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Review

Trophic cascades, invasive species and body-size hierarchies interactively modulate climate change responses of ecotonal temperate–boreal forest

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As the climate warms, boreal tree species are expected to be gradually replaced by temperate species within the southern boreal forest. Warming will be accompanied by changes in above- and below-ground consumers: large moose (*Alces alces*) replaced by smaller deer (*Odocoileus virginianus*) above-ground, and small detritivores replaced by larger exotic earthworms below-ground. These shifts may induce a cascade of ecological impacts across trophic levels that could alter the boreal to temperate forest transition. Deer are more likely to browse saplings of temperate tree species, and European earthworms favour seedlings of boreal tree species more than temperate species, potentially hindering the ability of temperate tree species to expand northwards. We hypothesize that warming-induced changes in consumers will lead to novel plant communities by changing the filter on plant species success, and that above- and below-ground cascades of trophic interactions will allow boreal tree species to persist during early phases of warming, leading to an abrupt change at a later time. The synthesis of evidence suggests that consumers can modify the climate change-induced transition of ecosystems.

Keywords: body mass; climate warming; exotic earthworms; trophic interactions; soil food webs

1. INTRODUCTION

A general trend exists towards smaller body mass in warmer climates in many taxa, ranging from bacteria to ectotherms and mammals [1–3]. However, an exception to this trend occurs in some taxa of below-ground fauna, which get larger in warmer climates; this includes annelids that dominate soil processes in large parts of the world, with small enchytraeid worms in the boreal forest and progressively larger earthworm species found from southern boreal forests through temperate and tropical forests [4,5]. This review and synthesis examines why body sizes of dominant above- and below-ground fauna responsible for important ecosystem processes in the temperate–

boreal forest ecotone are expected to change in opposite directions as the climate warms. These body size changes will influence ecosystem dynamics by causing trophic cascades that interact with climate change [6].

We examine dynamics of the boreal–temperate ecotone of eastern North America, which spans 1600 km, from Minnesota to New York and adjacent Canada (figure 1). Temperate forests on mesic sites along this ecotone (excluding sand plains and wetland forests beyond the scope of this paper) are dominated by sugar maple (*Acer saccharum*), American basswood (*Tilia americana*), yellow birch (*Betula alleghaniensis*), northern red oak (*Quercus rubra*), beech (*Fagus grandifolia*), white pine (*Pinus strobus*) and hemlock (*Tsuga canadensis*), while boreal forests are dominated by white spruce (*Picea glauca*), black spruce (*Picea mariana*), red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*) and aspen (*Populus tremuloides*). Change in forest composition from boreal to temperate species occurs over a narrow temperature range of about 3°C (figure 2).

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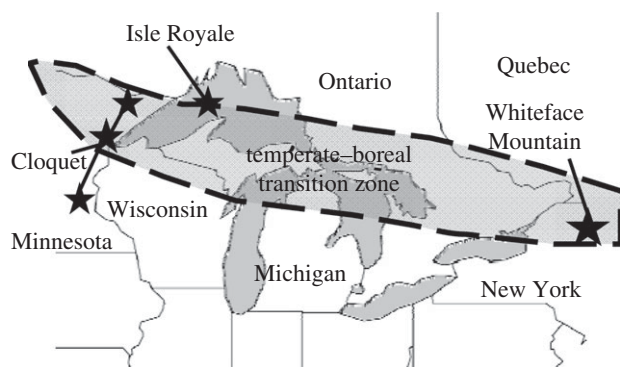


Figure 1. Map of study area showing the temperate–boreal transition (shaded). Locations mentioned in the text and figures 2–4 are labelled and marked with stars.

The magnitude of summer warming along this ecotone is expected to be 2–3°C by mid-century, leading to northward extension in temperate tree ranges by 150–200 km [9], and replacement of southern boreal forest by temperate forest.

We hypothesize that changes in above- and below-ground consumers will interact with climate change to become drivers of change in forest vegetation. As the southern boreal forest warms, it is expected that the dominant herbivore species within the deer family (Cervidae) will switch from moose (*Alces alces*) to the smaller white-tailed deer (*Odocoileus virginianus*), while relatively large earthworms will replace the existing enchytraeid and microarthropod dominated soil food webs. We hypothesize that trophic cascades emanating from these faunal changes will have complex impacts on vegetation, both reinforcing and delaying the impacts of warming climate. Furthermore, landscape-level dynamics of deer today are different than before European settlement (1700–1900), and European earthworms now dominate, so that plant species forming future forests will pass through a new filter, leading to novel forest communities. In the following sections, we consider why changes from moose to deer and changes in the detritivore community are likely in the southern boreal forest, and how these changes interact with plant communities, and we synthesize across trophic levels to show likely plant community responses.

2. HERBIVORE DYNAMICS IN A CHANGING CLIMATE

(a) *Deer replace moose*

Presently, moose are the dominant large herbivore in the North American boreal forest, with a range approximately coincident with the boreal forest [10]. Two factors are thought to limit moose at the southern edge of their range—warm climate and the deer brainworm (*Paraelaphostrongylus tenuis*), which is carried by deer but lethal to moose [11,12]. Differences in body-size scaling of thermoregulation and metabolic processing of plant materials consumed by deer and moose lead to differing ability to dissipate or retain heat at critical times. This results in the size-dependent inability of moose to continue eating during summer warm spells and, similarly, the inability of deer to store sufficient body fat to meet the energetic demands

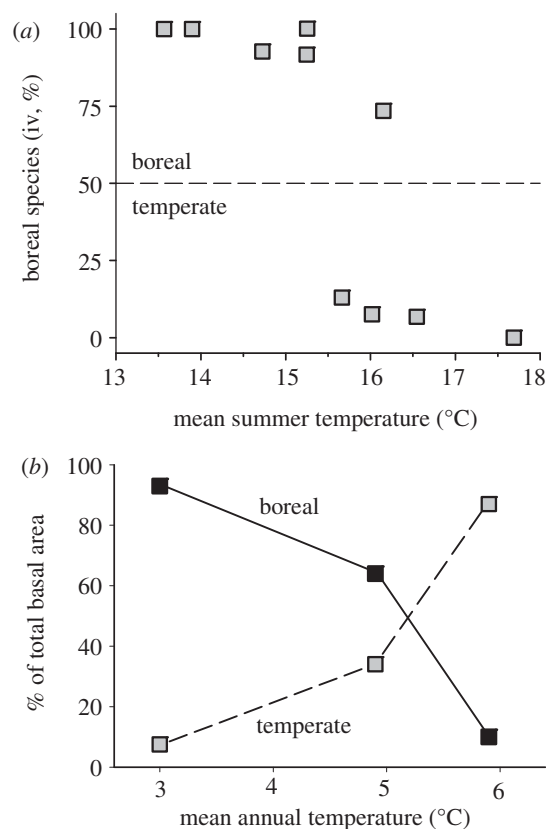


Figure 2. (a) Change in overstory tree species composition along an elevational gradient in summer climate on Mount Whiteface in the Adirondacks, NY, USA. Percentage of temperate species is expressed as their importance value (iv) calculated from tree species relative density and relative basal area following [7]. Air temperature was measured 1 m above the ground every 2 h during the vegetation season of 2009. Each data point represent means from 15 plots and three temperature loggers placed along a 225 m long transect spanning elevations from approximately 500 to 1200 m above sea level. (b) The percentage of total basal area by group in three regions in northeastern Minnesota, trending north–south and centred on Cloquet, in relation to the mean annual temperature in each region [8]. Boreal tree species, black squares; temperate tree species, light grey squares.

of winter and maintain predator avoidance strategies [13–16]. The ability of either species to adapt to differing climates by intraspecific variation in body size is also limited [1], therefore moose live in colder climates than deer, with limited overlap in their ranges.

Moose populations have recently declined dramatically in parts of the southern distribution, including areas from North Dakota to Nova Scotia, coincident with some combination of increased temperature and growing deer density [13,17]. Moose have also declined where deer are not present, on Isle Royale in Lake Superior [17], and where deer are present but climate has been relatively stable, in Nova Scotia [18]. As large herbivore species identity and/or abundance will be altered faster than their forest habitats, herbivore effects on forest vegetation will affect the trajectory of forest change.

(b) *Canid complications*

Herbivore impact on future forest development will depend on status of the wolf, the primary predator of

large boreal forest herbivores. The top-down influence of predation on future ungulate populations will vary, depending on the species of ‘wolf’ present. It is generally recognized that two wolf species are involved, the larger gray wolf (*Canis lupus*) in the western Great Lakes and the mid-sized eastern wolf (*Canis lycaon*) in eastern Ontario [19]. A smaller canid, commonly called ‘coyote’ or, more properly, ‘New England canid’, occurs today throughout most of New England and New York, and is likely a hybrid between the eastern wolf and coyote. The gray wolf is an effective predator of moose and deer; the eastern wolf primarily preys on deer and scavenges moose carcasses, while the smaller canid in New England is a less important deer predator. These differences in canid species will mean that ‘wolf’ predation effects will be more prominent in the western Great Lakes than in the east.

(c) *Heterogeneous predation impacts*

An important question is the extent to which predation will limit future ungulate density as winters become more moderate and deer expand north of their historic range. Throughout most of the present boreal forest, the gray wolf probably limits moose density [20,21]. From British Columbia to southern Quebec, the combined density of all cervids (primarily moose) is approximately 62 kg km^{-2} , in contrast with 299 kg km^{-2} in the gray wolf-free Maritime provinces and New England [20]. At a smaller scale, the effect of wolf presence is even clearer—moose biomass was 100 kg km^{-2} in gray wolf range north of the Saint Lawrence River in southern Quebec, while across the river, where the wolf was absent, moose biomass was 740 kg km^{-2} [22].

Future predation on ungulate populations will be heterogeneous across the boreal–temperate forest transition. As levels of human tolerance have increased in recent decades, the gray wolf has increased its distribution and density in the western Great Lakes [23], but not in New England. This may result in divergent trajectories for future forests in these regions as ungulates respond to climate change. If wolves effectively limit density of expanding deer populations in the Midwest, the ecological effects of deer replacing moose there may be partially mitigated. However, social attitudes towards wolves and deer that influence populations of both could favour rapid population growth of deer as they thrive further north.

(d) *Isle Royale: climate change in progress*

Isle Royale National Park in Lake Superior currently supports ecotonal forest—boreal forest of fir and spruce occupies the relatively cool northeast end and a fringe around the entire island, while temperate forest occupies the relatively large interior landmass at the southwest end [24]. Moose colonized predator-free Isle Royale early in the twentieth century and increased initially to a density of *ca* 6 moose km^{-2} by 1930. Starvation during the 1930s, followed by arrival of gray wolves in the 1940s [25], has generally limited moose density to *ca* 2 moose km^{-2} since that time, about 5–10 times the density on the adjacent mainland where black bears (*Ursus americanus*) provide additional predation pressure on newborn calves [21].

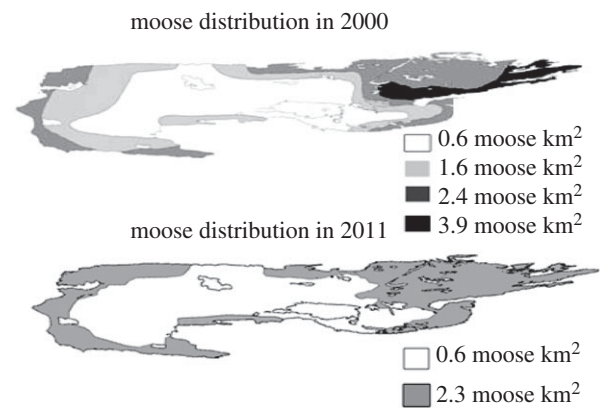


Figure 3. Moose density declined in Isle Royale National Park during 2000–2011, but spatial distribution changed little, with most moose occupying boreal habitats at the northeast end [17]. Moose densities are based on mid-winter aerial moose counts on 91 permanent plots of 1 km^2 in a stratified random array. Note that criteria for mapping contours changed between the two surveys.

During the last two decades, a number of changes have occurred that coincided with warming of the climate and waters of Lake Superior [26]. The moose population declined to about 500 animals (a historically low number), but the decline was larger at the southwest end than at the relatively cool northeast end (figure 3). During this period, calf recruitment consistently remained below the 50-year average, wolf: moose ratio was above average, and following warm years winter tick infestation of moose led to more than 50 per cent hair loss in late winter [17]. During the late 2000s, breeding wolf packs were reduced from four to one as the number of old moose (singular wolf prey) declined dramatically, and wolf numbers declined to nine (36% of 50-year average). Poor moose recruitment will result in an extended period of low food availability for wolves in 2010–2020, accentuating the risk of wolf extinction from random events [17].

Balsam fir is a critical winter forage species for moose, and despite the relatively low moose densities at the southwest end, the moose: fir ratio is still high and regeneration of balsam fir has been severely restricted. Fir is disappearing from the forest canopy as trees that emerged before the arrival of moose die without replacement (figure 4). Therefore, boreal floral and faunal elements (fir and moose) are being reduced in abundance at the temperate southwest end of the island. Even at the northeast end, where spruce and fir are found in thick stands, the temperate species red maple, red oak and white pine are regenerating well [27]. In contrast, the unpalatable boreal tree white spruce has persisted at the southwest end of the island, forming a ‘spruce–moose savannah’ [27], illustrating the variable effects of plant–herbivore interactions on forest change in a warming climate.

There are no white-tailed deer on Isle Royale, so future comparisons of population trends for moose on Isle Royale and the mainland will provide a rough measure of the significance of brainworm carried by deer as a cause of region-wide moose decline. As moderating winters allow deer to expand northward, only the cold water of Lake Superior prevents them from

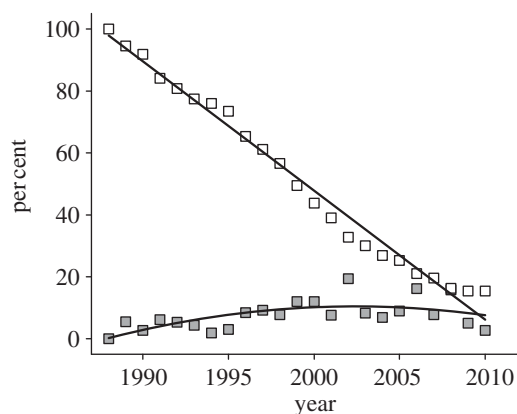


Figure 4. The percentage survival (open squares) and annual percentage mortality (light grey squares) of balsam fir trees more than 2 m in height at the southwest end of Isle Royale National Park, 1988–2010 [17]. As 473 trees tagged in 1988 have died, they have been replaced by only 12 new recruits. During the same period, there has been a slow increase in the annual mortality rate of these trees, which were all recruited prior to the arrival of moose in the early 1900s. This phenomenon of mortality without replacement characterizes fir demography on approximately half of Isle Royale.

colonizing Isle Royale. At Sleeping Giant Provincial Park, on the Ontario mainland adjacent to Isle Royale, with boreal forest, deer have almost completely displaced moose over the past three decades [28]. The number of dead deer found washed up on Isle Royale shorelines has increased from one in the 1980s to seven in the 2000s. Perhaps one day a warmer Lake Superior will allow dispersing deer to survive, resulting in major alteration of the ecosystem.

3. DETRITIVORE DYNAMICS

(a) *Soil biota in boreal versus temperate forests*

Soil community composition differs considerably between boreal and temperate forests. Boreal forests with coniferous tree species typically have poor litter quality and acidic (moder) soils. These soils often support a high diversity of soil mesofauna, in particular collembolans, enchytraeids and oribatid mites, but—in comparison with soil of deciduous forests (mostly mull soils)—only low densities and biomass of earthworms [4,29]. However, the presence of boreal deciduous tree species (e.g. aspen and birch) in coniferous stands allows earthworms to invade [30]. Thus, temperature is not the limiting factor for earthworm invasion in boreal forest; high earthworm biomass can occur in aspen-dominated or mixed aspen–conifer boreal forests (greater than 1000 earthworms m^{-2} ; greater than 250 $g m^{-2}$, [31]). Moreover, as the climate warms more palatable species with calcium-rich litter [32], such as sugar maple, red maple and basswood, will dominate the landscape, facilitating the spread and impact of relatively large-bodied earthworms, which in turn will increase processing rates of leaf litter [33].

(b) *Exotic earthworm effects on native soil food webs*

Earthworms are ecosystem engineers in many terrestrial ecosystems, as they structure the environment of other

soil biota [34]. They typically dominate the biomass of soil invertebrates in non-acidic soils and influence a plethora of chemical, physical and biotic ecosystem properties [34]. However, the impacts of earthworms on their environment depend on their feeding strategy, with three major ecological groups commonly distinguished: (i) epigeic species reside mainly in the upper organic soil layers and cause limited mixing of mineral and organic layers by feeding on litter materials; (ii) endogeic species live in the upper mineral soil layers primarily consuming mineral soil materials mixed with organic matter and forming horizontal non-permanent burrows; and (iii) anecic species feed on soil surface litter but live in deep vertical burrows.

Earthworms are important biological invaders in ecosystems worldwide, including the previously earthworm-free North American temperate–boreal ecotone [30]. Although pronounced changes in soil food webs owing to earthworm invasion are likely, only a handful of studies have experimentally investigated this topic [31,35]. According to a recent meta-analysis [33], earthworm ecological groups differ markedly in impacts on microarthropods, with epigeic and endogeic earthworm species likely having the largest influence. Effects of epigeic species on soil microarthropods are positive at moderate densities, but negative at high densities owing to accompanying changes in physical structure of the organic layers [33]. By contrast, endogeic earthworms have large negative impacts on microarthropod density and species richness, primarily due to competition with microarthropods for food resources [31]. Density and species richness of soil macrofauna, mainly consisting of Diptera larvae and predator and detritivore beetle species, decreased significantly in the presence of endogeic earthworms, roughly halving the biomass of indigenous soil macrofauna (N. Eisenhauer 2004, unpublished data). In addition, particularly small oribatid mite taxa (e.g. Brachychthoniidae, Oppiidae) were negatively affected by the physical disturbance caused by exotic epigeic and endogeic earthworms [31,36]. This suggests that invasive earthworms induce compositional shifts, and also change the size structure of soil food webs.

In sum, earthworm invasion induces considerable shifts in composition and biomass distribution of soil food webs. As competitively superior species compared with indigenous detritivores, earthworms retain an enormous amount of biomass previously fixed in organic soil layers, indigenous soil micro-organisms and arthropods. Thus, earthworm invasion is likely to lead to simplification of soil food webs [31,35].

4. INTERACTIONS OF HERBIVORES, DETRITIVORES AND THE PLANT COMMUNITY

The expected course of plant community change in mesic southern boreal forest in a warming climate would be for temperate species, principally sugar maple (usually the dominant species), red maple, northern red oak, white pine, yellow birch, American basswood, beech and hemlock to replace the boreal spruce, balsam fir, paper birch and aspen [37]. However, the complex effects of deer replacing moose and earthworms replacing the native soil fauna will

place a unique filter on success of tree species, altering the course of forest adjustment to changing climate.

Replacement of native soil fauna by earthworms in this region leads to changes in soil structure. Earthworms (i) consume the organic horizon, making soils warmer and drier during the growing season, reinforcing the impact of a warming climate while also changing seedbed conditions to favour a different suite of plant species that germinate on mineral soil [38,39]; (ii) raise soil bulk density [38], thereby lowering infiltration of rainfall and reinforcing the drying effect of organic horizon removal; (iii) lower nitrogen and phosphorus availability [38]; and (iv) disrupt hyphal networks of mycorrhizal fungi which live in the organic horizon [30]. These changes in turn strongly disfavour sugar maple, which germinates in leaf litter, relies on certain mycorrhizal fungi, grows best on nutrient-rich sites with good moisture supply, and because of its calcium-rich litter is a preferred earthworm food [32]. Most other temperate and all boreal tree species germinate well on bare mineral soil created by earthworms. Although these species are negatively affected by drier, more nutrient-poor soils, they are also more tolerant of those conditions than sugar maple, and thus can gain a competitive advantage when earthworms invade.

Earthworms also directly interact with seeds [40]. Earthworms may be important seed and seedling predators with potentially strong effects on plant community composition [41]. Although interactions between earthworms and tree seeds have, to our knowledge, not been investigated, studies on herbaceous species stress strong selective pressure by earthworms on the fate of seeds, which is likely to change plant community composition of North American forest ecosystems [42]. Plant species not adapted to the presence of earthworms may suffer from their invasion, resulting in simplified herbaceous communities [39], which also play an important role in forest ecosystem function [43].

Moose and deer have complex browsing preferences for boreal tree species. They do not browse spruce saplings, have a moderate preference for balsam fir and highly prefer aspen and paper birch. However, deer also browse several temperate tree species that are not browsed intensively by moose and that are expected to replace the boreal tree species under climate warming. Deer browsing has been shown to limit recruitment of temperate species, such as northern red oak, yellow birch, basswood and hemlock, on decadal and landscape scales [44]. Although sugar maple is a moderately preferred browse species, deer can limit sugar maple recruitment when more preferred species have been consumed [44], potentially hindering the ability of maple to invade boreal forests.

To summarize potential herbivore–detritivore–plant interactions, the net impact of deer and moose browsing in mesic forests of the boreal–temperate ecotone will be to promote persistence of boreal conifers, which are favoured by a lack of browsing and earthworm invasion. The temperate species hemlock, yellow birch, red maple and northern red oak will likely benefit from earthworm invasion relative to their main competitor, sugar maple.

5. SYNTHESIS AND CONCLUSIONS

(a) *Novel, variable recruitment filters for future plant communities*

Novel communities are expected to develop if climate change leads to new species interactions [45]. In the boreal–temperate forest ecotone, a cascade of trophic interactions starting with changes in body masses of large herbivores and soil fauna in a warming climate will lead to altered browsing patterns among tree species and soil suitability, creating plant communities that are different, and perhaps more novel than climate change alone would cause. Without the changes in soil fauna, the tree species currently dominant in temperate forests—sugar maple—would probably dominate future temperate forests that replace southern boreal forests. However, European earthworms discriminate against sugar maple and a wide variety of temperate forest understory plant species [39], and will probably broaden the forest niches of red maple, northern red oak, yellow birch, hemlock and beech. How well top-level predators like the wolf are able to regulate deer will also have an effect at the landscape scale, because several of the species favoured by the new soil conditions are also preferred browse species.

Existing mature trees in temperate forests near their northern range limits were established prior to European earthworm invasion at a time when herbivory by deer was modest. Thus, the historic legacy established with the historic filter on species success still has a lot of influence on current plant community composition. Now that new filters have been introduced, change will come as old trees die and new ones are recruited. However, the future temperate forest that emerges in areas now occupied by boreal forest will develop with the new filter in place from the start. This new filter will also include important factors beyond the scope of this paper, such as exotic tree pests and diseases (e.g. insect folivores, phloem-feeders and microbes) and nitrogen deposition, which can interact with earthworm invasion to simplify plant communities [37,46].

The differing strength of filters caused by variation in herbivory (regulated in the southern boreal forest at spatial scales of a few thousand square kilometres by landscape context and large predators) and earthworms (regulated at similar scales by points of introduction by humans, rate of spread, soil quality and palatability of leaf litter) will create a new pattern of vegetation across the landscape, with varying degrees of community novelty (figure 5a). There is uncertainty in that several potential trajectories exist for any given location, depending on temporal dynamics of replacement of moose by deer and earthworm invasion.

(b) *Abrupt versus gradual change in a warming climate*

We find support for the hypothesis that changes in above- and below-ground fauna accompanying a warming climate can lead to more abrupt change than from temperature change alone, i.e. a nonlinear vegetation response over time to a constant rate of warming (figure 5b). We posit this to be likely whether those

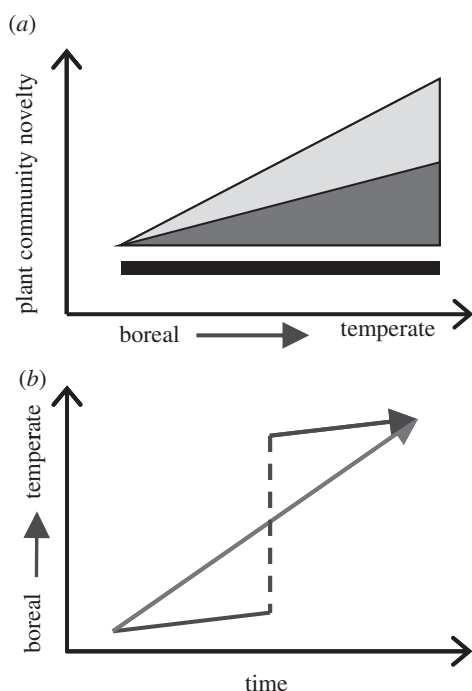


Figure 5. (a) Conceptual diagram of plant community novelty created by herbivore–detritivore interactions as the climate warms. Thick line at bottom; transition with minimal earthworm and ungulate herbivore impacts. Grey wedges, range of possibilities in future plant community novelty caused by trophic cascades from either ungulate changes from moose to deer, or earthworm invasion (dark grey), and with both (light grey). (b) Conceptual diagram on the hypothesized time course of temperate–boreal transition with low (straight line) and high (line with dashed segment) ungulate and earthworm effects.

factors reinforce the temperature effect (e.g. earthworm disturbance causing drier, warmer soils), or oppose it (e.g. initial resistance to change when earthworms and deer favour boreal trees). Because deer and earthworms have little effect on establishment of the dominant boreal spruce species, but have negative impacts on the current dominant temperate species, sugar maple, boreal species could stay in place during early phases of climate warming. This could lead to abrupt disappearance of spruce when some climate threshold has been breached, as opposed to gradual replacement of spruce by temperate species through gap dynamics.

In conclusion, changes in above- and below-ground fauna and the resulting trophic cascades are likely to play important roles in shaping plant community response to a warmer climate. For the boreal–temperate ecotone of eastern North America, reduction in body size of the dominant herbivores (moose to deer) will be driven by thermodynamics and metabolic processing of plant materials consumed. Below-ground, the indirect effects of a warmer climate leading to higher litter quality will allow large-bodied earthworms to replace smaller soil fauna. Higher-quality litter and larger-bodied detritivores in turn lead to higher litter processing rates [47] and changes in forest floor conditions that alter tree species success. It is not clear whether body size *per se*, or the unique characteristics of species that result from body size adjustment to climate change, may cause these trophic cascades; idiosyncratic species effects on

ecosystem function are expected [48]. This question could be answered by future research, including field and modelling studies with different combinations of climate, moose, deer, wolves and earthworm impacts.

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