Will environmental changes reinforce the impact of global warming on the prairie–forest border of central North America?

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Within the next 50–100 years, the warming climate will have major effects on boreal and northern hardwood forests situated near the prairie–forest border of central North America. This biome boundary shifted to the northeast during past episodes of global warming, and is expected to do so again. The climate of the future will likely lead to higher mortality among mature trees, because of the greater frequency of droughts, fires, forest-leveling windstorms, and outbreaks of native and exotic insect pests and diseases. In addition, increasing populations of native deer and European earthworm invasions will inhibit the establishment of tree seedlings. The expected net impact of these factors will be a "savannification" of the forest, owing to the loss of adult trees at a rate faster than that at which they can be replaced. This will cause a greater magnitude and more rapid northeastward shift of the prairie–forest border, as compared with a shift solely attributable to the direct effects of temperature change.

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Continental interiors have biome boundaries that are highly sensitive to climate change. The northern prairie–forest biome border in central North America is such a case; it is ~2700 km in length, extending from northern Alberta, Canada, southeastward across the Canadian prairie provinces, and into the western Great Lakes region of the US (DeFries *et al.* 2000; Figure 1). Positioned more or less perpendicular to the border is a steep gradient from a prairie climate – featuring frequent droughts, summer heat waves, and a historically high fire frequency – to a forest climate, with rainfall evenly distributed throughout the year and cool summers (Changnon *et al.* 2002).

Although woody expansion into North American grasslands has been documented in the past (Samson and Knopf 1994), it is widely expected that, under a scenario of human-induced global warming, the prairie biome will shift to the northeast and displace existing forests. The paleoecological record shows that this pattern of biome change occurred during previous climate-warming episodes; during the mid-Holocene warm period 7500 years before present (ybp), for example, a warmer climate and interactions between climate and fire frequency allowed grassland to replace boreal forests (dominated by jack pine [*Pinus banksiana*], black spruce [*Picea mariana*], balsam fir [*Abies balsamea*], aspen [*Populus tremuloides*], and paper birch [*Betula papyrifera*]) as well as hardwood forests (dominated by northern red oak [*Quercus rubra*], white oak [*Quercus alba*], sugar maple [*Acer saccharum*], American basswood [*Tilia americana*], and elm [*Ulmus* spp]; Camill and Clark 2000; Umbanhowar 2004). Future projections for a "2 x CO_2" climate (ie 560 parts per million [ppm] atmospheric CO_2, or twice the preindustrial concentration of 280 ppm) suggest a northeastward shift of biomes and tree ranges of 100–500 km (Lenihan and Neilson 1995; Walker *et al.* 2002), resulting in the potential loss of forests on 200 000 to 1 million km^2 of land in central North America. The upper estimate is more than twice the size of the state of California.

These projections, however, take into account only the climatic envelope within which certain tree species and biomes currently exist. Several other human-induced drivers of change will influence prairie–forest border dynamics, so that the types or magnitudes of future changes may differ from those in the paleoecological record, probably leading to no-analog plant communities (ie there is no past or current community of a similar composition; Williams and Jackson 2007). These drivers include invasive earthworms, tree diseases and pests, changes in dynamics of native insect populations, increasing deer

In a nutshell:

- Global warming is expected to cause the existing prairie–forest border of central North America to shift to the northeast; a substantial area of currently forested lands will change to savannas or grasslands
- More frequent droughts, fires, and windstorms – in addition to increased incidence of exotic tree diseases/pests and population growth of native insects, native deer, and non-native earthworms – will reinforce the impacts of warmer temperatures on existing forests
- Society will face important decisions regarding forest management; namely, whether to resist or facilitate change and how to manage the new boundary areas in light of invasive species and climate change

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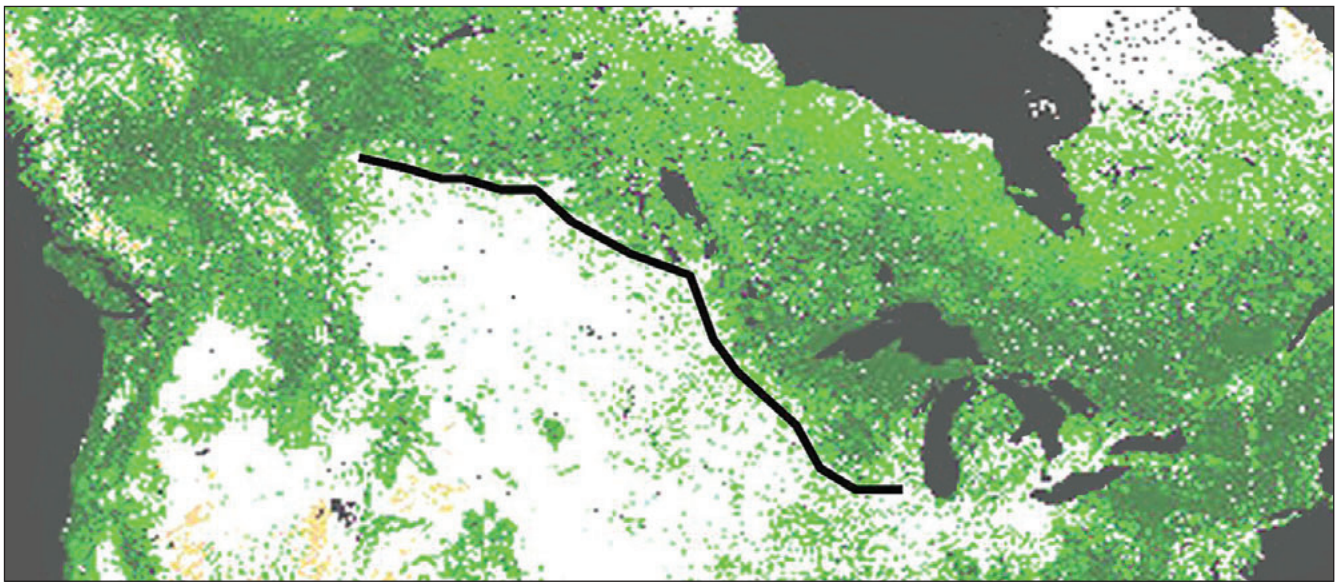

Figure 1. *Prairie–forest border in central North America (thick black line). Forest cover shown in green, non-forest is white, and water is black. Modified from DeFries* et al. *(2000).*

populations, changing disturbance type and frequency, increased plant growth due to higher availability of CO_2 (CO_2 fertilization), and nitrogen deposition. All of these drivers are capable of causing ecosystem change individually, but their impacts will occur concurrently with the direct impacts of climate change. In some systems with multiple drivers, simultaneous changes in two or more of them might result in no net change, because various drivers may counteract one another. However, for the prairie–forest border of central North America, global warming will interact with these drivers of change by facilitating faster and greater impacts, which will in turn reinforce the impacts of warming itself. The objective of this paper is to review important drivers of change along the prairie–forest border in central North America and how their interactions with the warming climate may influence forests.

Climate change and impacts on forests

Given the anticipated degree of warming, the most important direct impact on forests will probably be drought. For the continued existence of a given forest, all else being equal, trees must survive the longest summer dry period that occurs at a multidecadal scale. A warmer, drier climate would have much greater consequences for the northern prairie–forest border of central North America than would a warmer, wetter climate, which would still support forests, although of different composition. The best available projections for central North America for summer (June, July, and August) temperatures by the late 21st century are +3–9°C (range between low and high CO_2 emission scenarios established by the Intergovernmental Panel on Climate Change [IPCC]; Wuebbles and Hayhoe 2004; Christensen *et al.* 2007). Although long-term forecasts are uncertain, the most probable scenario for summer precipitation is that it will remain similar to that from 1970–1999 or decline 10–30% by the end of the 21st century; there is only a slight chance that it will increase (Wuebbles and Hayhoe 2004; Christensen *et al.* 2007). A negative change in the precipitation-to-evaporation ratio and drier summers are therefore thought to be the most probable scenario. This is consistent with observations in the region during the late 20th century, which show increases in temperature twice that of the global mean temperature rise and greater temporal variability in precipitation, leading to more droughts, shorter winters, and longer growing seasons (M Seeley pers comm).

The projected change toward lower precipitation-to-evaporation ratios and higher temperatures drives climate-envelope predictions that major tree species will shift their ranges northward by up to 500 km in central North America (Prasad *et al.* 2008). This is consistent with northward range shifts observed during episodes of Holocene warming that were similar in magnitude to those predicted for the 21st century, although the rate of change during the 21st century may be an order of magnitude faster than that of mid-Holocene warming, possibly outstripping the ability of tree species to keep pace with climate change (Davis and Shaw 2001).

Several simulations of modern and future biome boundaries show substantial differences (eg Lenihan and Neilson 1995; Notaro *et al.* 2007). However, they all suggest that large-magnitude northward shifts of biome boundaries are likely to occur at mid-continental, mid-to-high latitude regions, such as the central North American prairie–forest border and the interior forests of Siberia.

Foresters have reported dieback of mature tree crowns and regeneration failures throughout the northern hardwood forest region in Minnesota, Wisconsin, and Michigan in recent years (USDA 2008; Figure 2), although the underlying mechanisms remain unclear.

Increasing drought frequency, in combination with shallow soils, soils poor in base cations, and secondary impacts of insects, have led to sugar maple dieback in the past (Auclair *et al.* 1996). Warmer and longer growing seasons have also contributed to dieback of paper birch (Jones *et al.* 1993).

Warming climates generally do not follow a smooth upward trajectory. Forests will experience runs of several unusually warm years, with temperatures equal to predicted mean temperatures a few decades in the future, thus hastening the rate of forest change (Cohen and Pastor 1991). The paleoecological record shows that changes in the location of the prairie–forest border and in tree species distribution have occurred within a few decades in response to periods of drought and resulting stress (Camill and Clark 2000; Foster *et al.* 2006).


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Figure 2. *Forest dieback on the north shore of Lake Superior, Minnesota. This type of drought-induced dieback has become common in boreal birch–spruce–fir forests and northern hardwood forests of the prairie–forest border region in recent years.*

In summary, multiple lines of evidence – including recent climate trends, recent observations of forest response to episodes of warm and dry climate, future projections of climate, future projections of tree species ranges, and the best available predictions for future biome boundaries – indicate that a warmer climate will be less favorable for the continued existence of forests near the current prairie–forest border. This conclusion is reinforced by the paleoecological record of changes that occurred during previous periods of warming climate.

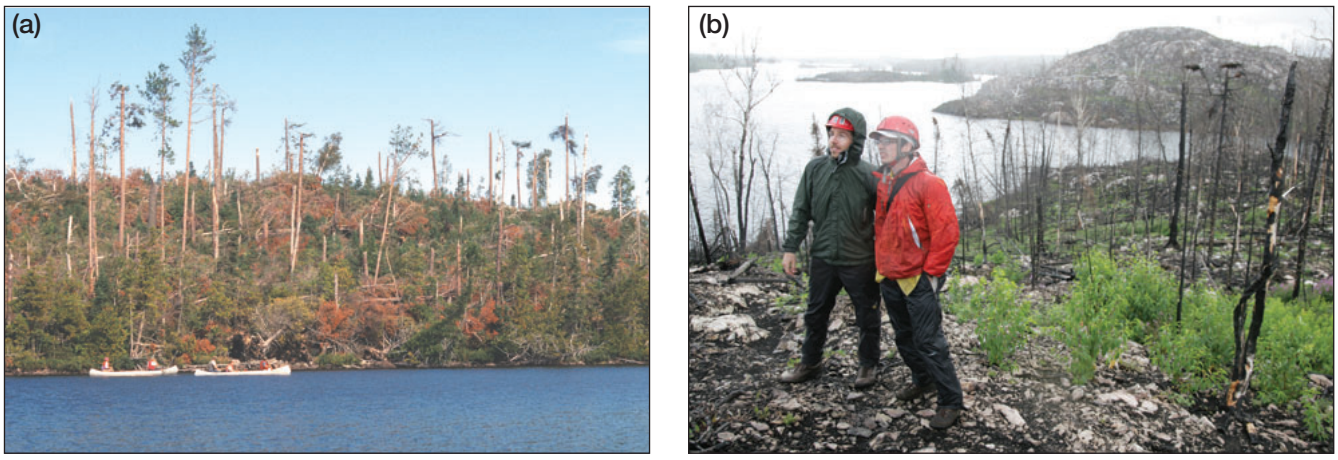
Indirect impacts of climate change

Changing disturbance regimes

Stand-killing disturbances, such as fire and wind, can give tree species adapted to a warmer climate a chance to replace existing species (Overpeck *et al.* 1990). Fire has been an important factor influencing the location of the prairie–forest border, and decreases in fire frequency due to land use, fragmentation, and fire suppression (coupled with several relatively moist decades) have led to the expansion of woody species into the prairie biome over the past 50 years (Samson and Knopf 1994). Thus, changes in fire frequency due to climate warming are likely to have important impacts throughout the prairie–forest region. Although climate warming will create conditions more conducive to increased fire frequency and severity at any given level of landscape fragmentation, other factors may result in divergent fire regimes close to and distant from the prairie–forest ecotone. For instance, land-use patterns in the geographic zone at the interface between the forest and prairie biomes, coupled with active fire suppression, will result in lower frequency and greater severity of forest fires. This is because much of that landscape is agricultural and unlikely to burn, and the generally high levels of fragmentation in the area will reduce fire spread. Although fragmentation has positive (more human access for ignition) and negative (more fire breaks) effects on fire frequency, the latter will dominate in areas with mixed land types and land uses, reducing the impacts climate change might otherwise have on fire incidence and spread.

In contrast, in densely forested areas with little fragmentation – such as conifer forests several tens of kilometers away from the prairie–forest interface, but still within the area that will experience a substantially warmer and drier climate – fires may become more frequent and more severe. This would include large tracts of boreal forest in Canada and the northern lake states of the US, where fire frequency is predicted to increase with global warming (Flannigan *et al.* 2001). A variety of vegetation types found to the south of the prairie–forest border, including prairie, aspen parkland, pine savanna, and oak savanna, could expand into currently forested areas (Curtis 1959; Young *et al.* 2006). These new vegetation types would also support more frequent fires than would closed-canopy forests, thus reinforcing their persistence.

Wind storms are also important factors in forest development. Severe thunderstorms, known as *derechos*, are capable of producing forest-leveling winds across millions of hectares (Rich *et al.* 2007). The highest frequency of these storms occurs within the "*derecho* triangle", which – with vertices in western Pennsylvania, north-central Texas, and central Minnesota – includes the traditional "tornado alley" of central North America, as well as the prairie biome to the southwest. *Derechos* require warm and humid summer days, meteorological conditions that are expected



(a) and (b) D Hansen, Univ of Minnesota

Figure 3. *Major disturbance events will be more common with global warming and transform the composition of large tracts of forest. (a) Unlogged, 200-year-old boreal forest with upper canopy destroyed by the* derecho *of 4 July 1999, Boundary Waters Canoe Area Wilderness, Minnesota. (b) The same forest as in (a), one year after the exceptionally severe Cavity Lake Fire of 2006, illustrating the combined impact of severe wind and fire disturbance.*

to occur more often in this region with climate warming (Trapp *et al.* 2007). Currently, the frequency of *derechos* in the prairie biome is 5–20 times that in the interior of the forest biome (Coniglio and Stensrud 2004), and a northeastward shift in climatic conditions could bring large increases in *derecho* frequency to the forest biome.

These windstorms are capable of transforming the species composition of vast swaths of forest (>200 km in length) within a day, because certain tree species have a higher risk of blowing down than others (Rich *et al.* 2007; Figure 3). These storms also present an opportunity for understory species adapted to a warmer climate to increase their dominance through regeneration. In addition, the alteration in fuel structure created by blowndown trees greatly increases the chances of severe fires (Figure 3), even in hardwood and hemlock forests that did not formerly experience such events. These very severe fires could convert the forest to early successional aspen and birch (Frelich and Reich 1999), or give species adapted to a warmer climate a chance to invade.

Insects and diseases

Many exotic insects and diseases that affect trees have arrived at, or are approaching, the prairie–forest border. Survival of insects and disease organisms is generally greater when winters are less severe, and their populations can increase faster with higher survival and longer breeding seasons, leading to greater rates of spread (Logan *et al.* 2003). Dutch elm disease (*Ophiostoma ulmi* and *Ophiostoma novo-ulmi*), hemlock wooly adelgid (*Adelges tsugae*), and emerald ash borer (*Agrilus planipennis*) are either present at, or moving toward, the prairie–forest border and threaten seven species of native trees. The adelgid is limited by the cold winters of the current climate (Evans and Gregoire 2007), but it could survive winters in the area under the IPCC low emissions climate scenarios. Asian long-horned beetle (*Anoplophora glabripennis*), although so far confined to urban areas, has the potential to greatly diminish the genera *Populus* (four species present) and *Acer* (four species present, including the ecologically and commercially important sugar maple, *A saccharum*). Sudden oak death (caused by the fungus *Phytopthora ramorum*) has the potential to reduce abundance of two oak species; currently, *Phytopthora* is not thought to be capable of surviving near the prairie–forest border, because of the cold climate (Smith and Coulston 2002), but that could change in the future.

Native insect pests (including species from elsewhere in North America) are also expected to play a major role in forest change in a warming climate. Insect populations that may have been in dynamic equilibrium with forests while the climate was relatively cool can experience outbreaks when longer growing seasons and milder winters facilitate reproduction and survival. For example, mountain pine beetles (*Dendroctonus ponderosae*), native to British Columbia, Canada, have killed 12 million ha of lodgepole pine (*Pinus contorta*) forest in that province in recent years; the large extent of the outbreak is partly attributable to a warmer, more favorable climate for the insects, especially in winter (Taylor *et al.* 2007). With warmer winters, the mountain pine beetle has the potential to cause major mortality in jack pine-dominated forests along the southern margin of the boreal forest across the continent (Logan 2007).

Exotic earthworms

European earthworms, principally the nightcrawler (*Lumbricus terrestris*), leaf worm (*Lumbricus rubellus*), and angleworms (*Aporrectodea* spp), are invading forests along the entire prairie–forest border, including boreal forests from Alberta to northern Minnesota, and hardwood forests from Minnesota to Indiana (Frelich *et al.* 2006; Cameron *et al.* 2007). The northern part of the prairie–forest border, from northern Wisconsin through Alberta, has no native earthworms. Earthworm invasions

Figure 4. *Forest change caused by earthworm invasion and deer grazing. (a) Intact forest of sugar maple, basswood, and red oak. (b) Forest with high deer population and earthworm invasion. Note the absence of tree seedlings, herbs, and duff on the forest floor.*

have been linked to dieback and reproductive failure in mature northern hardwood trees, and loss of native plant species richness through a cascade of ecological effects (Holdsworth *et al.* 2007). These include raising soil bulk density, decreasing availability of nitrogen (N) and phosphorus by 20–40%, and removing the organic horizon (ie the leaf litter or duff), leaving the forest floor without the insulating and moisture-holding capacities of the previously thick litter layer (Hale *et al.* 2005; Figure 4). The tree species most impacted is sugar maple.

Deer overabundance

White-tailed deer (*Odocoileus virginianus*) have been an important factor negatively impacting survival and recruitment of trees in central and eastern North America (Coté *et al.* 2004; Figure 4). Deer browse woody plants during the winter, when herbs are unavailable, and prefer seedlings of certain species of trees: northern white cedar (*Thuja occidentalis*), yellow birch (*Betula alleghaniensis*), northern red oak, eastern hemlock (*Tsuga canadensis*), and, in some areas, white pine (*Pinus strobus*). Reproduction of these species has been nearly eliminated in large tracts of forest within 500 km of the prairie–forest border (Cornett *et al.* 2000; Rooney *et al.* 2000). Deer populations in the boreal forest along the northwestern segment of the prairie–forest border are currently low, but are expected to increase as winters become milder, since winter mortality has been a historically limiting factor (Fieberg *et al.* 2008). Increasing acreage of aspen forest and fragmentation as logging proceeds into the boreal forest also favor expansion of deer populations (Alverson *et al.* 1988).

CO_2 fertilization and nitrogen deposition

Projected increases in atmospheric CO_2 concentrations and in N deposition may counteract some impacts of climate change by enhancing forest productivity and drought resistance. Enhanced productivity due to CO_2 fertilization and reduced water stress may occur in forests of the prairie–forest border region (Reich *et al.* 2006). The latter is more relevant to a consideration of possible climate-change interactions in this region. The ubiquitous water savings under elevated CO_2 are achieved via reduced stomatal conductance (Ainsworth and Long 2005) and can result in heightened seedling establishment (Davis *et al.* 2007). However, this should be offset to some extent by modest increases in leaf area index (projected green leaf area per unit ground area) under elevated CO_2 (Ainsworth and Long 2005; Reich *et al.* 2006), such that soil moisture patterns will be only modestly enhanced in most situations. Elevated CO_2 levels will constrain the rise in evapotranspiration under warmer (and especially warmer and drier) conditions to some extent, and will therefore partially counteract the effects of warming on plant and soil moisture relations. Given evidence from the free-air CO_2 enrichment literature, it is likely that these effects will be modest (Ainsworth and Long 2005; Reich *et al.* 2006).

Much of the northern hardwood and southern boreal forest near the prairie–forest border receives low-to-intermediate levels of N deposition (Keene *et al.* 2002). Given that these systems are known to be N-limited in terms of productivity (Reich *et al.* 1997, 2001), the continuing N additions will result in a modest average increase in productivity (Magill *et al.* 2004). Deciduous hardwoods should gain some advantage in comparison with prairie species under heightened N deposition levels, because the relative competitiveness of deciduous trees versus grasses increases with increasing N supply (Köchy and Wilson 2001). Furthermore, feedback effects of deciduous trees on N cycling will lead to conditions that are more conducive to trees than grasses (Reich *et al.* 2001; Dijkstra *et al.* 2006), possibly amplifying any influence of N deposition on tree–grass competitive interactions.

It seems probable that the effects of higher CO_2 concentrations will partially offset the impacts of future droughts, and that N-deposition effects will partially offset the impacts of earthworm invasion on nutrient availability. However, these two factors will not reduce the

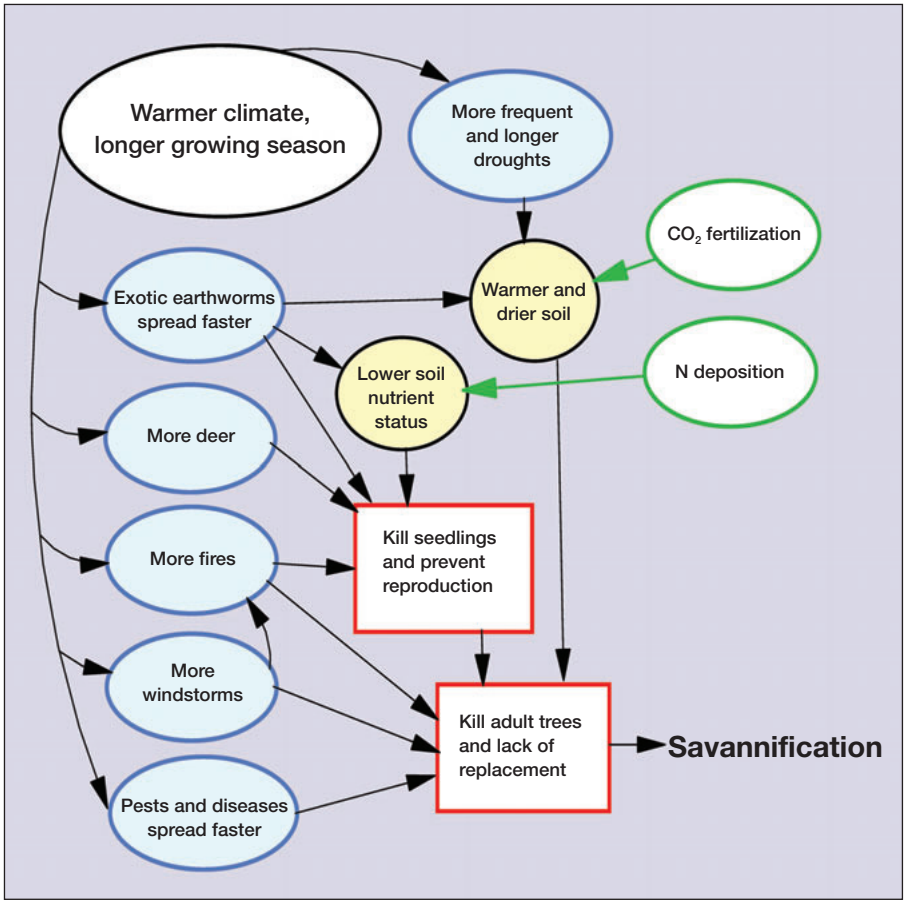


Figure 5. *Interactions between global warming and other drivers of change affecting the prairie–forest border of central North America, and their impact on trees. Blue ovals represent drivers with potential negative impacts on trees that are likely to be enhanced by a warmer climate. Yellow circles represent basic resources that may be changed by a warmer climate or by its interactions with other drivers. Green ovals represent drivers that may counteract negative impacts on trees to some extent. Red rectangles show the results of drivers on trees and their reproduction.*

negative impacts that storms, fires, exotic insects and diseases, and deer grazing have on forests.

Cumulative impacts of multiple drivers

Cumulative negative impacts of all drivers of change on trees in the prairie–forest border region may be quite large (Figure 5). Storms, fires, invasive insects, and unsuitable climate will remove mature forests from the landscape, while other factors, such as deer and European earthworms, will prevent tree reproduction. The loss of mature trees will also contribute to lack of reproduction through reduction in propagule availability. The net result for forests within a few hundred kilometers of the prairie–forest border is that tree mortality will increase and regeneration may not be able to keep pace.

Most genera and species of trees present along the prairie–forest border are sensitive to at least one potential negative impact. Fir, spruce, and larch will not find a warmer climate suitable. Both invasive and native insects and diseases have the potential to remove or greatly reduce several genera, such as maple, ash, pine, aspen, oak, hemlock, and elm, from large swaths of forest close to the prairie–forest border. Deer populations will prevent reproduction of several species that would otherwise be resistant to the impacts of a warmer climate, including white pine, northern red oak, yellow birch, and northern white cedar. Even tree species that experience a positive impact from one driver may respond negatively to other factors. Hemlock provides a good example. Earthworms create a bare mineral soil seedbed, which is better for hemlock than thick litter. However, some researchers have predicted the extinction of hemlock due to the hemlock wooly adelgid; deer grazing has also been shown to have a widespread negative impact on hemlock regeneration (Rooney *et al.* 2000), and increased drought and fire frequency will negatively affect this species.

Conclusions

Climate warming is predicted to lead to savannification of the forest near the northern prairie–forest border. The cumulative impacts of droughts, storms, fires, insects and diseases, invasive species, and deer grazing may be partially offset by CO_2 fertilization and N deposition. However, the net impact of all these drivers is expected to reinforce negative impacts of global warming, thereby hastening the decline of forests (Figure 5).

The relatively cool temperatures and frequent precipitation of the historic climate of the past several centuries, coupled with periodic crown fires for jack pine, have allowed boreal forest tree species, such as jack pine and black spruce, to exist from bogs to rocky hilltops, and northern hardwoods to spread across a soil gradient from clays to loamy sands. In a warmer climate, more differentiation among vegetation types is expected across soil types and slope positions (Pastor and Post 1988). Mesic forests are expected to narrow their niche, "abandoning" drier sites, and if the density of forested sites becomes low enough, people may perceive that the location of the prairie–forest border has shifted. Important decisions regarding forest management will need to be made as the climate warms: do we prioritize the maintenance of as much of our recent forest heritage as is possible? Do we let nature takes its (human-aided) course? Or do we proac-

tively use adaptive management strategies to accelerate the shift toward new vegetation, better suited to the conditions of the late 21st century? The answers to these questions are not simple and effective management will probably include a combination of all three approaches, guided by input from a wide array of stakeholders, including citizens, the timber industry, and public and private land management agencies.

Tracts of forests close to the prairie–forest border – destined to become grassland or savanna as the climate warms, and currently designated as wilderness – may represent a restoration opportunity for native grasslands and savannas, most of which have been converted to agriculture during the previous century. Remnant grasslands and savannas must be preserved, to serve as a seed source for future expansion into forested areas, thus allowing forests to make a "graceful" transition to prairie and/or savanna. These future grasslands may be no-analog communities, but a no-analog community of native species is probably more desirable than a no-analog community composed of non-native species.

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