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# Ecosystem Responses to Global Climate Change: Moving Beyond Color Mapping

OSWALD J. SCHMITZ, ERIC POST, CATHERINE E. BURNS, AND KEVIN M. JOHNSTON

*Current assessments of climate-change effects on ecosystems use two key approaches: (1) empirical synthesis and modeling of species range shifts and life-cycle processes that coincide with recent evidence of climate warming, from which scenarios of ecosystem change are inferred; and (2) experiments examining plant–soil interactions under simulated climate warming. Both kinds of assessment offer indisputable evidence that climate change and its effects on ecosystems are ongoing. However, both approaches often provide conservative estimates of the effects of climate change on ecosystems, because they do not consider the interplay and feedback among higher trophic levels in ecosystems, which may have a large effect on plant species composition and on ecosystem services such as productivity. Understanding the impacts of these top-down processes on ecosystems is critical for determining large-scale ecosystem response to climate change. Using examples of links between climate forcing, trophic interactions, and changes in ecosystem state in selected terrestrial, freshwater, and marine systems, we show that the ability to understand and accurately forecast future effects of climate change requires an integrated perspective, linking climate and the biotic components of the ecosystem as a whole.*

*Keywords: climate, fauna, global warming, trophic levels, ecosystem function*

**T**he scientific community has worked feverishly for most of the last two decades to offer quantitative insight into the fate of species and ecosystems faced with the changing climate that is expected to result from a doubling of atmospheric carbon dioxide (CO<sub>2</sub>). These assessments are usually done by (a) using simulation analyses that couple large-scale models of climate forcing (general circulation models, or GCMs) with process-based ecophysiological and biogeochemical models (Cameron and Scheel 1993, VEMAP 1995, Johnston and Schmitz 1997, Batchelet et al. 2001, Currie 2001, Iverson and Prasad 2001, Peterson et al. 2002) or (b) synthesizing empirical information that coincides with recent evidence of climate warming (Hughes 2000, Parmesan and Yohe 2003, Root et al. 2003). The results of these analyses are routinely displayed on color-coded maps that depict current and future geographic distribution of species and ecosystems. Because they present easily interpretable insights, color-coded maps have been used as the basis for political and economic analyses of climate-change effects on ecosystems (e.g., IPCC 2001, Mendelsohn 2001, NAST 2001).

Such assessments should, however, be considered first-cut approximations, because their prognosis of the nature and extent of climate-change effects hinges on three key assumptions that are unlikely to be met in reality. First, it is assumed that ecosystems can be conceptualized on the basis of their dominant plant life forms or functional plant groups (e.g., conifer forest, southeastern mixed forest, C<sub>3</sub> grasslands),

ignoring the effects of animal species at higher trophic levels (i.e., herbivores and carnivores) on ecosystem structure and function. This assumption stems from a long-standing view in ecology that ecosystems are driven by bottom-up processes, in which the composition and productivity of vegetation, determined by climate-driven soil–plant interactions, is the primary determinant of species abundances at higher trophic levels (Shaver et al. 2000, Loreau et al. 2001). This reasoning leads to a second assumption, that the line of dependency between animal species and the plants that compose animal habitats is unidirectional and upward. Accordingly, animal species are expected to redistribute themselves geographically by passively following the range shifts of plants that make up their habitats. But such redistributions did not occur among, for example, most mammal species during the last episode of rapid climatic warming at the Pleistocene–Holocene transition; instead, extinctions were

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widespread. Even under current environmental conditions, animal species are not passive components of ecosystems (Chapin et al. 1997). Indeed, top-down processes—that is, the interplay and feedback among different trophic levels in food webs—may have a large effect on plant species composition and on ecosystem services such as productivity (Krebs et al. 1995, Post et al. 1999, Terborgh et al. 2001, Schmitz 2003). Thus, the top-down chain from carnivores through herbivores to plants may be an important conduit for transmitting climate effects throughout ecosystems (Post et al. 1999). Moreover, faunal species have the potential to engineer new ecosystem structure and function (Jones et al. 1997, Wardle 2002) as a consequence of climate-driven shifts in the nature of species interactions. Finally, simple mapping approaches implicitly force a third assumption that, while ecosystem types may shift geographically under climate change, the nature and timing of fundamental life-cycle processes and trophic interactions will remain intact at the new locations.

Through focused evaluations of these assumptions, we show that mapping approaches may paint a very conservative portrait of climate-change effects on ecosystems. We identify how climate warming may lead to changes in trophic interactions and ecosystem structure that cannot be revealed through current mapping approaches. Our goal is to motivate the scientific community to a greater effort to quantify the effects of climate change on interactions and lines of dependency among species in all trophic levels of ecosystems, in order to develop more accurate assessments of the cumulative effects of climate change. We begin with a well-studied top-down food chain involving wolves (*Canis lupus*), moose (*Alces alces*), and vegetation in northern forest ecosystems. We contrast the results of a mapping analysis with a detailed empirical analysis of climate-change effects on ecosystem structure and function. This is followed by examples of climate-change effects on multitrophic interactions in three other large-scale ecosystems.

### **Color mapping versus species interactions: A case study of wolves, moose, and northern forest ecosystem function**

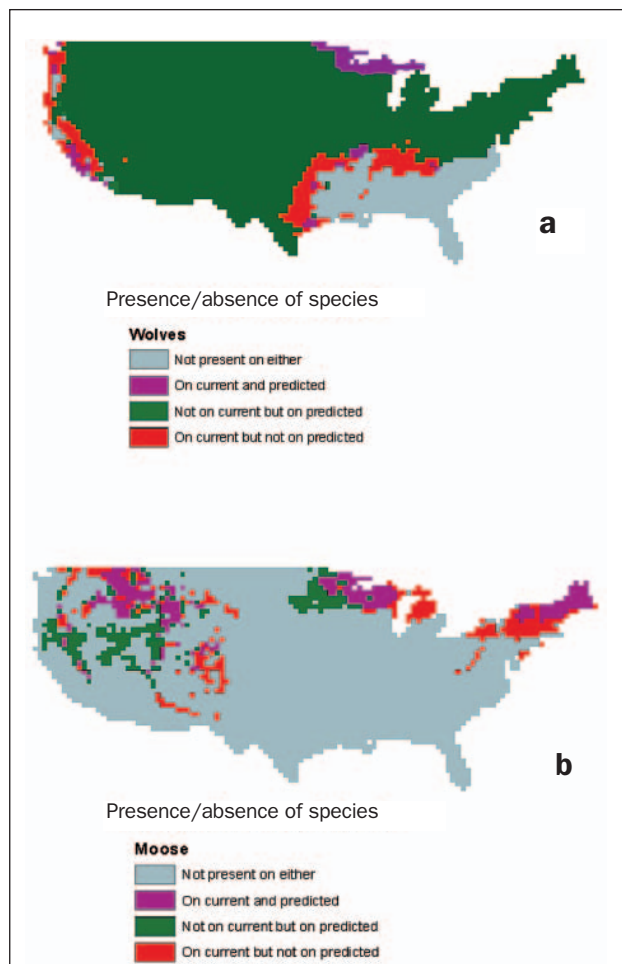
Current assessments indicate that northern forest ecosystems in the United States will undergo major northward shifts in range and a 40% to 80% reduction in geographical extent (Batchelet et al. 2001). We examined how shifts in northern forest ecosystems affect the geographic distribution of wolves and moose, two dominant species inhabiting these northern forests. A standard approach for assessing the effects of climate change on shifts in the range of animal species is to (a) link information on ecosystem types within the current distribution of selected species, (b) predict how the ecosystems will shift geographically under a doubling of CO<sub>2</sub>, and (c) predict how the animal species' geographic distribution will change as a consequence of geographical shifts in ecosystems (Cameron and Scheel 1993, Scheel et al. 1996, Johnston and Schmitz 1997, Currie 2001, Peterson et al. 2002). We used the protocol developed by Johnston and Schmitz (1997)

to quantify the association between the current geographic distribution of wolves and moose and the current distribution of the northern forest ecosystems that they inhabit. Wolf and moose distribution data were obtained from the Faunmap Project ([www.museum.state.il.us/research/faunmap/](http://www.museum.state.il.us/research/faunmap/)). We obtained data from the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP; [www.cgd.ucar.edu/vemap/](http://www.cgd.ucar.edu/vemap/)) on current and predicted future distribution of ecosystem types, assuming CGCM2 GCM (Second Generation Canadian Global Coupled Model, General Circulation Model) atmospheric conditions.

We quantified the association between current wolf and moose distributions and VEMAP data on current ecosystem types within each species' distribution range using logistic regression on geographic information system (GIS) software. Logistic regression requires an a priori specification of likelihood for predicting the presence or absence of an entity at a location. To identify a reasonable likelihood value, we ran a series of calibrations. First we chose an initial likelihood level, predicted the range distribution for the species, and compared the predicted range distribution with current distributions of mammal species based on the Faunmap data. Next, we increased the likelihood value and repeated the calibration steps. We stopped the iteration for a species when 80% or more of the pixels in the predicted and current distribution matched. The average likelihood value that produced these results was 50%; this value was used in subsequent logistic regressions. This statistical estimator of each species' habitat associations was then used in conjunction with a new map, depicting ecosystem change under climate warming, to assess the extent to which the geographic range of each species would change. This analysis (figure 1) indicates that both wolves and moose will remain over a good part of their geographic range and thus should fare well under doubled CO<sub>2</sub> levels. Any local losses of moose should be compensated by expansion into new geographic locations. This type of mapping analysis is representative of current techniques used to forecast the response of wildlife to climate change.

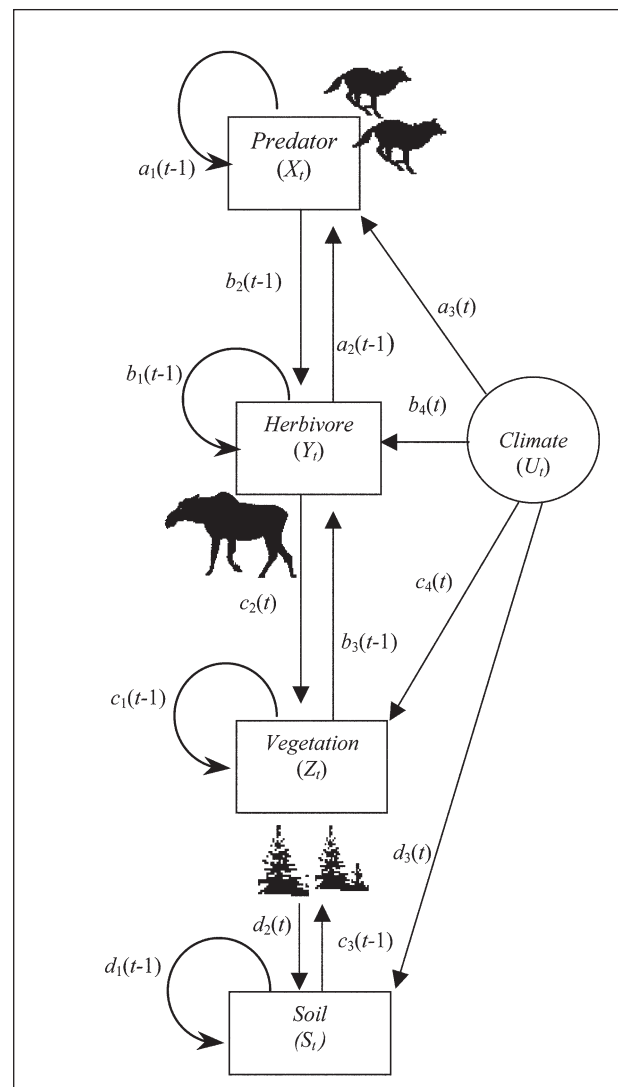
Data from a system of wolves, moose, and balsam fir (*Abies balsamea*) on Isle Royale, Michigan (Post et al. 1999), reveal an entirely different picture of ecosystem structure and function, and consequent response to global warming, than does the mapping analysis described above. More than 40 years of annual data indicate that a cyclic weather phenomenon with a decadal trend in temperature, moisture, and winter snowfall—the North Atlantic Oscillation (NAO)—has a strong influence on northern forest ecosystem structure and function. Moreover, NAO forcing can create environmental conditions expected under a doubling of CO<sub>2</sub>—namely, winters with anomalously warm temperatures and little snowfall (NAST 2001). Whenever snowfall levels are high, wolves are extremely efficient predators of moose, which are encumbered by deep snow. Consequently, by reducing moose populations to levels at which they cause only limited damage to balsam fir, wolves play an important role in determining the compositional makeup of forest vegetation (figure 2). The role

of wolves becomes diminished when NAO forcing causes snowfall levels to decline to levels expected under CO<sub>2</sub> doubling, decreasing the wolves' capture efficiency. Over the long term, climate warming can cause a cascade of effects, including declining wolf populations, rising moose populations, and declining balsam fir productivity (Post et al. 1999).



**Figure 1.** The traditional color mapping approach to understanding the effects of climate change on ecosystems. Depiction of the effect of doubling atmospheric carbon dioxide (CO<sub>2</sub>) on (a) wolves and (b) moose within the continental United States. Current moose and wolf distribution data were obtained from the Faunmap Project ([www.museum.state.il.us/research/faunmap/](http://www.museum.state.il.us/research/faunmap/)). Current and predicted future vegetation distribution, assuming CGCM2 GCM (Second Generation Canadian Global Coupled Model, General Circulation Model) atmospheric conditions, was obtained from the Vegetation/Ecosystem Modeling and Analysis Project ([www.cgd.ucar.edu/vemap/](http://www.cgd.ucar.edu/vemap/)). Under both current and predicted conditions, there is a 50% or greater likelihood that wolves and moose will remain in most of their range. Under current conditions, any climate-caused range loss is compensated by range expansion to other locations; however, this is not true under predicted conditions.

Moreover, moose may increasingly suppress sapling tree recruitment, resulting in a more open forest canopy with a changed understory of shrub and herb species (McInnes et al. 1992). If these conditions persist, the entire system may undergo a state transition to chronically low balsam fir abundance in the face of high moose abundance (Schmitz and



**Figure 2.** Schematic of a dynamic system, linking climate with three trophic levels (plants, herbivores, and carnivores) in an ecosystem. The figure illustrates the top-down processes, or interplay and feedback among different trophic levels in food webs, that may have a large effect on plant species abundance and ecosystem services such as productivity. Thus, the top-down chain from carnivores through herbivores to plants may be an important conduit for transmitting climate effects throughout ecosystems. The next generation of models must quantify the magnitude of trophic interactions and feedbacks (represented by arrows and corresponding coefficients) and the emergent nonlinearities to accurately forecast climate-change effects on ecosystems.

Sinclair 1997). This switch in ecosystem state is akin to nonlinearities long known for forest insect pests and their host plants (Holling 1992).

Studies of moose–vegetation dynamics in other boreal forest systems indicate that browsing-induced reduction of canopy height and closure by as little as 12% to 50% results in higher light intensity, lower humidity, warmer and drier soils, and lower primary productivity of tree species (Bonan 1992, Kielland and Bryant 1998). Over the long term, soil chemistry can become altered through reductions in litter quality and rate of litter decomposition, causing a buildup of soil carbon that feeds from the bottom up to exacerbate the reduction in ecosystem productivity (Pastor et al. 1993). Lowered diversity and abundance of habitat types, resulting from the attendant herbivory, can also result in loss of animal species diversity (McShea et al. 1997).

The only congruence between the mapping analysis and detailed examination of ecosystem structure and function is that the major species in the different trophic levels should continue to coexist under climate warming. Unlike the mapping analysis, however, the more focused assessment of ecosystem function reveals that the nature and strength of trophic interactions are likely to be transformed, leading to dramatic changes in the relative abundance of species in different trophic levels. This, in turn, may alter vital ecosystem services, including productivity. Such alterations would not be apparent in an analysis based on a mapping approach alone.

### **Moving beyond color mapping: Climate effects on ecosystems**

Global climate change is a massive, ongoing perturbation to Earth's ecosystems that has only recently received focused scientific attention. One of the challenges in characterizing the likely effects of climate change is that ecology has had insufficient time to conduct perturbation experiments to evaluate the cause-and-effect links between climate and multitrophic interactions on ecosystem functioning. To make inferences, scientists must look for signals using other kinds of data (Harrington et al. 1999). One method is to piece together how recorded historical patterns of climate fluctuations relate to long-term measures of ecosystem function. The link between NAO forcing and alteration of the wolf–moose–northern forest ecosystem is one such example.

Linking NAO forcing with ecosystem functioning is a useful first step in anticipating climate-change effects. The NAO is a long-term alternation of air mass and air pressure that has a huge effect on the westerly flow of air across the North Atlantic region. It is active over a large geographic scale, from the subtropical Azores to subarctic Iceland; its reach extends from northwestern North America to northeastern Europe (Stenseth et al. 1999, 2002), and its ecological impacts have been detected as far from the center of its activity as southern Africa (Oba et al. 2001). It causes fluctuations in winter temperature and precipitation. During certain phases, it produces regional (e.g., northeastern United States and Canada)

climate effects that resemble the predicted effects of rising CO<sub>2</sub>, such as anomalously warm winters with limited snowfall. In addition, the NAO seems to synchronize species interactions that shape ecosystem processes over large spatial scales (Post and Forchhammer 2001, Straile 2002). Below, we highlight several examples to illustrate further how climate change may affect multitrophic level processes that cascade from the top of the food chain down to lower levels. In these cases, the species composition of ecosystems is not expected to change with global warming, but alterations in species abundance, interaction strength, and ecosystem function are altogether likely.

**Lynx, snowshoe hare, and boreal vegetation.** The interaction between lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*) is a textbook example of the way tight coupling between predator and prey species can give rise to the celebrated 10-year cycling of species abundances in nature. This view, however, is now being reconsidered in light of recent evidence that a complete understanding of the cyclic dynamics requires a perspective that includes three trophic levels (lynx, hares, and the hares' plant resources; Krebs et al. 1995, 2001). More than 200 years of empirical data indicate that, as in the wolf–moose–northern forest system, the periodicity in lynx, snowshoe hare, and plants may be triggered by NAO climate effects on lynx abundance (Stenseth et al. 1999). The lynx–hare cycle appears to arise from trophic interactions whose strength varies with region-specific vegetation (e.g., forest–tundra, boreal conifer–deciduous mixed woods) and winter conditions. However, the timing and decadal periodicity of the regional cycles seem to be synchronized by the state of winter atmospheric circulation determined by the NAO. The proposed mechanism is that NAO-determined winter snow levels mediate lynx hunting efficiency, the effects of which then cascade down through snowshoe hares to the plants (Stenseth et al. 1999, Krebs et al. 2001). Environmental warming that produces anomalously warm temperatures and little snowfall may result in more efficient lynx predation, leading to a chronic decline in hare abundance. The prediction of a negative effect of low snowfall on snowshoe hare survival is entirely opposite to the prediction of a model that ignores top-predator effects in boreal ecosystems (e.g. Niemelä et al. 2001). Declines in snowshoe hare abundance can result in substantial shifts in plant species composition, litter decomposition, and nitrogen cycling of boreal ecosystems (Krebs et al. 2001). In addition, alteration of this trophic structure can affect a host of other predator and prey species that are linked to this focal food chain (Krebs et al. 2001, Niemelä et al. 2001).

### **Zooplankton, algae, and food web interactions in lakes.**

During late spring and early summer each year, many freshwater lakes undergo a distinct regime shift in which they become transformed from highly opaque to clear (Scheffer et al. 2001, Straile 2002). This clear-water state appears to result from a highly temperature-sensitive interaction between algae and herbivorous zooplankton, caused by climatic effects



on zooplankton population dynamics. The event is triggered by natural environmental warming, which causes rapid zooplankton life-cycle development and consequent proliferation in herbivorous zooplankton abundance. This, in turn, leads to a rapid suppression of algal abundance through a plant–herbivore trophic interaction (Straile 2000). Whether or not clear-water events occur depends on very small changes in temperature (Scheffer et al. 2001).

The NAO has a remarkable capacity to determine both the likelihood of occurrence and the interannual variability in timing of clear-water events (Scheffer et al. 2001). As in the lynx–hare cycle, the NAO can synchronize the occurrence of the clear-water state over several hundreds of kilometers (Straile 2002). Warm winter and spring conditions, indicated by high NAO winter index values, can lead to earlier and longer-lasting clear-water phases than in cold winters, owing to earlier life-cycle development of zooplankton and longer periods of zooplankton survival (Straile 2000). Protracted periods of clear-water conditions may also trigger larger ecosystem state changes by creating environmental conditions that are highly suitable for the invasion of submerged vegetation, which is important for the recovery of lake biodiversity (Scheffer et al. 2001).

**Cod, shrimp, and oceanic ecosystems.** Pelagic marine ecosystems remain a frontier for experimental research aimed at elucidating the relative importance of top-down control of ecosystem function, owing to the difficulty of conducting and monitoring trophic manipulations on a large enough scale and over a long enough time period. Nevertheless, ecologists have recently capitalized on the availability of long-term catch data for many commercial species and the occurrence of a large-scale perturbation, the regime shift in abundance of a top predator, Atlantic cod (*Gadus morhua*). Long-term biomass data indicate predator–prey coupling between cod and prey species such as shrimp (*Pandalus borealis*), snow crabs (*Chionocetes opilio*), and lobster (*Homarus americanus*) (Worm and Myers 2003). Overfishing in the last 30 years has caused a rapid decline in the abundance of many cod stocks and a corresponding increase in prey species abundance across the north Atlantic, offering strong evidence for top-down control of this food web (Worm and Myers 2003). Additional evidence indicates that, historically, the strength of this trophic interaction is sensitive to ocean temperature, whereby cooler temperatures probably weaken the interaction strength (Worm and Myers 2003).

As in the lake system described above, the effect of temperature on trophic interactions appears to arise largely from temperature effects on consumer (in this case, cod) life-cycle processes, such as recruitment and somatic growth (Ottersen and Stenseth 2001, Worm and Myers 2003). Such temperature-mediated effects on the life history of cod appear to be influenced also by NAO forcing (Ottersen and Stenseth 2001). Thus, climate warming has the potential to increase the strength of top-down effects that cascade from invertebrate

and fish prey down to benthic components of the food web (Stenseth et al. 2002, Worm and Myers 2003).

### Climate change and trophic interactions in ecosystems

The examples above indicate that in response to global climate change, the composition of key players in ecosystems may remain intact, but the fundamental character and complexion of the ecosystem and its feedbacks may become uniquely transformed. Likewise, the possibility of shifts in ecosystem state driven by top predators indicates that higher-order trophic interactions are likely to play an important role in determining ecosystem structure and function. The implications of losing or gaining top predators or integral prey species have not been incorporated into current models that attempt to forecast ecosystem response to climate change. Moreover, these implications are not being widely explored as part of an agenda for experimental research on the effects of global change on ecosystems (Shaver et al. 2000, Niemelä et al. 2001).

We recognize that the idea that ecosystems are driven by top-down or bottom-up effects exclusively is unlikely to hold true in general (Polis and Strong 1996, Wardle 2002). We do not suggest, therefore, that researchers should supplant the bottom-up perspective with a purely top-down viewpoint. Indeed, our example of climate effects on the Isle Royale ecosystem demonstrates the need to consider the interplay between top-down and bottom-up effects. The Isle Royale system may contain an even greater interplay between top-down and bottom-up control than described above, in that moose may initially prefer highly palatable deciduous species that have higher nutrient composition and litter decomposition rates than less preferred species (Pastor and Cohen 1997). This diet preference (a top-down effect), especially in the face of rising moose populations under climate change, may reduce the abundance of preferred resource species, allowing the proliferation of less preferred species, such as balsam fir. This, in turn, accelerates the transformation of nutrient turnover and ecosystem productivity from high to low, as described above (Pastor and Cohen 1997). Eventually, diminished abundance of highly nutritious, preferred species can force moose to consume less preferred resources, leading to declines in moose population (a bottom-up effect).

Animal responses to climate change—especially to abrupt changes in temperature, such as the rapid warming at the end of the Younger Dryas event, when temperatures rose by 7°C in as little as 10 years (Alley et al. 1993)—may be much more immediate than more gradual plant responses. For example, many species of vertebrates show numerical responses to major climatic perturbations with as little lag time as 1 to 3 years (Walther et al. 2002), while the most immediate population- and species-level plant responses to past climate change appear to be on the order of decades (Williams et al. 2002). Moreover, the rapid numerical response of large herbivores such as Irish elk (*Megaloceros giganteus*) during this period may be driven by changes in the nutrient status of

plants. This is because a change in vegetation due both to climate change and to herbivory may have resulted in a declining supply of essential nutrients, such as calcium and phosphorus, in plants (Moen et al. 1999)—another interplay between top-down and bottom-up processes.

Developing models of climate–ecosystem linkages (e.g., figure 2) should allow researchers to develop concrete working hypotheses about species interactions and the kinds of parameters that need to be measured to more accurately predict the long-term effects of global climate change (e.g., changes in the strength of trophic interactions). The model shown in figure 2 has been used to quantify direct and indirect climatic pathways on primary production in the Isle Royale ecosystem. The time series on interannual variability in growth increments of balsam fir from Isle Royale correlate with the winter NAO index (Post et al. 1999). Using such data in the absence of concurrent data on herbivore, and even predator, densities from the same system, one might be led to conclude that climate influences primary production in this system only in a direct way. However, applying the model in figure 2 to data at all three trophic levels from Isle Royale reveals that the NAO also influences balsam fir productivity through its influence on moose population dynamics (Post and Forchhammer 2001) and selective foraging (Pastor and Cohen 1997).

In addition, measuring the strength of trophic interactions leads to the discovery that increased temperatures can have huge impacts on plant resource consumption by several herbivores, including species that are known to have devastating effects on plant resources when climatic conditions favor their abundance. For example, Watt and colleagues (1995) showed that under temperature increases that mirror those forecast in climate change scenarios, vegetation consumption by herbivorous lepidopteran and orthopteran species increased between 25% and more than 100% above the levels observed under extant temperatures.

The examples provided here illustrate that species in higher trophic levels of ecosystems can have dramatic effects on ecosystem function (primary production) by altering plant species composition through direct and indirect interaction pathways. By abstracting higher trophic-level complexity, scientists run the risk of oversimplifying the response to global climate change and of generating prognoses that are overly conservative. The ability to develop tools that reliably forecast future effects of climate on ecosystem function rests squarely on approaches that include a more integrated perspective on the links and feedbacks between climate forcing and the biotic components of the ecosystem as a whole (figure 2). Therefore, in seeking to understand community-level consequences of climate change, researchers must investigate how ecological detail at the level of individual populations can lead to complexity that creates the context for emergent phenomena at the ecosystem level. Finally, deriving creative new answers to emerging environmental problems requires that researchers begin exploring how to scale across key organizational hierarchies in ecosystems.

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