REVIEW / SYNTHÈSE

# Composition and carbon dynamics of forests in northeastern North America in a future, warmer world[1]

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**Abstract:** Increasing temperatures, precipitation extremes, and other anthropogenic influences (pollutant deposition, increasing carbon dioxide) will influence future forest composition and productivity in the northeastern United States and eastern Canada. This synthesis of empirical and modeling studies includes tree DNA evidence suggesting tree migrations since the last glaciation were much slower, at least under postglacial conditions, than is needed to keep up with current and future climate warming. Exceedances of US and Canadian ozone air quality standards are apparent and offset $CO_2$-induced gains in biomass and predispose trees to other stresses. The deposition of nitrogen and sulfate in the northeastern United States changes forest nutrient availability and retention, reduces reproductive success and frost hardiness, causes physical damage to leaf surfaces, and alters performance of forest pests and diseases. These interacting stresses may increase future tree declines and ecosystem disturbances during transition to a warmer climate. Recent modeling work predicts warmer climates will increase suitable habitat (not necessarily actual distribution) for most tree species in the northeastern United States. Species whose habitat is declining in the northeastern United States currently occur in Canadian forests and may expand northward with warming. Paleoecological studies suggest local factors may interact with, even overwhelm, climatic effects, causing lags and thresholds leading to sudden large shifts in vegetation.

**Résumé :** L'augmentation des températures, les extrêmes de précipitation et d'autres facteurs anthropogéniques (les dépôts d'agents polluants, l'augmentation du dioxyde de carbone) influenceront la composition et la productivité future des forêts du nord-est des États-Unis et de l'est du Canada. Cette synthèse d'études empiriques et de modélisation inclut des preuves basées sur l'ADN des arbres qui indiquent que les migrations d'arbres depuis la dernière glaciation ont été beaucoup plus lentes, du moins dans les conditions qui ont suivi la glaciation, qu'elles devraient l'être pour suivre le rythme du réchauffement actuel et futur du climat. Les dépassements des normes de qualité de l'air des États-Unis et du Canada pour l'ozone sont apparents; ils annulent les gains de biomasse dus au $CO_2^-$ et prédisposent les arbres à d'autres stress. Les dépôts d'azote et de sulfates dans le nord-est modifient la disponibilité et la rétention des nutriments dans les forêts, réduisent le succès de reproduction et la résistance au gel, causent des dommages physiques à la surface des feuilles et modifient la performance des organismes nuisibles et des maladies des arbres. Ces stress qui interagissent les uns avec les autres pourraient accentuer le dépérissement des arbres et la perturbation des écosystèmes durant la période de transition vers un climat plus chaud. Des travaux récents de modélisation prédisent que des conditions climatiques plus chaudes augmenteront les habitats (pas nécessairement l'aire de répartition actuelle) qui conviennent à la plupart des espèces d'arbres dans le nord-est des États-Unis. Des espèces dont l'habitat est en déclin aux États-Unis sont présentes dans les forêts canadiennes aujourd'hui et pourraient s'étendre vers le nord avec le réchauffement. Des études paléoécologiques indiquent que des facteurs locaux pourraient interagir avec les effets du climat, voir même les éclipser, causant des décalages et des seuils entraînant des changements soudains et importants dans la végétation.

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## Introduction

Climate change will restructure forests of northeastern North America over the coming century, although the details of this restructuring remain uncertain. This paper synthesizes recent empirical and modeling work to give scientists, managers, and policy makers a sense of how forests of the region may look and function over the next century, and to highlight areas requiring future research efforts. For the purpose of this synthesis, we define the region as the New England states and the state of New York in the United States and New Brunswick, Nova Scotia, Prince Edward Island, and the southern portions of Quebec and Ontario in Canada. In this paper we examine potential changes in forest composition and carbon acquisition in the absence of human intervention (facilitated migration, silvicultural practices, fire suppression, etc.). We examine the response of forest recruitment and migration to climate change, and consider the effects of increasing atmospheric carbon dioxide ($CO_2$) and of nonclimatic factors of global change, such as tropospheric ozone ($O_3$), nitrogen (N) deposition, and sulfate ($SO_4$) deposition, as well as interactions of these factors with climate, on forest vegetation and ecosystems. We then cover work on current and historical declines in hardwood and softwood species in northeastern forests and present results from recent modeling work on the future distribution of suitable habitat for trees and forest types in the United States. We consider empirical evidence, both paleoecological and current, of climate change impacts on forest composition and carbon acquisition. We conclude with a section on future research and implications to address future research challenges and possible unexpected consequences of global change for northeastern forest ecosystems. Refining abilities to forecast future forest composition, distribution, and productivity is a critical goal for improving ecological understanding as well as economic and policy decision making.

## Global change impacts on forest reproduction, recruitment, and migration

The mid- and long-term composition of northeastern forests will be profoundly influenced by climate change impacts on tree reproduction and establishment success, and by the migration potential of eastern tree species. Climate change may perturb the connection between the timing of tree reproductive events (flowering times, pollen availability, and seed development) and the availability of necessary faunal agents. The animals that pollinate and disperse the seeds of many plants may themselves respond independently to climate change, resulting in a "decoupling" of the plant–animal pollination and dispersal systems (Bethke and Nudds 1995; Visser et al. 1998; Dunn and Winkler 1999; Vellend et al. 2006). Other work implicates extreme winter storms in reducing populations of passerine bird species and causing contractions away from range edges (Mehlman 1997). In Mehlman's (1997) study extreme weather not only reduced total avian abundance, but did so particularly in the northern portions of the range that will be most crucial for future seed dispersal and poleward migration by plants. Reductions in winter snowpack may delay or reduce plant reproductive efforts, which, in turn, may diminish future abundance of animal pollinators and seed dispersers (Inouye and McGuire 1991).

How physiological impacts of future atmospheric chemistry will influence seed quality and quantity, and interact with climate change, is uncertain. Seed production has been observed to increase (Farnsworth and Bazzaz 1995; Thomas et al. 1999; LaDeau and Clark 2001, 2006) or decrease (Farnsworth and Bazzaz 1995; Fischer et al. 1997; Thomas et al. 1999), and to occur earlier (Farnsworth et al. 1996) under elevated atmospheric $CO_2$. Mohan et al. (2004) found that red maple (*Acer rubrum*) seeds exhibited increasing germination probabilities with increasing atmospheric $CO_2$ concentrations. This effect may result from interactions with ethylene, a C-based plant hormone that stimulates germination. Other studies have found that seeds from parental plants reared in elevated $CO_2$ may have higher C:N ratios and develop into smaller, slower-growing seedlings (Huxman et al. 1998; Ward et al. 2000). Reproductive impacts of increased N deposition are equivocal: plant fecundity may increase or remain unchanged as a result of increased N availability (Gordon et al. 1999; Callahan et al. 2008). Bergweiler and Manning (1999) found that, even when $O_3$ levels caused only nominal damage in vegetative tissue, flower production and reproductive success were significantly reduced.

How fast must species migrate to keep up with their respective "climatic envelopes" (i.e., the range of climatic variables describing the current distribution of a species)? Many eastern North American trees will have to migrate or expand their ranges as fast as 3000–5000 $m \cdot year^{-1}$ to track predicted climate change over this century (Petit et al. 2008). Yet the likelihood of such rates actually occurring in nature is low. Although early-Holocene conditions following the last glaciation differed from those of today (i.e., glacial retreat uncovered rocky substrates that would be different from the relatively developed soils of today and generally lower in nutrients and moisture retention; there were no areas of human development to impede migration), paleoecological studies can provide insights into past migration by eastern tree species in response to climate warming (Petit et al. 2008). Some empirical studies using fossil pollen data do suggest the possibility of relatively rapid migration, with rates of 100–1000 $m \cdot year^{-1}$ during the late Quaternary – early Holocene with the melting of the Laurentide ice sheet in eastern North America (Davis 1981; Delcourt and Delcourt 1987; MacDonald et al. 1993). These studies generally employ the concept of a Pleistocene refugia located in the southern United States that provided source populations for Holocene recolonization of northeastern United States and eastern Canada (Davis 1981; Delcourt and Delcourt 1987). But others studies cast doubt on the potential for rapid migration by most species. Dyer (1995) modeled early-Holocene migration rates using pollen data and found that the fastest rate of migration was only 136 $m \cdot year^{-1}$ for one animal-dispersed species, whereas all other species had much lower rates. Recent molecular work using chloroplast DNA suggests late-Quaternary migration rates in North America were much less than 100 $m \cdot year^{-1}$ (McLachlan et al. 2005; Anderson et al. 2006). Migration rates for plant populations are largely governed by extremely rare long-distance seed dispersal events (LDD; Clark 1998; Clark et al. 1999; Schwartz et al. 2001), which may not be frequent enough to instigate timely, rapid migration for most species. Furthermore, successful colonization following LDD is typically limited by subsequent germination, seedling establishment, and survival (Clark et al. 1999; Ibañez et al. 2007; Mohan et al. 2007). Molecular work also suggests that, rather than migrating from coastal refugia in the southern United States, some eastern tree species existed at the end of the Pleistocene in cryptic, very small, or low-density populations (McLachlan et al. 2005; Petit et al. 2008) with too few individuals to leave clear pollen evidence (Stewart and Lister 2001) near the edge of the Laurentide ice sheet. This suggests that early-Holocene migration rates of eastern trees were actually much less than the 3000–5000 m·year$^{-1}$ rates required to keep up with current and future climate change. These slower migration rates are also consistent with observed and modeled rate estimates based on life-history traits and seed dispersal data (Reid 1899; Clark 1998; Clark et al. 1998, 2003, 2004).

## Nonclimatic factors affecting species composition and carbon gain and their interaction with climate

The reality of industrial development and urbanization is the regional concentration of air pollutants and the long-distance transport to downwind receptor ecosystems. The deposition of both acidifying N and sulfur (S) compounds, as well as $O_3$ and $CO_2$ exposure from industrial and mobile sources, can change productivity and competitive relations between species and how they respond to climate.

### Ozone trends over forested regions and its effects

$O_3$ is considered the most pervasive of air pollutants (Fowler et al. 1999) and an important greenhouse gas (Rawaswamy et al. 2001), requiring newly established air quality metric and standards for the United States and Canada. When mapped, this metric shows that a substantial area of forested land in northeastern North America is exposed to levels in excess of the new Canada-wide Standard of 65 ppm (Canadian Council of Ministers of the Environment 2000) and the current US Environmental Protection Agency primary National Ambient Air Quality Standard of 80 ppb (Percy et al. 2007). Background levels over the mid-latitudes have increased by 0.5%–2% per year (Vingarzan 2004), in part as a result of the historic increases in emissions of oxides of N and volatile organic C compounds (VOC), which are precursors in the photochemical production of $O_3$ in the northern hemisphere (Finlayson-Pitts and Pitts 2000). Increases in temperatures due to climate change are likely to increase tropospheric $O_3$ production, i.e., by increasing VOC production by plants.

### Ozone effects

Needle blights of eastern white pine (*Pinus strobus*) have been reported since the turn of the twentieth century (Clinton 1907; Faull 1920). Later this injury was linked to $O_3$ exposure by Linzon (1967) and Berry and Ripperton (1963). Sensitive phenotypes of this species developed foliage symptoms after fumigation of 30 ppb $O_3$ for 48 h (Costonis and Sinclair 1969; Linzon 1973; Blanchard et al. 1979), indicating that the resource is threatened and that sensitive phenotypes may disappear by 2020 (Bennett et al. 1986). Moreover, the effects of $O_3$ exposure are augmented in the presence of sulfur dioxide ($SO_2$) (Dochinger et al. 1970).

Chappelka and Samuelson (1998) and Laurence and Andersen (2003) concluded that $O_3$ symptom expression was much influenced by endogenous and exogenous factors. They also concluded that compensatory processes (C partitioning and allocation) that change the deployment of plant resources to aboveground tissues under $O_3$ exposure might reduce root growth with its implications for tree water and nutrient acquisition in a warmer climate. Using free-air C enrichment technology, Karnosky et al. (2003, 2007) established that the negative effects of $O_3$ offset production gains due to $CO_2$ enrichment, reduced competitive N acquisition by birch roots, and changed competitive abilities among various aspen clones (Zak et al. 2007).

Abundant empirical evidence indicates that $O_3$ exposure reduces stomatal control of transpiration and in larger trees leads to greater stomatal apertures, increased transpiration, and delayed stomatal closure at nightfall, leading to decreased water-use efficiency (McLaughlin et al. 2007). Slowdowns in seasonal tree growth patterns in the southern Appalachians by 30%–50% were attributed, in part, to $O_3$-induced poor water-use efficiency (McLaughlin et al. 2007). The effect of $O_3$ will offset expected gains in forest water-use efficiency with increased $CO_2$ and is likely to increase water stress (Hsiao et al. 1976) in a warmer climate with more droughts (Hanson and Weltzin 2000). Ollinger et al. (2002) have suggested that the effects of $O_3$ and forest disturbance on tree growth could offset expected growth gains induced by N deposition and enriched $CO_2$ in northeastern forests; these authors also proposed that novel atmospheric effects may have very different long-term implications.

Indirect effects of $O_3$ on forest production and forest community structure may also occur as a result of $O_3$-induced changes in the quantity and chemistry of plant tissues, and these changes may moderate the responses of temperate hardwood forests to elevated $CO_2$ (Karnosky et al. 2003).

$O_3$ exposure is also known to change secondary plant metabolism in leaves of eastern white pine (Shadkami et al. 2007), sugar maple (*Acer saccharum*) (Sager et al. 2005), and European silver birch (*Betula pendula*) (Saleem et al. 2001), as well as the quality and quantity of biogenic volatile organic compounds (Paré and Tumlinson 1999). These changes in leaf chemical composition and volatile emissions may change nutritional value and attractiveness to herbivores and may contribute to plant defense mechanisms, alter forest pest performance (Percy et al. 2002), and change behavior of the natural enemies of plant herbivores (Pinto et al. 2007). These complex interactions need to be better understood in the light of increased stress caused by invasive insects as climate warms.

### Acid deposition

The continued anthropogenic acid deposition and depletion of soil calcium (Ca) with an increase in soil aluminum: calcium ratios in sugar maple stands, and associated foliar imbalances of these elements, have been linked to growth and health reduction of this species in Vermont and Quebec (Duchesne et al. 2002; Schaberg et al. 2006). An additional stress in these sugar maple stands is the reduction in depth and duration of insulating snow cover that accompanies a warmer climate. When these changes in snow cover reduce soil freezing, pronounced acidification of the soil solution driven by nitrification occurs. Increased acid leaching of Ca and magnesium (Mg) would enhance the already low soil Ca status in high-acid deposition sites.

Acid cloud–fog deposition is a common feature of high-elevation and coastal red spruce (*Picea rubens*) habitat (Schemenauer 1986; Cox et al. 1989; Jagels et al. 2002). There is strong evidence that interception of this often highly acidic aerosol by red spruce foliage increases the risk of freezing injury by reducing frost hardiness of current-year needles by anywhere from 5 to 12 °C (reviewed by Schaberg and DeHayes (2000), and see "Declines" section below). Interception of acidic marine fogs with pH values as low as 3.0 has been documented in coastal red spruce and mountain paper birch (*Betula cordifolia*) stands adjacent to the Bay of Fundy in New Brunswick and Nova Scotia, and has been linked to episodes of birch foliar browning and early leaf loss due to leaf cuticular erosion followed by invasion by the leaf fungus *Septoria betulae* (Cox et al. 1989, 1996; Kouterick et al. 2001). This periodic defoliation of coastal birches exacerbates their deteriorating condition caused by warmer winters (Bourque et al. 2005, and see the "Decline" section).

### Nitrogen deposition

Computations have indicated that 10.1% of the global natural terrestrial ecosystems is exposed to N deposition above the critical load of 1 $g \cdot m^{-2} \cdot year^{-1}$, and this area will increase to 25% by 2030 under the Intergovernmental Panel on Climate Change's Special Report on Emissions Scenarios A2 scenario of emission reductions (Dentener et al. 2006). Modeling ecosystem responses to increased $CO_2$ and N deposition indicated that the increase in productivity doubles compared with that occurring under a $CO_2$ increase alone, and that the terrestrial C sink, due to $CO_2$ fertilization and N deposition, accounts for 0.2 $Pmol \cdot year^{-1}$ of C (Lloyd 1999).

Although N deposition is certainly altering the N status of northeastern forests (Aber et al. 2003), the impacts of anthropogenic N deposition for forest productivity are unclear. Studies indicate that in the last century 0.1–2.3 $Pg \cdot year^{-1}$ of C may be stored as a result of anthropogenic increases in N deposition, mostly on northern continents in aggrading forests, and may help balance global C losses to the atmosphere prior to potential future soil N saturation (Peterson and Melillo 1985; Schindler and Bayley 1993; Townsend et al. 1996).

However, Nadelhoffer et al. (1999) used N15 tracer studies to conclude N deposition played a minor role in temperate forest carbon sequestration, with most of the N15 tracer ending up in soils (with low C:N ratios), not tree biomass (with high C:N ratios). Caspersen et al. (2000) found that land-use history accounts for the postagricultural carbon accumulation in eastern US forests, not $CO_2$ fertilization or N deposition.

Some negative aspects of excess N deposition include decreased resistance to summer drought-induced xylem cavitation in hybrid poplars, which may compromise growth in plantations on dry sites (Harvey and van den Driessche 1997), and increased winter xylem cavitation, caused by a freeze–thaw cycle, in yellow birch (*Betula alleghaniensis*) saplings (Zhu et al. 2001). Production may be further compromised in these species by greater seasonality in precipitation patterns and increased winter thaws under climate change.

### Carbon dioxide

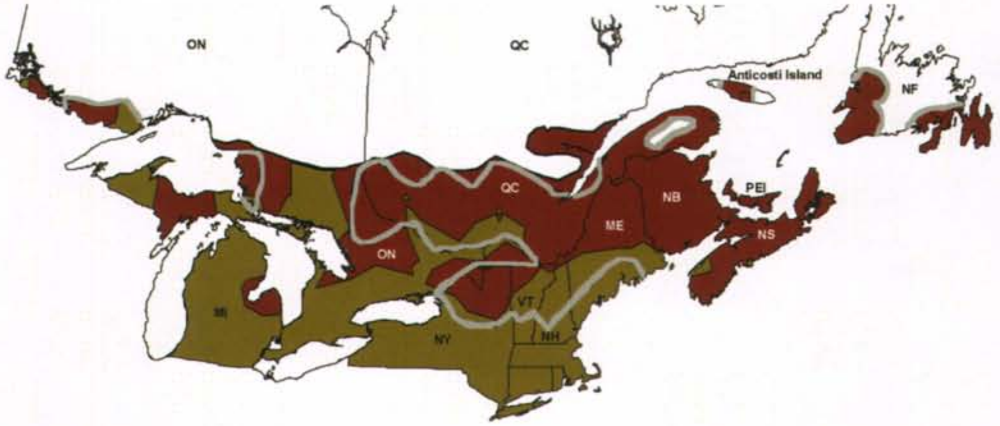
$CO_2$ concentrations in the earth's atmosphere have fluctuated widely over geological and paleoecological time scales (Petit et al. 1999). During each of the Pleistocene glacial stages, levels dropped to below 200 $\mu L \cdot L^{-1}$ and rose again during subsequent interglacial events. Owing to fossil fuel emissions and land-use change, the current concentration of ~380 $\mu L \cdot L^{-1}$ is expected to increase to 580 $\mu L \cdot L^{-1}$ by the middle of this century, representing the highest $CO_2$ level in the past 650 000 years (Jansen et al. 2007; ice core data) or even 15 million years (Pearson and Palmer 2000; fossil leaf data). The current rate of increase has never before been experienced by earth's vegetation (Schlesinger 1997). Understanding how forests respond to rising $CO_2$ concentrations is critical for predicting future forest composition, diversity, and productivity. Forests dominated by productive early-successional trees are typically net C sinks (Barford et al. 2001; Deckmyn et al. 2004). Such forests exhibit maximum rates of net ecosystem productivity, representing sequestered C (Ryan et al. 1997, 2004; Bonan 2008). Forests of the eastern United States, in particular, are accumulating biomass as they recover from nineteenth- and twentieth-century land clearance (Delcourt and Harris 1980; Dixon et al. 1994; Foster et al. 2004), and C sequestration by such forests is an important component of the global C and climate cycles (Ciais et al. 1995; Bonan 2008).

Although a few glasshouse and chamber studies suggest that productive early-successional species preferentially benefit from increased atmospheric $CO_2$ (Brown and Higginbotham 1986; Hoddinott and Scott 1996; Hättenschwiler and Körner 1996), most such work finds later-successional shade-tolerant species to be favored by elevated $CO_2$ (Bazzaz and Miao 1993; Kubiske and Pregitzer 1996; Hättenschwiler and Körner 2000; Kerstiens 2001, 1998). A successional study done in an intact forest setting concluded that shade-tolerant species were at a clear advantage over intolerant competitors when grown at elevated $CO_2$ (Mohan et al. 2007). The species that benefited the most from elevated $CO_2$ in this study were southern sugar maple (*Acer barbatum*), winged elm (*Ulmus alata*), red maple, and black cherry (*Prunus serotina*). Predicting species-specific responses is further complicated by the large degree of within-species genetic variation in response to $CO_2$ (Curtis et al. 1994; Wang et al. 2000; Ward et al. 2000; Mohan et al. 2004).

## Declines and dieback in northern tree species in relation to changes in the physical and chemical climate

What is a tree decline? This major type of forest disturbance is often described as a decline disease, involving progressive deteriorating of tree condition derived by complex responses to multiple stresses. This disease can involve background factors that predispose or weaken the tree, making it more vulnerable to an inciting or severe acute stress event that leads to attack by secondary organisms (contributing stress) that would normally be resisted. This etiology of

**Fig. 1.** Overlay of projected biologically significant refreeze areas (dark red) and documented birch dieback (after Braathe 1995) for 1930–1960 (enclosed by light gray line). The proportion of the birch range (colored area) covered by the calculated refreeze area is 43.1%, and the documented birch dieback area is 37.2%. The calculated refreeze area is ~1.2 times larger than the documented birch dieback area. (After Bourque et al. 2005, Glob. Change Biol., Vol. 11, pp. 1477–1492, ©2005 Blackwell Publishing Ltd., Reproduced by permission of John Wiley & Sons Ltd.)



decline has been elegantly described by forest pathologists (Houston 1981; Manion 1981), and tree decline is considered a major category of plant diseases. This paradigm helps to elucidate the forms of stress, temporally and spatially, whereas knowledge of the ecology, biophysical properties, and physiology may resolve some key adaptive limits of a particular tree species.

## Hardwood declines

### *Birch decline*

Widespread dieback and decline of birches (yellow birch and white birch (*Betula papyrifera*)) have been a major problem in eastern North America (history reviewed by Millers et al. 1989; Braathe 1995; Bourque et al. 2005). Since first reported by Balch (1944), severe birch dieback has been noted from the Maritimes region (Pomerleau 1953) to eastern Ontario (Sinclair 1952; Walker et al. 1990). Birch decline led to a 19% loss of the $368 \times 10^6$ $m^3$ growing stock of yellow birch in North America (Ward and Stephens 1997). Following up on suggestions (Pomerleau 1953; Auclair 1987; Braathe 1995) that winter climate may be involved, the work of Cox and Malcolm (1997) and Cox and Zhu (2003) indicated that various aspects of the biophysics and physiological responses of northern birches to extended winter thaws may play an important role in their decline. Using the climate records over the yellow birch range and knowledge of potentially damaging thaw–freeze events, Bourque et al. (2005) projected areas of birch decline and overlaid these projections on maps of observed 1930–1960 declines (prepared by Auclair 1987; Braathe 1995; Auclair et al. 1997). The projected and observed areas demonstrated similar geographic patterns (Fig. 1). This finding supports the importance of extended thaws in the health of northern birches and has negative implications for these populations, as climate and winter temperatures continue to warm.

### *Maple decline*

Widespread decline episodes in sugar maple have been recorded as far back as 1912–1913, with 26 episodes recorded up to 1986. Millers et al. (1989) attributed decline episodes to many causes, including some climatic factors (root freezing during midwinter thaws) and various contributing stresses from insects and diseases. More recently, prolonged thaw–freeze events have again been implicated in declines in sugar maple. The effects of these events have increased fine-root mortality (Bertrand et al. 1994; Decker et al. 2003), changed soil acidity and nutrient availability (Fitzhugh et al. 2003), and reduced xylem conductivity and sapflow (Bertrand et al. 1994). The above findings point to increased disturbance in this species as climate warms.

### *Oak decline*

At the beginning of the twentieth century, large areas of oak (*Quercus* spp.) mortality were noted in New England and the Appalachian Mountains and were followed by declines in red oak (*Quercus rubra*) and white oak (*Quercus alba*) during the 1920s in North Carolina and Virginia. In 1925, 3 million board feet of white oak were lost in a single county of Virginia. Drought was again implicated (Millers et al. 1989). In the 1930s an episode of large-scale oak mortality in Pennsylvania was attributed to drought and insect attack. Drought stresses have been reported as initiating the decline in oaks both in the southeastern and in the northeastern United States, whereas other abiotic stresses such as frost and ice storms have been implicated locally, but with secondary pathogens often killing the trees. The implication of drought as an inciting factor in oak declines would put certain species (see Millers et al. 1989) at risk with the increased seasonality of rainfall projected under a warmer climate.

### *Ash decline*

White ash (*Fraxinus americana*) dieback has been noted in the northeastern United States and eastern Canada (Quebec) since the 1920s. By the 1940s ash dieback had become increasingly severe in New York and New England. By the 1960s a New York census showed 31% of ash trees were dying, with 6% already dead. By 1963 a survey of New Hampshire, Vermont, Massachusetts, Connecticut, New Jersey, and Pennsylvania ashes found 27.2% of the trees were dying, with 8.9% already dead. Climate factors, especially drought and also freezing damage, have been implicated as inciting factors (Millers et al. 1989), and several biotic agents have been found to act as primary or contributory factors, including ash yellows, a phytoplasmal disease thought to be implicated with aggravated drought susceptibility. As drought is especially associated with the dieback of ash, this species is likely to respond negatively to increases in the frequency of extended droughts — a likely scenario with climate change in the Northeast (Hayhoe et al. 2007).

Recently, an invasive Asian beetle, the emerald ash borer (*Agrilus planipennis*), has emerged as a threat to ash trees in the midwestern United States and Canada (Poland and McCullough 2006). Already at the northern limits of white ash, this beetles native presence in Asia indicates a tolerance for current climatic conditions in North America, such that a severe threat exists for all native ashes on the continent regardless of climate change.

### Declines in softwoods

#### *High-elevation and coastal red spruce*

Widespread decline of red spruce was observed in the northeastern United States from the 1960s through the 1980s and has increased over the last few decades (Friedland et al. 1984; Johnson 1992). Late-winter reddening and subsequent abscission of current-year foliage are signs of this winter injury, attributed to rapid freezing (DeHayes 1992; Perkins and Adams 1995). Lazarus et al. (2004) documented widespread winter injury to the current-year foliage of red spruce in the northeastern United States (Vermont and surrounding states and the province of New Brunswick) in late winter of 2003. In southern New Brunswick 90% of all trees assessed showed winter injury, with an average of 46% loss of the current-year foliage, and in the worst cases, 1- to 3-year-old trees had up to 32% bud mortality, with all crown classes affected (Magasi and Hurley 1994; Hurley and Harrison 1997). This new type of damage in New Brunswick was more frequent and severe on the top third of the crowns. The suggested cause was a unique and perhaps complex weather anomaly, but the synergistic effects of acidic deposition were not ruled out.

There is growing evidence that air pollution and changing winter conditions have predisposed red spruce to winter damage at high elevations by reducing its cold hardiness, which was originally only just sufficient for the winter habitat conditions in Vermont (Schaberg and DeHayes 2000), southern New Hampshire, and Massachusetts. These are areas where climatic factors such as repeated freeze–thaw events (Lund and Livingstone 1998), rapid rates of thaw (Manter and Livingstone 1996), and subsequent exposure to refreezing conditions decreased the shoot cold tolerance. Reduced cold tolerance is of concern under a warming climate, where variation in winter temperatures may increase as will the frequency and duration of winter thaws (Bourque et al. 2005).

## Modeling results of climate change impacts on potential suitable habitat for tree species and forest type estimates and changes in area of suitable habitat

We used forest inventory and analysis (FIA) data (Miles et al. 2001) along with 38 environmental variables (including 7 climate variables, 22 soil variables, 5 topographic variables, and 4 land-use or fragmentation variables) to model the primary environmental drivers to the importance values (calculated equally from basal area and number of stems from each of over 100 000 plots across the eastern United States) for 134 tree species for each 20 km × 20 km cell across the eastern United States (Iverson et al. 2008*b*). It is critical to realize that we do not model potential species ranges by the year 2100, but only the area of suitable habitat for each species. In this analysis, we consider only New England, New York, Pennsylvania, and New Jersey. We were unable to conduct this work on the Canadian side of the border because of data inconsistencies between countries. We then changed the seven climate variables according to three climate models (Parallel Climate Model (PCM), Geophysical Fluid Dynamics Laboratory (GFDL), and HadleyCM3) and two emission scenarios (low emissions — considerable conservation of energy; high emissions — continue on our current trajectory until about 2050) for the year 2100. All models were also run on the average climate model output (GCM3) for low and high emissions, for an overall total of eight scenarios. We used a statistical modeling tool called Random Forests for this analysis. For details, see Iverson et al. (2008*b*). Details for each species output can be found at our Web site: http://www.nrs.fs.fed.us/atlas (Prasad et al. 2007).

The northeastern United States is an extremely diverse region in terms of tree species, and most of the 134 species used in this study occur there: the FIA data record 98 species for the region. In addition, our models for the current climate showed that habitat for an additional 24 species could exist in the region.

Random Forests model outputs yielded percentage estimates of the area coverage for each of 134 species for the current time and for year 2100, according to the eight scenarios discussed above. In sum, over all the eight scenarios, three times more species are estimated to have increases than decreases in suitable habitat in the northeastern United States (Table 1). This pattern may be expected because of the large number of species occupying the southern half of the United States (often with climatic pressure to move north), and a lesser number across the northern tier. According to this assessment, using the HadleyCM3 – high emission scenario (the harshest scenario), 26 species could have a reduced habitat (by at least 2% of the northeastern area), and 84 species could have an increased habitat by year 2100 (Table 1). In contrast, for the PCM – low emission scenario (least harsh scenario), 22 species could have a decreased habitat, and 62 species could have an increased habitat. Note, however, that 72 of the 134 species bordered Canada, and as such, a full assessment of the potential change in suitable habitat is not possible, as only the habitat contained within the United States was analyzed. Our data show that most of the species with decreasing suitable habitat bordered Canada. On the other hand, most of the species for which suitable habitat is increasing are more southern and do not yet reach the Canadian boundary. In both cases, it is the northward shifting of habitat that is responsible for these patterns.

Calculating the numbers of species for which suitable habitat may newly enter or completely leave the region is difficult because of the issues mentioned above. For exam-

**Table 1.** Summary of decreasing and increasing species' area of suitable habitat by scenario for the northeastern United States.

| | No. of species by percentage change class | | | | |
|---|---|---|---|---|---|
| Scenario | Decrease >10% | Decrease 2%–10% | No change | Increase 2%–10% | Increase >10% |
| PCM low | 10 | 12 | 36 | 24 | 38 |
| GCM3 low | 13 | 9 | 32 | 25 | 42 |
| GCM3 high | 16 | 10 | 26 | 20 | 54 |
| Hadley high | 18 | 8 | 18 | 21 | 63 |

**Note:** The four scenarios listed represent the least harsh (PCM – low emissions), the most harsh (Hadley – high emissions), and the average low (GCM3 low) and high (GCM3 high) conditions for 2100.

ple, some species show very small amounts of newly available habitat, possibly as a result of model reliability issues or because of true gains in habitat. If we consider the 36 (of 134) species not currently found in the region's FIA plots, our modeling indicates that 11 of them could have a significant amount (>1% of region's area) of suitable habitat under the PCM – low emission scenario, and 24 of them could have newly available suitable habitat under the warmest, HadleyCM3 – high emission, scenario. However, our models indicate that most (20 of 24) of these species already have suitable habitat at a low level in the region (either in reality and missed by FIA plots or as model error), so it is not surprising to see these species expanding their habitat in the region under the GCM scenarios. Some of the species that could have a sizeable amount of newly suitable habitat include oaks (water oak (*Quercus nigra*), overcup oak (*Quercus lyrata*), Shumard oak (*Quercus shumardii*), and cherrybark oak (*Quercus falcata* var. *pagodifolia*)), some pines (pond pine (*Pinus serotina*), longleaf pine (*Pinus palustris*), slash pine (*Pinus elliottii*)), and others (sugarberry (*Celtis laevigata*), swamp tupelo (*Nyssa sylvatica* var. *biflora*)).

Our models indicate that no species will completely lose their suitable habitat from the region under any of the GCM scenarios, although the habitat of several species would be severely curtailed, especially under the more severe scenarios. Our models indicate that the following species would have the most reduced area of suitable habitat: black spruce (*Picea mariana*), mountain maple (*Acer spicatum*), butternut (*Juglans cinerea*), American mountain-ash (*Sorbus americana*), balsam poplar (*Populus balsamifera*), big-toothed aspen (*Populus grandidentata*), white birch, pin cherry (*Prunus pensylvanica*), and chokecherry (*Prunus virginiana*).

### Species importance values weighted by area

An analysis that simultaneously includes both species area and species importance (area-weighted importance value) perhaps yields a better indicator of potential change in overall species habitat under various scenarios of climate change. To evaluate this assumption, we calculated the ratios of future to current suitable habitat, so that values around 1 (0.9–1.1) indicated no change, values <0.9 were decreases (in two classes of 0.5–0.9 and <0.5), and values >1.1 were increases (in two classes of 1.1–2 and >2) under each of the scenarios. Averaged across all scenarios, a total of 73 species showed increases, 54 showed decreases, and seven had no change (Table 2). We also chose to calculate the same metrics after excluding 50 species that occurred in 20 or fewer cells in the FIA data (<2% of the northeastern United States), because these species tended to have less-stable models. For the 84 more common species, an average of 47 species showed increases and 31 species showed decreases, whereas six species had no change (Table 2).

**Table 2.** Potential species changes, as determined by ratios of current to future suitable habitat.

| Scenario | <0.5 | 0.5–0.9 | 0.9–1.1 | 1.1–2 | >2 |
|---|---|---|---|---|---|
| **For all 134 spp. studied in the NE United States** | | | | | |
| PCM low | 29 | 23 | 13 | 29 | 40 |
| GCM3 low | 28 | 25 | 8 | 24 | 49 |
| GCM3 high | 38 | 16 | 6 | 12 | 62 |
| Hadley high | 41 | 10 | 2 | 12 | 69 |
| **For 84 spp. found in 20 or more 20 km × 20 km cells in the NE United States** | | | | | |
| PCM low | 9 | 17 | 10 | 27 | 21 |
| GCM3 low | 10 | 19 | 7 | 18 | 30 |
| GCM3 high | 21 | 11 | 6 | 10 | 37 |
| Hadley high | 25 | 8 | 1 | 10 | 40 |

**Note:** Columns headings are ratios of suitable habitat in year 2100 to current suitable habitat, so that column headings less than 1 contain the number of species with declining habitat, and columns with ratios greater than 1 contain the number of species with increasing habitat. See Table 1 for scenario descriptions.

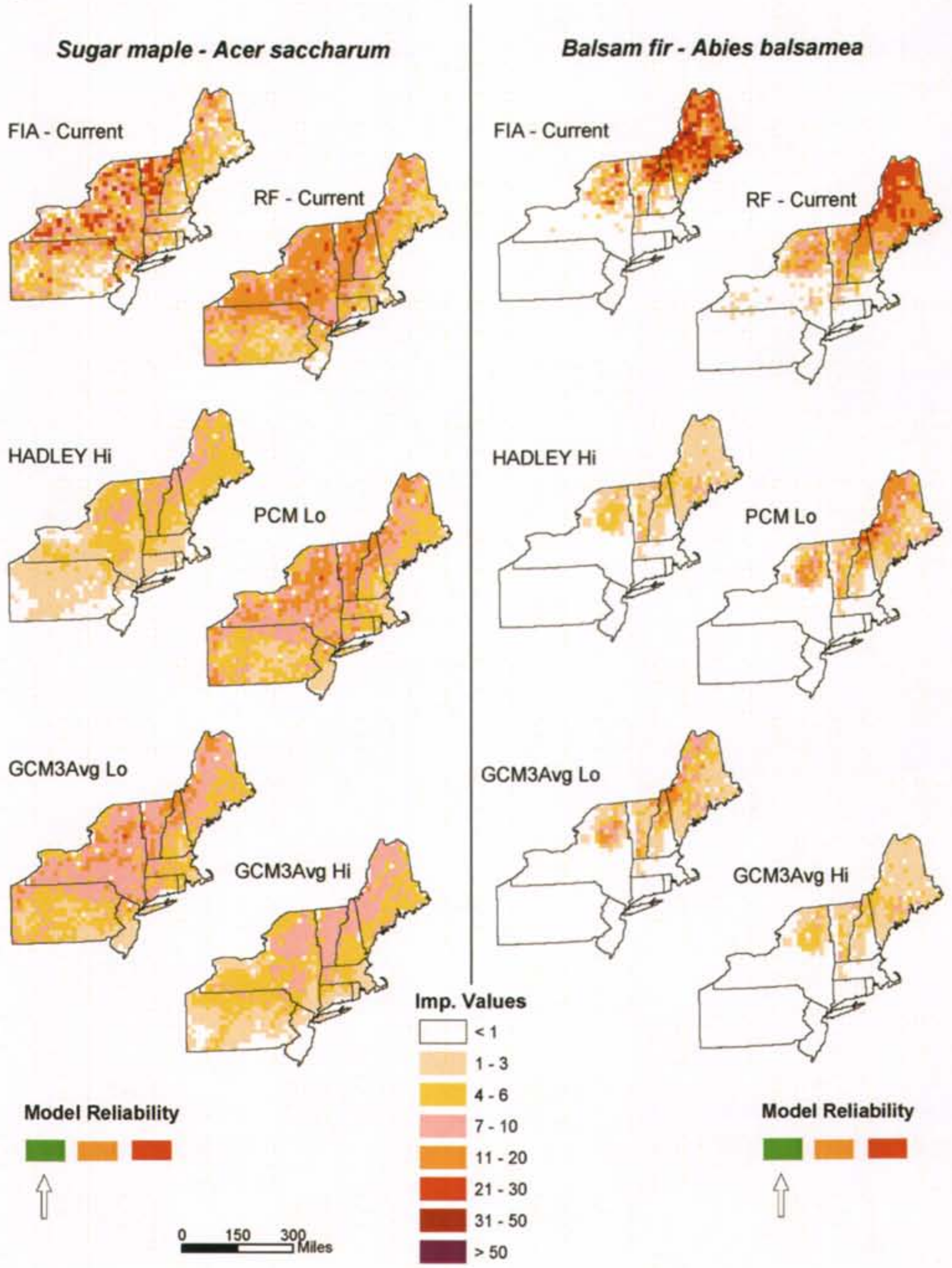
Some of the species for which suitable habitat decreases the most under this evaluation include relatively common northern species such as white birch, quaking aspen (*Populus tremuloides*), bigtooth aspen (*Populus grandidentata*), balsam fir (*Abies balsamea*), northern white-cedar (*Thuja occidentalis*), striped maple (*Acer pensylvanicum*), American beech (*Fagus grandifolia*), red spruce, sugar maple, and black cherry. (Interestingly, empirical data suggest sugar maple and black cherry may be at a demographic advantage in the Northeast with warming, see "Future research" section below.)

Species showing substantial increases of area-weighted importance values include post oak (*Quercus stellata*), shortleaf pine (*Pinus echinata*), loblolly pine (*Pinus taeda*), eastern redbud (*Cercis canadensis*), hackberry (*Celtis occidentalis*), bitternut hickory (*Carya cordiformis*), sweetgum (*Liquidambar styraciflua*), eastern redcedar (*Juniperus virginiana*), eastern cottonwood (*Populus deltoides*), sourwood (*Oxydendrum arboretum*), and sycamore (*Platanus occidentalis*).

### Species-level maps

We prepared maps for each species, with FIA actual data, current condition according to model outputs, HadleyCM3 – high emission (harshest scenario), average high and low emission for the three models, and PCM – low emission

**Fig. 2.** Potential values in suitable habitat for sugar maple and balsam fir according to the current FIA data, the current model, and future scenarios of Hadley high emissions (harshest), PCM low emissions (mildest), average of three models with low emissions, and average of three models with high emissions.

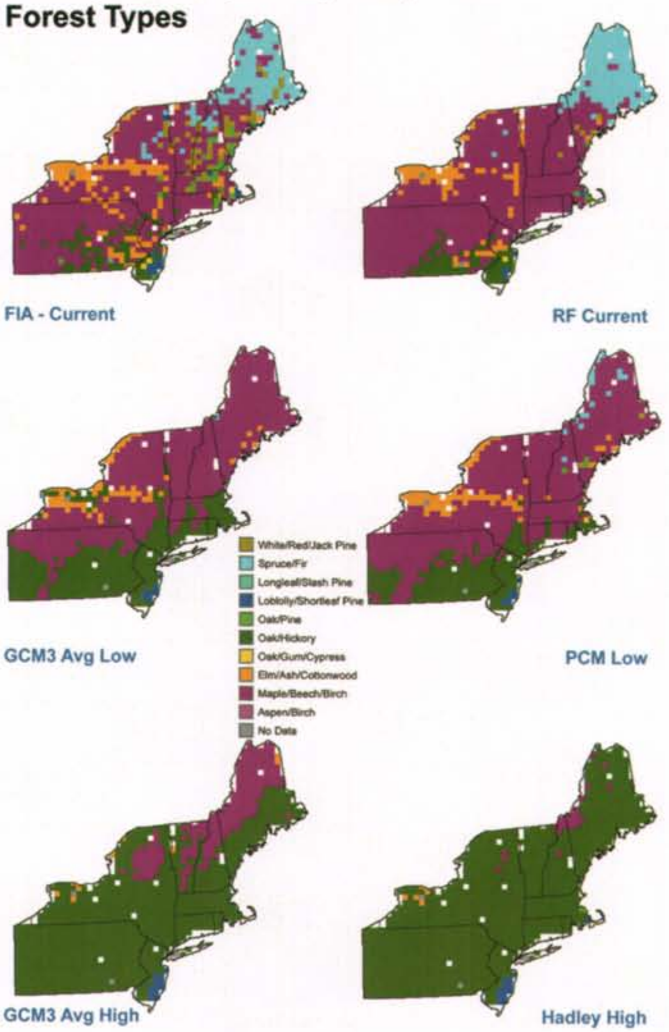


(mildest scenario). Model reliability was based on four metrics ($R^2$, fuzzy kappa, and consistency measures of 30-tree models using the bagging tree outputs) used to compare model outputs against the current distribution according to FIA data. We provide some examples here, and all 134 species-level maps are available from our Web site. The examples show two common species of large economic value for which suitable habitat will likely decrease: sugar maple and balsam fir (Fig. 2). The maps show that the suitable habitat for both species is especially reduced under the high levels of emissions by human activities — if we can substantially curtail greenhouse gas emissions, the suitable habitat for these species would remain much more intact. The PCM low emissions model shows relatively small changes compared with high emission scenarios and compared with the Hadley model. Though the spatial distribution of these species is not considerably affected by climate change, the overall habitat could be reduced drastically for both species.

## Forest-type maps

By combining individual species importance maps and developing rules for "who wins", we have created maps of forest types for the northeastern United States (Fig. 3). We find that in the future, only the PCM – low emission (the least harsh) scenario retains any spruce–fir habitat. The

Fig. 3. Forest-type map for the northeastern United States, based on combining individual species maps of importance.



oak–hickory habitat increases significantly at the expense of the maple–beech–birch habitat in all scenarios, especially under the high emission scenarios. Note, these maps reflect habitat suitability and not necessarily where the species will actually be within the next 100 years. For example, most oaks and hickories have difficulty regenerating (e.g., Sutherland and Hutchinson 2003), so that projected oak–hickory expansions may not materialize for a long time (Carmel and Flather 2006; Iverson et al. 2008*a*).

### Modeling — discussion

We do not expect the situation depicted in the maps presented here to be realized by 2100 or even many decades afterward. Trees live a long time and migrate slowly, so great lag times would need to be considered to determine actual estimated ranges. In other work, we have attempted to do so for a few species, using a companion model (SHIFT), and found that the lag times and fragmented nature of the remaining forests greatly slow migration rates. For five species we estimated that less than 15% of the suitable habitat would have a 1 in 50 chance of being colonized within 100 years (Iverson et al. 2004).

We also emphasize that there are several assumptions and limitations with this approach. We assume the species is in equilibrium with its environment. We cannot include $CO_2$ enrichment, land-use change, or most disturbances (e.g., fire, pests, diseases, extreme climatic events) directly but only indirectly as species legacies. Obviously, species trajectories could be altered significantly by such disturbances.

This study has shown that climate change could have large impacts on the suitable habitat for tree species in the northeastern United States. Overall, we show that climate change could bring some additional species into the region, but more importantly, there is a potential for expansion of area and importance for species that are in the region but have relatively minor prominence. Our models show that species with increasing suitable habitat substantially outnumber those with decreasing habitat. The geographical location of the tree species ranges can be used to explain this trend. In the northeastern United States, there is much territory to the south of the study area but none to the north (because we cannot model Canada without FIA data). However, the pressures, as indicated by paleoecological and current data, are for the species to move northward. So it is logical that many southern species, especially ones that are driven largely by climate (particularly temperature), would have suitable habitat appear or increase in the northeastern United States. Effects of nonclimate variables, such as disturbance regimes, dispersal mechanisms, and fragmentation, add complexity and uncertainty to the final outcomes.

Besides the possibility that there will be more habitat for less-common species, the habitat of some of the very common northern species, such as balsam fir, paper birch, red spruce, bigtooth and quaking aspen, and black cherry, will likely shrink. The models thus suggest a retreat of the spruce–fir zone back into Canada, as seen in the past (DeHayes et al. 2000).

Perhaps a better evaluation of potential species habitat changes is provided by the area-weighted importance value variable, instead of potential area changes (which are difficult to model at low importance levels). This variable includes both abundance and area of the species. In this case, the number of species with increasing area-weighted importance values is greater than the number of species with decreasing area-weighted importance values, but the difference is less than that when only area is considered.

Another set of recent modeling work by McKenny et al. (2007) also projects a northward shift of northeastern species, including sugar maple, red maple, northern red and white oaks, white ash, and yellow birch (for information on all 130 species used in this study, see http://planthardiness.gc.ca/).

## Paleoecological and modern evidence of climate change impacts on forest composition

Paleoecological data from northeastern forests reveal the importance of past changes in climate for species composition. Before the current-day Holocene interglacial period, beginning approximately 15 000 – 12 000 years before present (BP), the climate of the Pleistocene, covering the previous 2.5 million years, fluctuated fairly routinely between colder glacial cycles and shorter, warmer intervening interglacial periods (Webb et al. 1994). Generally, conditions in northeastern North America were drier and up to 2 °C warmer 6000 – 10 000 BP, changing to cooler and moister conditions at later Holocene stages (Webb et al. 1994; DeHayes et al. 2000). At the biome scale, most modern assemblages of eastern trees have only co-occurred over the last 6000–8000 BP, and individual species have responded to climate change over the last 20 000 years in unique manners (Davis 1983; Webb 1987; Overpeck et al. 1991; Webb et al. 1994). Hence, modern forest communities are "transitory combinations of taxa" (DeHayes et al. 2000), and paleoecological trends provide no evidence to expect that current species assemblages will respond in concert to current and future climate change.

Pollen and charcoal evidence from throughout New England and Nova Scotia suggest that in the very early Holocene this region was characterized by spruce (*Picea* spp.) and jack pine (*Pinus banksiana*) woodlands with fairly frequent fire events occurring every ~50–200 years (Webb et al. 1994; Clark et al. 1996). Also occurring in the pollen record of this time was evidence of *Artemesia* and grass and sedge taxa, suggesting more open vegetation that was compositionally and functionally distinct from the boreal forests of today. Within a few thousand years (by ~9000 BP in New York), the region became dominated by eastern white pine concomitant with a decline in *Picea* spp., followed by decreased jack pine abundance. During the warmer periods of the early to mid Holocene, both white pine and eastern hemlock (*Tsuga canadensis*) grew at elevations up to 400 m higher than where these taxa occur today in New Hampshire's White Mountains (Davis et al. 1980) and the Adirondack Mountains of New York (Jackson and Whitehead 1991). After the initial increase in white pine, oaks also became common. Charcoal evidence suggests fire continued to be a regular event, although it is unclear whether return times were less frequent than in the preceding spruce–jack pine woodland (Clark et al. 1996). The decline in graminoid and *Artemesia* pollen during this time suggests more closed forest physiognomies.

After this period (about 8000 BP), charcoal evidence in New York indicates a steep decline in the importance of fire, a decline in white pine pollen, and the rise of certain hardwood species, particularly American beech, elms (*Ulmus* spp.), and sugar maple, which codominate with the oaks that remain abundant (Clark et al. 1996; Foster et al. 2004). Hemlock also increases with the hardwoods, declines after 5000 BP, and then resurges after 4000 BP. Farther north, white pine reached its northernmost limit 4000 BP and then retreated back southward in response to the climate cooling that allowed boreal species to move further south (DeHayes et al. 2000). The modern boreal forests of eastern Canada only developed during the last 6000 years (Webb 1987) and apparently only shifted southward into Maine and Minnesota during the last 1000–1500 years, whereas white pine in these regions has been exhibiting declines in abundance during this cooling period (DeHayes et al. 2000).

Several efforts using current species' data also address issues of climate change impacts on future forest composition. However, in addition to dispersal, migration, and fragmentation — obstacles that may complicate species' establishment in potentially suitable habitat and climates — other factors not always accounted for in models of future species composition, such as differing abiotic conditions (e.g., water tables, disturbance frequencies) and biotic factors (pests, pathogens, and competition with native and exotic plants), make predicting future ranges of species and forest types complex. For example, although both models (Iverson and Prasad 1998, 2002; McKenny et al. 2007; Iverson et al. 2008*b*) and some empirical data (Duchesne et al. 2002; Schaberg et al. 2006) suggest a future decline in sugar maple in warmer northeastern US forests, data from a Harvard Forest soil warming experiment suggest this species to be one of the "winners", with enhanced growth of juveniles, under a 5 °C increase in soil temperatures, at least when not grown in competition with potential invading taxa from the south (J. Mohan and J. Melillo, unpublished data). Red oak juveniles in this oak-dominated forest survived and grew less well under warmer conditions. Conversely, Ibañez et al. (2007) found that red oak exhibited higher germination rates at lower soil moisture levels, suggesting, as some models predict (Iverson et al. 2008*b*), that this species may expand in the Northeast given more drought events in the future (Hayhoe et al. 2007).

A recent modeling study assessed the combined effects of increased atmospheric $CO_2$ and elevated temperatures on the transitional temperate–boreal forest system of the Boundary Water Canoe Area of northern Minnesota (Xu et al. 2007). When only increased temperatures were considered, this transitional forest shifted to a pine-dominated mixed forest, consistent with southern species moving northward with climate change. However, when the effects of increased atmospheric $CO_2$ on optimal temperature for photosynthesis were included ($C_3$ plants often exhibit higher photosynthetically optimal temperatures when grown at elevated $CO_2$), this system remained a fir-dominated boreal forest in areas of high water-holding capacity, suggesting that $CO_2$ enrichment could reduce global warming impacts on forest compositional change.

Finally, the increased abundance of woody vines that has been observed in temperate forests over the last few decades (Myster and Pickett 1992; Dillenburg et al. 1995; Allen et al. 2007), apparently associated with increases in atmospheric $CO_2$ (Mohan et al. 2006, 2008), and the related decline in forest regeneration (Myster and Pickett 1992; Dillenburg et al. 1995; Laurance et al. 2001; Phillips et al. 2002) make future forest establishment, composition, and structure even less certain.

## Paleoecological and modern evidence of climate change impacts on forest carbon dynamics

Natural forest C gain is directly linked to temperatures and precipitation, as well as to species composition, soil nutrients, and stand age (Ryan et al. 1997, 2004; Bonan 2008), highlighting the importance of both edaphic factors and climate for forest productivity. Many historical and paleoecological studies document the direct effects of altered temperature and (or) precipitation on northeastern forest productivity. A 400 year record of black spruce growth near the tree line in eastern Canada indicates that modern trees are larger and more productive than same-genet trees that grew during the Little Ice Age (Vallée and Payette 2004). Similarly, a 5200 year record of buried black spruce – jack pine trees in northern Quebec indicates higher productivity in association with milder, warmer climates (Arseneault and Sirois 2004). Cooler and drier periods during the twentieth century (1910–1930, 1965–1970) were associated with lower growth rates of an old-growth hemlock – white pine forest in Pennsylvania (Black and Abrams 2005). Reduced growth was primarily due to drought in winter and early fall, and to low March temperatures.

Research of modern forest dynamics also supports the importance of direct climate effects on forest growth in the Northeast. In eastern North America, winter is the season showing the greatest amount of warming (Schwartz et al. 2006), a phenomenon that bears important implications for the timing of spring leaf out. Schwartz and Reiter (2000) found an average 5 to 6 day advance in spring phenology of lilacs in North America between 1959 and 1993, owing to warmer seasonal temperatures largely in the Northwest and the Northeast. A 47 year phenological record from Hubbard Brook, New Hampshire, found significantly earlier spring leaf out and an increase in green canopy duration of about 10 days (Richardson et al. 2006). These findings suggest increasing periods of growth and productivity for northeastern forests, and they are similar to the results of a soil warming study at Harvard Forest that documents an average 4–7 day increase in spring bud break for canopy trees growing at a 5 °C increase in soil temperature (J. Melillo and J. Mohan, unpublished data). Similarly, White et al. (1999) found an increased growing season length for northeastern US forests and determined that such an increase in growing season length would have important consequences for net ecosystem C accumulation (i.e., a 1% increase in growing season length corresponds to a 1.6% increase in net ecosystem productivity).

Warmer climates, particularly with increased precipitation, may eventually lead to greater forest productivity, but interactions with nonclimatic variables make this relationship less than certain. Even with increased temperatures and precipitation, temperature-induced increases in evapotranspiration may lead to increased drought stress (Ollinger et al. 2008). In a PnET-BGC model simulation of Hubbard Brook's responses to four climate scenarios over this century, Campbell et al. (2009) found that even with warmer temperatures and increased precipitation, soil water content actually declined by 2100. In response to warmer conditions and increased precipitation, net primary productivity (NPP) increased by 8%–15% between 1999 and 2099, driven largely by longer growing seasons.

Elevated $CO_2$ has been shown to result in $\sim$23% increase in NPP in free-air C enrichment experiments in four forests representing a range of species compositions and climates (Norby et al. 2005). It remains unclear whether N limitation in northeastern forests will further constrain productivity enhancements from elevated temperatures and $CO_2$ (Oren et al. 2001; Luo et al. 2006), whether productivity will be enhanced by rising $CO_2$ even in the face of N limitation through a combination of increased plant N uptake and increased N-use efficiency (Norby et al. 2005; Finzi et al. 2007), or whether increases in N deposition and warming-induced increases in N mineralization rates will offset N limitation in northeastern forests systems. Simulating the 300 year change in NPP (1700–2000) on northeastern sites with differing land uses, Ollinger et al. (2002) compared the productivity impacts of increases in atmospheric $CO_2$, tropospheric $O_3$, and N deposition with "control" situations in which only past land use was considered (and altered atmospheric chemistries were not). This study found increases in NPP of 19% (1116 vs. 933 $g{\cdot}m^{-2}{\cdot}year^{-1}$) and $\sim$11% ($\sim$1100 vs. $\sim$1220 $g{\cdot}m^{-2}{\cdot}year^{-1}$) for historic agricultural and timber lands, respectively, compared with control simulations. Further, adding interannual climate variation greatly increased the temporal variability in net carbon exchange for Hubbard Brook and Harvard Forest, compared with considering land-use and pollution effects alone.

Using the PnET-CN ecosystem model to predict NPP over the current century, Ollinger et al. (2008) predict that deciduous northeastern forests exhibit neutral- to slight-increases in NPP due to climate change when effects of rising $CO_2$ are not considered. When $CO_2$ and climate change are both considered, NPP in deciduous forests increases from current-day levels of $\sim$380 $g\ C{\cdot}m^{-2}{\cdot}year^{-1}$ to $\sim$725–1000 $g\ C{\cdot}m^{-2}{\cdot}year^{-1}$ by 2100, depending on the global change model and $CO_2$ emission scenario used. This suggests that the productivity of current deciduous forests in the Northeast may significantly increase by the end of this century, barring edaphic limitations and natural and anthropogenic disturbance (i.e., fire frequency is currently increasing in boreal forests and may become more prominent given increased summer droughts in northeastern temperate forests). Conversely, current-day spruce forests exhibited much more variable results, with an overall decline in NPP under the warmest emissions scenario, regardless of the $CO_2$ effect.

Although Ollinger et al. (2008) are careful to point our that future shifts in species composition, and potential impacts on NPP, were beyond the scope of their paper, changes in productivity may further be mediated by shifts in forest species composition (Woods 2004; Mohan et al. 2007). Predicted increases in precipitation variability and storm events (Hayhoe et al. 2007) may lead to shifts in dominance toward shade-intolerant, productive tree species typical of recently disturbed environments (Woods 2004). Conversely, recent studies in the eastern United States determined that elevated $CO_2$ benefited the recruitment of shade-tolerant, less-productive taxa (Mohan et al. 2007). Local dynamics and indirect climatic effects further impact productivity and composition. Supporting the importance of edaphic factors, Gamache and Payette (2005) document that despite a milder twentieth century climate, local topographic factors primarily influenced black spruce tree line and seed establishment at high elevations. This study found little correlation between tree establishment and climate, likely owing to the difficulty of successful seed establishment on exposed, drought-prone tundra, and because black spruce produce semi-serotinous cones. This study demonstrates that local edaphic factors (e.g., exposed, drought prone soils) can still negatively impact current and future recruitment success, similar to conditions earlier in the Holocene. Chapin et al. (2004) suggest that boreal vegetation shifts due to climate change will be gradual near northern range limits, but abrupt in central regions as climatic thresholds are exceeded. Similarly, local effects in boreal peatlands can buffer climatic thawing of permafrost, making transient responses difficult to predict and potentially causing lags and thresholds leading to sudden, large shifts in vegetation (Camill and Clark 2000).

## Future research and implications

The merging of empirical data, particularly from field manipulations and natural gradients, with modeling studies and predictions is vital to increase the forecasting accuracy of future forest composition and carbon dynamics. For example, under harsh climate scenarios future habitat for sugar maple is expected to decrease by 10%–20% in the northeastern United States (Fig. 2). Yet empirical data suggests the recruitment success of sugar maple juveniles may be enhanced by warmer soils at Harvard Forest, possibly involving a biogeochemical feedback with N mineralization rates (J. Mohan and J. Melillo, unpublished data). Future efforts synthesizing species-specific modeled distributions with data documenting demographic responses to climate change will greatly improve forecasts of future forest composition and ecosystem functioning.

A related critical issue requiring more research effort is how potential changes in northeastern forest composition will affect future ecosystem services, including water and C balances. Hemlock forests of the Northeast lose 50% less moisture to the atmosphere during summer evapotranspiration than do nearby hardwood stands with similar leaf area indices (Ellison et al. 2005). As a result of the introduction of an exotic pest, hemlock wooly adelgid (*Adelges tsugae*), hemlock stands are shifting toward dominance by hardwoods, with direct implications for water balances — to the extent that small streams currently draining hemlock stands (and inhabited by salamanders and aquatic invertebrates of conservation concern) are predicted to diminish following hardwood dominance (Ellison et al. 2005). Similarly, shifts in species composition bear important implications for C and energy budgets. Will forests become more productive in a warmer climate with enhanced C and N fertilization? Or, will productivity decline as forest stands age and elevated $CO_2$ favors the establishment of less-productive species? Will increased drought negate any productivity boost stemming from warmer temperatures and longer growing seasons?

Another concern is to what extent interactions among global change components will alter future forest disturbance, declines, composition, and productivity. For example, several studies have determined that increased $O_3$ can offset productivity benefits of $CO_2$ fertilization (Karnosky et al. 2003, 2007). $O_3$ has also been linked to reduced C allocation to roots (Chappelka and Samuelson 1998; Laurence and Andersen 2003). How this reduction in roots will interact with future drought and disturbance events to affect forest composition and functioning remains uncertain. Similarly, higher atmospheric $CO_2$ can increase optimal temperatures for photosynthesis, which may reduce vegetation change due to global warming (Xu et al. 2007). It remains unclear how other factors, such as increased $O_3$ and drought, might affect this prediction.

Finally, more research is needed to pinpoint time scales of vegetation change. Will forest change be gradual or abrupt (Camill and Clark 2000; Chapin et al. 2004)? What are the implications of transient dynamics and disturbances such as tree declines for forest structure and productivity? How soon will most northeastern forests shift from being "fertilized" from N deposition and sinks for atmospheric $CO_2$, to being N saturated with nutrients leaching into stream systems? What might the enhanced N availability mean for future species competitive relations and composition? Further research addressing these questions and others will advance our ability to forecast changes in northeastern forest composition and associated modifications in productivity and other ecosystem services, in a future, warmer world.

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