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Losing Legacies, Ecological Release, and Transient Responses: Key Challenges for the Future of Northern Ecosystem Science

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ABSTRACT

Northern ecosystem processes play out across scales that are rare elsewhere on contemporary earth: large ranging predator–prey systems are still operational, invasive species are rare, and large-scale natural disturbances occur extensively. Disturbances in the far north affect huge areas of land and are difficult to control or manage. Historically, disturbance patterns and processes ranging across a number of spatio-temporal scales have played an important role in the resilience of northern ecosystems. However, due to interactions with a warming climate, these disturbances are now erasing key legacies of the last millennia of ecosystem processes. Building on the concepts of legacies and cross-scale interactions, we highlight several general conceptual issues that represent key challenges for the future of northern ecosystem science, but that also have relevance to other biomes.

Key words: arctic; boreal; succession; disturbance; permafrost; wildfire; carbon; diversity; trophic interactions; niche.

INTRODUCTION

The far north (boreal and arctic biomes) has long served as a source of inspiration for many, representing the notions of wilderness, survival, adventure, and exploration: a final frontier with less human activity than perhaps any other biome. Those who have spent their careers studying northern ecosystems understand that while the north is wild, rugged, and harsh, it is also extremely fragile and vulnerable to change. Of the billions of people on this planet, only a small percentage will experience the wonder of northern ecosystems directly. Yet due to polar amplification of climate change (Pithan and Mauritsen 2014), the north has already been profoundly influenced by human activities and greenhouse gas emissions from

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around the globe. Climate change is altering northern ecosystems through warming temperatures, changing precipitation regimes, lengthening growing seasons, and warmer and deeper seasonally thawed soils (Hinzman and others 2005). And what happens in the north will not stay in the north because of the importance of this region to both regional and global climate systems (Schuur and others 2015; Price and others 2013; Ruckstuhl and others 2008 and contributions therein). Here, we highlight several areas of research that we believe are important to northern regions and that present challenges for the field of ecosystem science as a whole.

Legacies of past ecosystem states play a critical role in shaping current and future ecological dynamics in the north. The cold climate and relative isolation of the boreal and arctic biomes mean that many ecosystem processes operate at a slower pace than in mid-latitude systems. As a result, physical and biological legacies of past ecosystem states influence ecosystem processes over a comparatively long time-span. These legacies constrain ecosystem responses to disturbance and thereby stabilize trajectories of system recovery. Physical legacies are slow-changing factors related to soils, topography, and climate that provide the context for faster ecological dynamics and are often considered as stable elements of an ecosystem (for example, the ‘‘state factors’’ described in Van Cleve and others 1991). The glacial history of the north has created physical legacies of soil characteristics, topography, and drainage that present unique constraints on northern ecosystem processes. Across shorter time scales, ecological and evolutionary processes interact with physical constraints to generate biological structures that persist and influence ecological dynamics through time. These biological legacies, in the form of surviving individuals, organic structures, and nutrient pools (Franklin and others 2000), translate materials and information across disturbance cycles and instill an ecological memory to the system that is a primary mechanism of ecological resilience (Johnstone and others 2016).

Unlike most biomes around the world, many northern regions are sparsely populated by humans. As a result, ecological processes in northern ecosystems play out across very broad scales of regional predator–prey systems and broad natural disturbances, in communities dominated by native flora and fauna with relatively few invasive species. Disturbances such as permafrost thaw, wildfires, and insect outbreaks affect huge areas of land and are difficult to control or manage. Cross-scale interactions arising from human activity and greenhouse gas emissions in the south are causing amplified climate change and more severe disturbances in the north. In turn, ecosystem responses to disturbance in the north may accelerate carbon emissions and feedback to influence global processes (Figure 1) . The non-linear, uncontrollable nature of these changing disturbance regimes is eroding key legacies of the last millennia of ecosystem processes. Below we highlight four important research questions related to legacies and cross-scale feedbacks in the north that should also have broad inference to other biomes.

Question #1 Will climate change erase the legacies of past disturbances in northern ecosystems, and what are the consequences for ecosystem function?

Northern regions are characterized by broad-scale and infrequent disturbances, primarily wildfire, and insect outbreaks (Figure 1). These disturbance events long have shaped northern ecosystems and are inherently tied to vegetation. Repeatable cycles of disturbance and succession have created legacies in northern vegetation that promote resilience. Disturbance extent and severity can increase when positive feedbacks amplify process rates across scales, as highlighted for fire (Peters and others 2007) and insect outbreaks (Raffa and others 2008). The mechanisms governing cross-scale feedbacks between boreal vegetation and fire, however, differ between upland and lowland (peatland) ecosystems. In upland forests, empirical and modeling studies suggest that increases in fire severity could trigger increases in the abundance of deciduous forests at the expense of conifer cover (Beck and others 2011; Mann and others 2012). In North America, black spruce (*Picea mariana*) regeneration is common on moist sites in which a soil organic layer persisted after less severe burning, whereas deciduous trees dominate the post-fire community in severely burned sites (Johnstone and others 2010). Multiple legacies are at play in stabilizing the conifer domain, including vegetation legacies (propagules) and other material legacies (the soil organic layer and associated permafrost; see Question #4). More severe fires will erase the material legacy of soil characteristics that favor black spruce, and may also erase the propagule legacy by combusting the areal seed bank. On top of this, more severe fires will also likely increase the patch size, and distance to unburned seed source. Accelerated fire regimes likely will push ecosystems away from local, within-scale controls to more complex and regional cross-scale

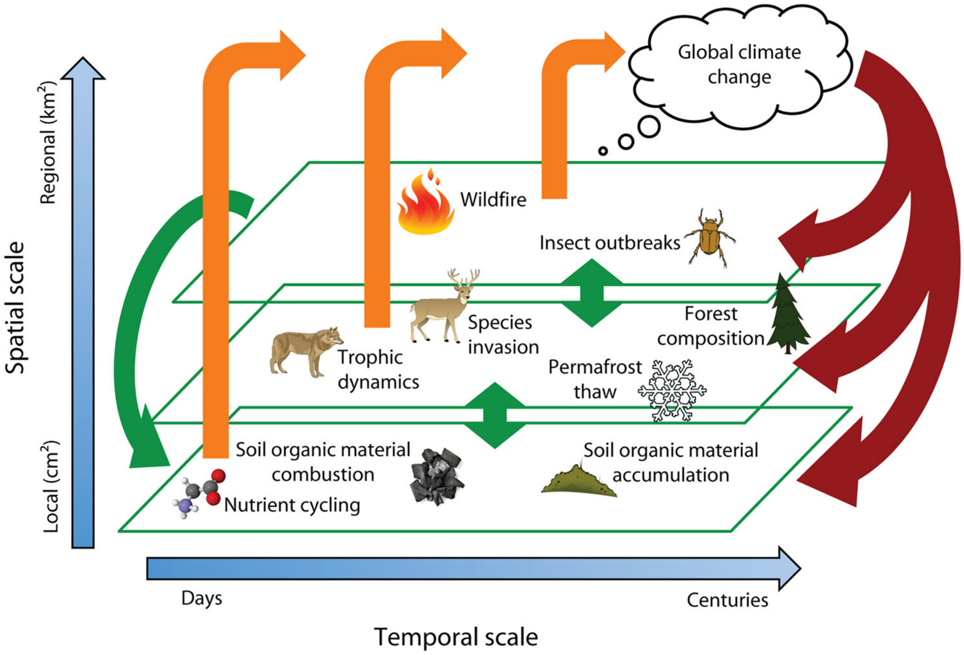

Figure 1. Conceptual illustration of cross-scale linkages among ecosystem processes that shape ecological memory and ecosystem dynamics in the north. Spatially nested scales (*green polygons*) are often well-represented in ecosystem models, while interactions across scales (*green arrows*) are more challenging to explore. Biological legacies of materials and information (images) influence the dynamics across scales. Finally, ecosystem processes in the north are both influenced by global processes such as climate change (*red arrows*) and return to affect those processes (*orange arrows*), largely through controls over carbon, water, and energy exchange. For example, processes at fine spatial scales related to soil organic material and nutrient cycling are connected across long time scales through the material legacies of organic material accumulation. Trophic and community dynamics at intermediate scales are heavily influenced by broad-scale disturbances and in turn shape fine-scale processes of element cycling. Large disturbances, such as wildfire and insect outbreaks further influence the transmission of material (for example, soil organic material) and information (for example, species traits) legacies that influence the trajectories of ecosystem recovery through time.

controls (Figure 1). For example, severe fires have the potential to shift the drivers of forest regeneration from local seeds and materials, to regional seed sources and perhaps newly exposed materials from thawing permafrost soils. Shifts between northern forest domains also involve shifts in coupled fast–slow cycles (Carpenter and Turner 2010). Conifer cover is stabilized by low fire severity and cool soils, whereas shifts to deciduous cover are initiated by high fire severity. However, decreased fire severity alone is not sufficient to favor a transition from a deciduous to conifer domain. That transition is also dependent on slow processes such as carbon accumulation in peat layers and thermal changes in the ground layer (Johnstone and others 2010). Because accumulation of a new organic soil layer is unlikely to occur under a warmer, drier climate, the legacy effect of organic soil on fires is likely to be substantially diminished or erased, which will fundamentally change fire activity in the north.

Within upland forests, fires often kill most of the standing trees quickly, creating evenly aged stands that become more heterogeneous in stand age with increasing time following fire. In northern peatlands, however, fire is a key mechanism in maintaining fine-scale heterogeneity as raised hummocks dominated by *Sphagnum* mosses resist burning relative to vegetation in depressional hollows (Benscoter and others 2015). By increasing the difference in surface elevation between hummocks and hollows, fire maintains heterogeneity and diversity of microhabitats, which tends to become more homogeneous over time with peat accumulation related to autogenic succession. More severe burning of hollow vegetation is an important fine-scale process that maintains diversity in plant species composition and ecosystem function in peatlands. Although most peatland ecologists view hummock formation as an example of niche construction, formed by the slow decomposition traits of *Sphagnum* hummock mosses, we view the hummock-hollow gradient in part as a legacy of past disturbance events. Related to this fine-scale legacy, peatlands tend to burn less severely than other northern ecosystem types. Although hummock *Sphagnum* mosses possess traits that allow them to resist burning, these resistance mechanisms are likely to be overwhelmed under a warmer, drier climate. A change in this fine-scale pattern (differential burning of hummocks and hollows) is likely to result in positive feedbacks that lead to much deeper burning in peatland ecosystems (Turetsky and others 2011) and also is likely to lead to greater increases in fire spread and severity at larger scales than what would be expected if the landscape comprised purely upland forests (Turetsky and others 2004). By altering these ecohydrological feedbacks that allow *Sphagnum* mosses to resist burning, climate change is erasing disturbance legacies in northern peatlands.

Future interactions between climate, vegetation, and disturbance will shape northern ecosystems and their feedbacks to climate. Yet there are large uncertainties about how disturbances ultimately will respond to both the direct and indirect effects of climate change, in large part because there is limited mechanistic understanding of cross-scale interactions and how these mechanisms might vary across the landscape (and between regions such as North America versus Eurasia). Many boreal ecosystems are dominated by disturbances such as insect outbreaks or windthrow that are associated with patchier and slower mortality than fire. With expected increases in severe fire activity, a greater proportion of northern forests may become controlled by the recurrence of large stand replacing fires at the expense of disturbances that generate more fine-scale heterogeneity. This is also likely to be true in northern peatlands. Although anthropogenic activity tends to homogenize landscapes, we believe that similar trends will occur in northern regions as climate change affects disturbance regimes and associated legacies.

Question #2 How are northern niches being impacted by a rapidly changing climate combined with increasing introductions of non-native species?

Northern communities are inherently species poor. This is a product of both the harsh environmental conditions that characterize the region, which dictate the northern limits of many species ranges and the potential productivity of the system (Willig and others 2003; Sanderson and others 2012), as well as the evolutionary history of the region. Compared to more southerly systems, northern ecosystems have had relatively little time to accumulate species due to recent glaciation. This biogeographic legacy means that northern ecosystems have limited diversification of species, which also filters down to more limited ranges of life histories and associated suites of functional traits than in other biomes. The biogeographic legacy of limited species diversity also decreases the likelihood of redundancy in functional traits, thereby impeding maintenance of ecosystem function in the face of disturbance or other environmental changes (Hooper and others 2005).

Low diversity systems also have been linked with greater invasibility, although the reverse (high diversity and high invasibility) has been linked as well. In low diversity situations, there are two potential drivers: vacant niches and competitive inferiority. In evolution, the term ‘‘vacant niche’’ is somewhat standard and the concept is viewed as a critical underpinning of theories such as adaptive radiation (Lekevicius 2010). In ecology, the term has generated long-standing debate about issues such as species versus habitat-based definitions of the niche and the non-equilibrium paradigm (Rodhe 1979; Lekevicius 2010). The term ‘‘ecological release’’ also can describe the availability of free resources and lack of competitors. Fridley and Sax (2014) review the idea that evolutionary lineages in regions that have had greater environmental stability through time should have been under greater selective pressures, therefore enhancing competitive ability compared to those in newer locations. Due to their biogeographical legacy, northern ecosystems likely have competitive inferiority in the face of invasion relative to other biomes. Also, competitive intensity, and biotic interactions more generally, in species-poor northern ecosystems are thought to be lower than in more southerly locations (Schemske and others 2009), which may be expected to lead to competitively inferior species in this region. Together these factors coupled with accelerating disturbance (Question #1) suggest that as physiological temperature constraints are lifted, the north may be poised for dramatic shifts in ecosystem composition and function (Louthan and others 2015). For example, as habitat suitability increases with climate change, it will be imperative to examine changes in propagule loads with habitat alteration related to natural or anthropogenic disturbance across this region. Will increasing human activity overwhelm the biogeographic legacy that has limited species and trait diversity in northern regions and allowed certain species (for example, black spruce) to dominate? With this legacy loss, how will fast processes such as human-related invasions shape northern communities? What are the feedbacks between human activity and legacy loss, for example relationships between loss of the sea ice legacy (see Question #3) and ship traffic, that will have strong implications for range expansions of organisms? How will changing biodiversity and suites of functional traits associated with biological invasion influence relationships with disturbance regimes (Question #1)? While ecologists are just at the beginning of addressing this major research issue as it relates to the diversity and niches of northern ecosystems, it surely will involve interesting interactions between ecological and evolutionary processes. For example, how will selective pressures on physiology and phenology be altered by a changing climate, and what influence will this have on competition for resources or food web function (see Question #3)?

Question #3 Moving beyond either a static bottom-up or top-down framework, should all food webs be viewed as transient systems that can enhance resilience through cross-scale feedbacks?

Much of the history of ecosystem ecology has been dominated by assumptions that bottom-up effects prevail, and that to a large extent the effects of climate change on animal populations will scale directly from these bottom-up effects (Van Hemert and others 2015; Parmesan and Yohe 2002). However, there is ample historical evidence that animal responses to past environmental change differ substantially from vegetation responses (Schmitz and others 2003; Walther and others 2002). As an extreme example, rather than tracking shifts in biome expansion, animal extinctions are common during some periods of historical climatic change (Schmitz and others 2003).

Studies of experimental food webs suggest that warming may enhance top-down effects because of the temperature sensitivity of consumer metabolism and population processes (Hoekman 2010). Although such studies are useful in shifting ecosystem scientists away from a bottom-up perspective, there is increasing recognition of the need to understand and study food webs more as a mosaic of changing conditions driven by behavior of consumers on the landscape (Eveleigh and others 2007; Poisot and others 2014). In both aquatic and terrestrial ecosystems, consumers move widely on the landscape as they respond to spatial and temporal heterogeneity in resources. Such movement couples habitats in terms of nutrient and energy flow, and drives strong but transient top-down effects that can serve to stabilize food webs (Figure 1) (McCann 2007). If high densities of local prey or resources attract regional predators, the resulting ''birdfeeder effect'' can stabilize fluctuations in prey densities (Eveleigh and others 2007). Because of their larger home ranges, organisms at higher trophic levels such as top predators often fulfill this stabilizing function of linking habitats. For example, arctic foxes exploit terrestrial productivity (lemmings) during peaks in the lemming population cycles but switch to alternative marine prey channels during low lemming years. Prey switching and other kinds of stabilizing behavior are expected to be stronger with increasing habitat or resource heterogeneity, which allows mobile consumers to exhibit switching behavior while foraging for example and to respond more strongly to changes in prey densities.

The interaction of bottom-up and top-down processes, due to coupling by highly mobile consumers on a heterogeneous landscape, is critical for understanding the cross-scale feedbacks that govern food web function and how these are likely to respond to future climate change. In general, climate change is expected to impact macrohabitats, or ecosystems, differentially (for example, forest versus field; aboveground versus belowground (Tunney and others 2014). For example, under Question #1, we outline how ecosystems vulnerable to fire might experience greater homogenization at the expense of fine-scale heterogeneity. Habitat alteration at this scale, in turn, has the potential to dramatically rewire the major energy pathways to mobile consumers that couple across major habitat compartments, potentially altering the structure and biodiversity across the landscape (Blanchard 2015; Kortsch and others 2015). The effects of climate change on arctic marine food webs is a compelling example of such rewiring of energy flow in ecosystems. Kortsch and others (2015) demonstrate that boreal fish species are moving northward to affect the architecture of arctic marine food webs. Relative to boreal food webs, arctic food webs are more modular and less connected in part due to narrow niches associated with sea ice habitat. The expansion of boreal generalists into the Arctic results in increased connectance and reduced modularity. Such a shift in food web architecture denotes a major shift in cross-scale feedbacks; these species for example are known not only to feed across trophic levels (omnivory) but they also increase the coupling of pelagic and benthic habitats.

Sea ice, particularly old sea ice that is more common in the Arctic than the Antarctic, is a key material legacy that influences trophic interactions in this marine system. Old sea ice is declining with warming, and as a result arctic sea ice is becoming younger and thinner (Rigor and Wallace 2004). Loss of this ice legacy is associated with the expansion of boreal generalists into arctic food webs (Kortsch and others 2015). Similar to the loss of disturbance legacies outlined in Question #1, loss of the sea ice legacy is shifting the system away from local controls to more complex cross-scale controls. As briefly introduced in Question #2, the loss of these material legacies also opens up these northern remote regions to increased introductions of nonindigenous species due to greater human access or expanding bioclimatic envelopes. This marine example helps to illustrate the linkages between loss of legacies (Question #1) and changes in diversity and niche breadth with climate change (Question #2), and illustrates important consequences for trophic interactions (Question #3). Across terrestrial, freshwater, and marine ecosystems, will climate change favor migratory generalists given their ability to move into new suitable regions, where they can exploit available niches? How will resultant shifts in food web architecture (greater connectance versus reduced modularity) influence diversity, productivity and nutrient cycling? Will mobile species that increase connectance provide flexibility in food web function and contribute to stability? Or will greater connectance across habitats mean that the macrosystem is more vulnerable to the flow of novel stressors such as disease?

Question #4 How can the transient state of ecosystems be predicted with models that often are limited by knowledge of boundary conditions, particularly those that relate to legacies?

Ecosystem models were initially developed for temperate ecosystems, and often focused on the soil-plant system, representing the movement of element pools such as carbon and nutrients rather than individual organisms. When these models were used to represent high latitude ecosystems, the underlying approach was generally portable but there were some aspects of northern ecosystems that affected model structure and forecasting in important ways. We argue that many of these are related to legacies of northern ecosystems, and require insight into cross-scale feedbacks that govern northern systems. For example, using temperate-based models for northern ecosystems required a much more resolved soil representation, in particular to describe the accumulation of the organic soil layer (the material legacy of both thin and thick peat soils that are characteristic of the region). Moss-derived organic layers differ in water holding capacity and heat conduction such that they act to insulate the mineral soils below. This has the effect of creating what is known as ecosystem-protected permafrost, for example perennially frozen soil layers that are kept frozen by the historic accumulation of an organic moss soil layer. Ecosystem-protected permafrost can exist in disequilibrium with current climate, as in sporadic permafrost peatlands that are relicts of the Little Ice Age and are preserved under current climate by the peat legacy (Halsey and others 1995). Representing the effects of the legacy organic layer on soil energy balance was a key conceptual advance for northern ecosystem models that more accurately simulated the distribution of permafrost soils.

Boundary conditions, which can be physically or mathematically based, are extremely important for understanding future ecosystem trajectories including resilience. In general, these are processes that are not described by the model but are important initial conditions needed to simulate the future state. In addition to the organic soil example, the material legacy of a deep soil column (>20 m) acts as a sink for added heat, enhances permafrost stability in response to environmental change, and likely is important in regulating the preservation of permafrost carbon. The non-homogenous distribution of water and ice in soils is another important example of a boundary condition that is relatively unique for northern ecosystems. This example also illustrates the challenges of representing processes across scales within northern ecosystem models. It is well known that ice in permafrost soils accumulates to form lenses, wedges, and pore ice that are not evenly distributed. The amount and distribution of ice in permafrost soils creates a legacy effect that then governs ecosystem function, including vegetation structure and productivity, the distribution of element pools, and how the ecosystem responds to thaw. Because ice occupies a greater volume than water, loss of ground ice leads to the redistribution of surface water and subsidence of the ground surface. Projecting the effects of permafrost thaw on future ecosystem succession or potential carbon release simply is not possible without an understanding of the legacy of ground ice. Initially triggered by surface subsidence (thermokarst), the trajectory and rate of change of these thermokarst features are governed by interactions between vegetation, hydrology, and the soil organic layer that amplify across scales due to positive feedbacks (Baltzer and others 2014). As a result of these positive feedbacks, the rate of change in ice-rich permafrost is greater than what is typically represented in models (Jafarov and others 2013). Because these cross-scale processes are unlikely to be incorporated into modeling soon, a description of the distribution of ground ice becomes a boundary condition problem. How can geophysical measurements be used not only to describe ground ice at the site level, but also to scale these observations across landscapes? Modeling experiments can be used to explore the sensitivity of current ecosystem behavior to boundary conditions. How can the results of these sensitivity analyses be used to guide future field activities in the north? In situations where boundary conditions are not expected to be entirely correct or realistic, model intercomparison studies are likely to be valuable for understanding how model structure influences key aspects of model output or performance.

CONCLUSIONS

Here we highlight four general research questions that we believe serve as important challenges for the next several decades of northern ecosystem ecology. Although these questions reveal the unique aspects of northern ecology (remoteness, low biodiversity, rapid climate change), they also reveal that Arctic and taiga ecosystems are ideal systems for examining the importance of legacies and cross-scale interactions within ecosystems. Across all of our questions, it seems evident that interactions between climate, disturbance, and biota are shifting northern systems away from local controls towards processes that involve more complex, regional cross-scale dynamics. There is a great need for empirical studies to examine the mechanisms involved in cross-scale feedbacks between climate change, biota, and disturbances, and for these mechanisms to be represented in process-based models in an integrated fashion. More generally, both empirical and modeling studies should aim to place their observations of contemporary change firmly in the broad context of legacies. Understanding the longer-term context that influences the outcome of ecosystem responses, whether that context be over biogeochemical, evolutionary, or geologic times, will allow us to develop and refine more sophisticated modeling approaches for forecasting ecological change in this region.

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