforest trees based on a long-term demographic study. *Forest Ecology and Management* 190: 131–143.
- LE ROUX, P. C., AND M. A. MCGEOCH. 2008. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* 14: 2950–2962.
- LENOIR, J., J. GÉGOUT, J. DUPOUEY, D. BERT, AND J.-C. SVENNING. 2010a. Forest plant community changes during 1989–2007 in response to climate warming in the Jura Mountains (France and Switzerland). *Journal of Vegetation Science* 21: 949–964.
- LENOIR, J., J.-C. GÉGOUT, A. GUISAN, P. VITTOZ, T. WOHLGEMUTH, N. E. ZIMMERMANN, S. DULLINGER, ET AL. 2010b. Going against the flow: Potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33: 295–303.
- LENOIR, J., J. C. GÉGOUT, P. A. MARQUET, P. DE RUFFRAY, AND H. BRISSE. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320: 1768–1771.
- LEVEY, D. J., B. M. BOLKER, J. J. TEWKSBURY, S. SARGENT, AND N. M. HADDAD. 2005. Effects of landscape corridors on seed dispersal by birds. *Science* 309: 146–148.
- LINHART, Y. B., AND M. C. GRANT. 1996. Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics* 27: 237–277.
- 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.
- LUYSSAERT, S., E.-D. SCHULZE, A. BÖRNER, A. KNOHL, D. HESSENMÖLLER, B. E. LAW, P. CIAIS, AND J. GRACE. 2008. Old-growth forests as global carbon sinks. *Nature* 455: 213–215.
- LYNCH, A. J. J., R. W. BARNES, R. E. VAILLANCOURT, AND J. CAMBÈCÈDES. 1998. Genetic evidence that *Lomatia tasmanica* (Proteaceae) is an ancient clone. *Australian Journal of Botany* 46: 25–33.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.
- MACDONALD, G. M., T. W. D. EDWARDS, K. A. MOSER, R. PIENITZ, AND J. P. SMOL. 1993. Rapid response of treeline vegetation and lakes to past climate warming. *Nature* 361: 243–246.
- MACDONALD, G. M., K. V. KREMENETSKI, AND D. W. BEILMAN. 2008. Climate change and the northern Russian treeline zone. *Philosophical Transactions of the Royal Society B, Biological Sciences* 363: 2283–2299.
- MACK, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: An ecological chronicle. *Agro-ecosystems* 7: 145–165.
- MATLACK, G. R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* 75: 1491–1502.
- MATLACK, G. R. 2005. Slow plants in a fast forest: Local dispersal as a predictor of species frequencies in a dynamic landscape. *Journal of Ecology* 93: 50–59.
- MCGLONE, M. S., J. M. WILMSHURST, AND S. K. WISER. 2000. Lateglacial and Holocene vegetation and climatic change on Auckland Island, Subantarctic New Zealand. *Holocene* 10: 719–728.
- MCINERNEY, G., J. M. J. TRAVIS, AND C. DYTHAM. 2007. Range shifting on a fragmented landscape. *Ecological Informatics* 2: 1–8.

- 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.
- McLACHLAN, J. S., J. J. HELLMANN, AND M. W. SCHWARTZ. 2007. A framework for debate of assisted migration in an era of climate change. *Conservation Biology* 21: 297–302.
- McLANE, S. C., AND S. N. AITKEN. 2012. Whitebark pine (*Pinus albicaulis*) assisted migration potential: Testing establishment north of the species range. *Ecological Applications* 22: 142–153.
- MEJÍAS, J. A., J. ARROYO, AND F. OJEDA. 2002. Reproductive ecology of *Rhododendron ponticum* (Ericaceae) in relict Mediterranean populations. *Botanical Journal of the Linnean Society* 140: 297–311.
- MILES, J. 1985. The pedogenic effects of different species and vegetation types and the implications of succession. *Journal of Soil Science* 36: 571–584.
- MOESLUND, J., L. ARGE, P. BØCHER, B. NYGAARD, AND J.-C. SVENNING. 2011. Geographically comprehensive assessment of salt-meadow vegetation–elevation relations using LiDAR. *Wetlands* 31: 471–482.
- 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.
- MORI, A. S. 2011. Ecosystem management based on natural disturbances: Hierarchical context and non-equilibrium paradigm. *Journal of Applied Ecology* 48: 280–292.
- MORRIS, W. F., C. A. PFISTER, S. TULJAPURKAR, C. V. HARIDAS, C. L. BOGGS, M. S. BOYCE, E. M. BRUNA, ET AL. 2008. Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* 89: 19–25.
- MUELLER, R. C., C. M. SCUDDER, M. E. PORTER, R. T. TROTTER III, C. A. GEHRING, AND T. G. WHITHAM. 2005. Differential tree mortality in response to severe drought: Evidence for long-term vegetation shifts. *Journal of Ecology* 93: 1085–1093.
- NORBÝ, R. J., AND D. R. ZAK. 2011. Ecological lessons from free-air CO<sub>2</sub> enrichment (FACE) experiments. *Annual Review of Ecology, Evolution and Systematics* 42: 181–203.
- NORMAND, S., R. E. RICKLEFS, F. SKOV, J. BLADT, O. TACKENBERG, AND J.-C. SVENNING. 2011. Postglacial migration supplements climate in determining plant species ranges in Europe. *Proceedings. Biological Sciences* 278: 3644–3653.
- NORMAND, S., J.-C. SVENNING, AND F. SKOV. 2007. National and European perspectives on climate change sensitivity of the habitats directive characteristic plant species. *Journal for Nature Conservation* 15: 41–53.
- ÓDOR, P., J. HEILMANN-CLAUSEN, M. CHRISTENSEN, E. AUDE, K. W. VAN DORT, A. PILTAVER, I. SILLER, ET AL. 2006. Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. *Biological Conservation* 131: 58–71.
- ORWIG, D. A. 2002. Ecosystem to regional impacts of introduced pests and pathogens: Historical context, questions and issues. *Journal of Biogeography* 29: 1471–1474.
- PACALA, S. W., C. D. CANHAM, J. SAPONARA, J. A. SILANDER JR., R. K. KOBE, AND E. RIBBENS. 1996. Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecological Monographs* 66: 1–43.
- PACKHAM, J. R., P. A. THOMAS, M. D. ATKINSON, AND T. DEGEN. 2012. Biological flora of the British Isles: *Fagus sylvatica*. *Journal of Ecology* 100: 1557–1608.
- PARADIS, A., J. ELKINTON, K. HAYHOE, AND J. BUONACCORSI. 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. *Mitigation and Adaptation Strategies for Global Change* 13: 541–554.
- PARMESAN, C., AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- PAROLO, G., AND G. ROSSI. 2008. Upward migration of vascular plants following a climate warming trend in the Alps. *Basic and Applied Ecology* 9: 100–107.
- PAUS, A. 1995. The Late Weichselian and early Holocene history of tree birch in south Norway and the Bølling *Betula* time-lag in northwest Europe. *Review of Palaeobotany and Palynology* 85: 243–262.
- PAYETTE, S. 2007. Contrasted dynamics of northern Labrador tree lines caused by climate change and migrational lags. *Ecology* 88: 770–780.
- PEARMAN, P. B., C. F. RANDIN, O. BROENNIMANN, P. VITTOZ, W. O. KNAAP, R. ENGLER, G. L. LAY, N. E. ZIMMERMANN, AND A. GUIBAN. 2008. Prediction of plant species distributions across six millennia. *Ecology Letters* 11: 357–369.
- 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.
- PENNINGTON, W. 1986. Lags in adjustment of vegetation to climate caused by the pace of soil development. Evidence from Britain. *Vegetatio* 67: 105–118.
- PETERKEN, G. F. 1996. Natural woodland: Ecology and conservation in northern temperate regions. Cambridge University Press, Cambridge, UK.
- PETERKEN, G. F., AND M. GAME. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *Journal of Ecology* 72: 155–182.
- PICKETT, S. T. A., AND P. S. WHITE. 1985. Patch dynamics: A synthesis. In S. T. A. Pickett and P. S. White [eds.], *The ecology of natural disturbance and patch dynamics* 371–384. Academic Press, Orlando, Florida, USA.
- PITELKA, L. F., AND PLANT MIGRATION WORKSHOP GROUP. 1997. Plant migration and climate change. *American Scientist* 85: 464–473.
- PRENTICE, I. C. 1986. Vegetation responses to past climatic variation. *Vegetatio* 67: 131–141.
- PRENTICE, I. C., P. J. BARTLEIN, AND T. WEBB III. 1991. Vegetation and climate change in eastern North America since the Last Glacial Maximum. *Ecology* 72: 2038–2056.
- PRENTICE, I. C., W. CRAMER, S. P. HARRISON, R. LEEMANS, R. A. MONSERUD, AND A. M. SOLOMON. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography* 19: 117–134.
- PRESTON, K., J. T. ROTENBERRY, R. A. REDAK, AND M. F. ALLEN. 2008. Habitat shifts of endangered species under altered climate conditions: Importance of biotic interactions. *Global Change Biology* 14: 2501–2515.
- RANDIN, C. F., R. ENGLER, S. NORMAND, M. ZAPPA, N. E. ZIMMERMAN, P. B. PEARMAN, P. VITTOZ, W. THULLER, AND A. GUIBAN. 2009. Climate change and plant distribution: Local models predict high-elevation persistence. *Global Change Biology* 15: 1557–1569.
- RAKOTOARINIVO, M., A. BLACH-OVERGAARD, W. J. BAKER, J. DRANSFIELD, J. MOAT, AND J.-C. SVENNING. 2013. Palaeo-precipitation is a major determinant of palm species richness patterns across Madagascar—A tropical biodiversity hotspot. *Proceedings of the Royal Society, B, Biological Sciences* 280: 20123048.
- RANIUS, T., AND N. JANSSON. 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biological Conservation* 95: 85–94.
- REICH, P. B., AND J. OLEKSYN. 2008. Climate warming will reduce growth and survival of Scots pine except in the far north. *Ecology Letters* 11: 588–597.
- RICKEBUSCH, S., W. THULLER, T. HICKLER, M. B. ARAÚJO, M. T. SYKES, O. SCHWEIGER, AND B. LAFOURCADE. 2008. Incorporating the effects of changes in vegetation functioning and CO<sub>2</sub> on water availability in plant habitat models. *Biology Letters* 4: 556–559.
- RUSTAD, L. 2006. From transient to steady-state response of ecosystems to atmospheric CO<sub>2</sub>-enrichment and global climate change: Conceptual challenges and need for an integrated approach. *Plant Ecology* 182: 43–62.
- SAKAI, A. K., F. W. ALLENDORF, J. S. HOLT, D. M. LODGE, J. MOLOFSKY, K. A. WITH, S. BAUGHMAN, ET AL. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305–332.
- SALA, O. E., F. S. CHAPIN III, J. J. ARMESTO, E. BERLOW, J. BLOOMFIELD, R. DIRZO, E. HUBER-SANWALD, ET AL. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.
- SANDEL, B., L. ARGE, B. DALSGAARD, R. G. DAVIES, K. J. GASTON, W. J. SUTHERLAND, AND J.-C. SVENNING. 2011. The influence of Late

- Quaternary climate-change velocity on species endemism. *Science* 334: 660–664.
- SANDEL, B., L. J. GOLDSTEIN, N. J. B. KRAFT, J. G. OKIE, M. I. SHULDMAN, D. D. ACKERLY, E. E. CLELAND, AND K. N. SUDING. 2010. Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. *New Phytologist* 188: 565–575.
- SCHNEIDER, S., AND S. I. HIGGINS. 2009. Impacts of climate change on the vegetation of Africa: An adaptive dynamic vegetation modelling approach. *Global Change Biology* 15: 2224–2246.
- SCHWARTZ, M. W. 2012. Using niche models with climate projections to inform conservation management decisions. *Biological Conservation* 155: 149–156.
- SCHWEIGER, O., J. SETTELE, O. KUDRNA, S. KLOTZ, AND I. KÜHN. 2008. Climatic change can cause spatial mismatch of trophically interacting species. *Ecology* 89: 3472–3479.
- SHAVER, G. R., J. CANADELL, F. S. CHAPIN III, J. GUREVITCH, J. HARTE, G. HENRY, P. INESON, ET AL. 2000. Global warming and terrestrial ecosystems: A conceptual framework for analysis. *Bioscience* 50: 871–882.
- SILVERTOWN, J. 1985. History of a latitudinal diversity gradient: Woody plants in Europe 13,000–1000 years B.P. *Journal of Biogeography* 12: 519–525.
- SKOV, F., AND J.-C. SVENNING. 2004. Potential impact of climatic change on the distribution of forest herbs in Europe. *Ecography* 27: 366–380.
- SMITH, A. G. 1965. Problems of inertia and threshold related to post-glacial habitat changes. *Proceedings of the Royal Society of London, B, Biological Sciences* 161: 331–342.
- SOONS, M. B., J. H. MESSELINK, E. JONGEJANS, AND G. W. HEIL. 2005. Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. *Journal of Ecology* 93: 1214–1225.
- SOUZA, L., R. T. BELOTE, P. KARDOL, J. F. WELTZIN, AND R. J. NORBY. 2010. CO<sub>2</sub> enrichment accelerates successional development of an understory plant community. *Journal of Plant Ecology* 3: 33–39.
- STADLER, B., T. MÜLLER, D. ORWIG, AND R. COBB. 2005. Hemlock woolly adelgid in New England forests: Canopy impacts transforming ecosystem processes and landscapes. *Ecosystems* 8: 233–247.
- STROPP, J., H. TER STEEGE, Y. MALHI, ADTN, AND RAINFOR. 2009. Disentangling regional and local tree diversity in the Amazon. *Ecography* 32: 46–54.
- SUTTLE, K. B., M. A. THOMSEN, AND M. E. POWER. 2007. Species interactions reverse grassland responses to changing climate. *Science* 315: 640–642.
- SVENNING, J.-C. 2003. Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecology Letters* 6: 646–653.
- SVENNING, J.-C., K. H. BAKTOFT, AND H. BALSLEV. 2009. Land-use history affects understory plant species distributions in a large temperate-forest complex, Denmark. *Plant Ecology* 201: 221–234.
- SVENNING, J.-C., AND R. CONDIT. 2008. Biodiversity in a warmer world. *Science* 322: 206–207.
- SVENNING, J.-C., D. A. KINNER, R. F. STALLARD, B. M. J. ENGELBRECHT, AND S. J. WRIGHT. 2004. Ecological determinism in plant community structure across a tropical forest landscape. *Ecology* 85: 2526–2538.
- SVENNING, J.-C., S. NORMAND, AND F. SKOV. 2008. Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. *Ecography* 31: 316–326.
- SVENNING, J.-C., AND F. SKOV. 2004. Limited filling of the potential range in European tree species. *Ecology Letters* 7: 565–573.
- TAKAHASHI, M. K., L. M. HORNER, T. KUBOTA, N. A. KELLER, AND W. G. ABRAHAMSON. 2011. Extensive clonal spread and extreme longevity in saw palmetto, a foundation clonal plant. *Molecular Ecology* 20: 3730–3742.
- THOMPSON, D. Q., R. L. STUCKEY, AND E. B. THOMPSON. 1987. Spread, impact, and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands (online version 04JUN1999). U.S. Fish and Wildlife Service, Jamestown, North Dakota, USA: Northern Prairie Wildlife Research Center Online.
- THOMSON, F. J., A. T. MOLES, T. D. AULD, AND R. T. KINGSFORD. 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology* 99: 1299–1307.
- THULLER, W., S. LAVOREL, M. B. ARAÚJO, M. T. SYKES, AND I. C. PRENTICE. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA* 102: 8245–8250.
- TINNER, W., AND A. F. LOTTER. 2006. Holocene expansions of *Fagus sylvatica* and *Abies alba* in Central Europe: Where are we after eight decades of debate? *Quaternary Science Reviews* 25: 526–549.
- TURNBULL, L. A., M. J. CRAWLEY, AND M. REES. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88: 225–238.
- TYRRELL, L. E., AND T. R. CROW. 1994. Structural characteristics of old-growth hemlock–hardwood forests in relation to age. *Ecology* 75: 370–386.
- URBAN, M. C., J. J. TEWKSBURY, AND K. S. SHELDON. 2012. On a collision course: Competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society, B, Biological Sciences* 279: 2072–2080.
- VAN DER VEKEN, S., P. DE FRENNE, L. BAETEN, E. VAN BEEK, K. VERHEYEN, AND M. HERMY. 2012. Experimental assessment of the survival and performance of forest herbs transplanted beyond their range limit. *Basic and Applied Ecology* 13: 10–19.
- VAN DER VEKEN, S., J. ROGISTER, K. VERHEYEN, M. HERMY, AND R. NATHAN. 2007. Over the (range) edge: A 45-year transplant experiment with the perennial forest herb *Hyacinthoides non-scripta*. *Journal of Ecology* 95: 343–351.
- VON HUMBOLDT, A., AND A. BONPLAND. 1807. Essay on the geography of plants with a physical tableau of the equinoctial regions. Fr. Schoell, Paris. In S. T. Jackson [ed.], 2009, A. von Humboldt and A. Bonpland, Essay on the geography of plants, 57–143. University of Chicago Press, Chicago, Illinois, USA.
- WALTHER, G.-R. 2000. Climatic forcing on the dispersal of exotic species. *Phytocoenologia* 30: 409–430.
- WALTHER, G.-R., S. BERGER, AND M. T. SYKES. 2005. An ecological ‘footprint’ of climate change. *Proceedings of the Royal Society, B, Biological Sciences* 272: 1427–1432.
- WANGEN, S. R., AND C. R. WEBSTER. 2006. Potential for multiple lag phases during biotic invasions: Reconstructing an invasion of the exotic tree *Acer platanoides*. *Journal of Applied Ecology* 43: 258–268.
- WEBB, T., III. 1986. Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio* 67: 75–91.
- WELK, E. 2004. Constraints in range predictions of invasive plant species due to non-equilibrium distribution patterns: Purple loosestrife (*Lythrum salicaria*) in North America. *Ecological Modelling* 179: 551–567.
- WILKINSON, D. M. 1998. Mycorrhizal fungi and Quaternary plant migrations. *Global Ecology and Biogeography Letters* 7: 137–140.
- WILLIAMS, J. W., B. N. SHUMAN, AND T. WEBB III. 2001. Dissimilarity analyses of Late-Quaternary vegetation and climate in eastern North America. *Ecology* 82: 3346–3362.
- WILLIS, K. J., M. BRAUN, P. SÜMEGI, AND A. TÓTH. 1997. Does soil change cause vegetation change or vice versa: A temporal perspective from Hungary. *Ecology* 78: 740–750.
- WILLIS, K. J., A. KLECZKOWSKI, M. NEW, AND R. J. WHITTAKER. 2007. Testing the impact of climate variability on European plant diversity: 320000 years of water-energy dynamics and its long-term influence on plant taxonomic richness. *Ecology Letters* 10: 673–679.
- WILLNER, W., R. DI PIETRO, AND E. BERGMEIER. 2009. Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species. *Ecography* 32: 1011–1018.
- WOODWARD, F. I. 1990. The impact of low temperatures in controlling the geographical distribution of plants. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences* 326: 585–593.
- WOODWARD, F. I., AND D. J. BEERLING. 1997. The dynamics of vegetation change: Health warnings for equilibrium ‘dodo’ models. *Global Ecology and Biogeography Letters* 6: 413–418.
- ZHANG, Z., R. R. SWAISGOOD, S. ZHANG, L. A. NORDSTROM, H. WANG, X. GU, J. HU, AND F. WEI. 2011. Old-growth forest is what giant pandas really need. *Biological Letters* 7: 403–406.
- 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.