Cascading effects: insights from the U.S. Long Term Ecological Research Network

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Abstract.   Ecosystems across the United States are changing in complex and unpredictable ways and analysis of these changes requires coordinated, long-term research. This paper is a product of a synthesis effort of the U.S. National Science Foundation funded Long-Term Ecological Research (LTER) network addressing the LTER core research area of "populations and communities." This analysis revealed that each LTER site had at least one compelling "story" about what their site would look like in 50–100 yr. As the stories were prepared, themes emerged, and the stories were group into papers along five themes: state change, connectivity, resilience, time lags, and cascading effects. This paper addresses the cascading effects theme and includes stories from the Bonanza Creek (boreal), Kellogg Biological Station (agricultural and freshwater), Palmer (Antarctica), and Harvard Forest (temperate forest) LTER sites. We define cascading effects very broadly to include a wide array of unforeseen chains of events that result from a variety of actions or changes in a system. While climate change is having important direct effects on boreal forests, indirect effects mediated by fire activity—severity, size, and return interval—have large cascading effects over the long term. In northeastern temperate forests, legacies of human management and disturbance affect the composition of current forests, which creates a cascade of effects that interact with the climate-facilitated invasion of an exotic pest. In Antarctica, declining sea ice creates a cascade of effects including declines in Adélie and increases in Gentoo penguins, changes in phytoplankton, and consequent changes in zooplankton populations. An invasion of an exotic species of lady beetle is likely to have important future effects on pest control and conservation of native species in agricultural landscapes. New studies of zebra mussels, a well-studied invader, have established links between climate, the heat tolerance of the

mussels, and harmful algal blooms. Collectively, these stories highlight the need for long-term studies to sort out the complexities of different types of ecological cascades. The diversity of sites within the LTER network facilitates the emergence of overarching concepts about trophic interactions as an important driver of ecosystem structure, function, services, and futures.

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INTRODUCTION

Ecosystems across the United States are changing in complex and unpredictable ways (Grimm et al. 2013), and analyses of these changes require coordinated long-term ecological research. The challenge of ecosystem change has only intensified in recent years, along with the nature and extent of global environmental changes in climate, air and water pollution, land-use change, agricultural intensification, and species movement (Steffen et al. 2005). Addressing the diverse and changing needs of human society requires an in-depth understanding of how ecosystems are changing, presenting a fundamental challenge to ecological science. How will today's dominant populations and communities change in the coming decades? What will be the consequences for ecosystem structure and function, and the values and services these ecosystems provide to people?

The capacity of ecological science to provide societally relevant information on ecosystem change is greatly facilitated by the presence of research and monitoring networks, which date back to the 1960s (Golley 1996). The U.S. National Science Foundation (NSF) funds the Long-Term Ecological Research (LTER) network, a group of long-term, site-based research programs aimed at understanding ecological processes within and across a wide range of ecosystems. The LTER network began in 1980, with roots in earlier network efforts such as the International Biosphere Program (Callahan 1984). In contrast to prior efforts, LTER sites were not selected to represent major ecosystem types systematically or natural biomes necessarily, but rather via a competitive process based on the combination of question-driven research frameworks, locations to study critical phenomena over long time periods, and the synergistic use of experiments, long-term monitoring, modeling, and comparative studies. As part of this design, LTER sites often carry out integrative, cross-site, network-wide research, enabled by organized data collection, categorization methods, and adherence to common metadata standards. The organization of hypotheses, experiments, and measurements at each site focuses on five core research areas: primary production, population studies, movement of organic matter, movement of inorganic matter, and disturbance patterns.

Synthetic analysis to facilitate the flow of information from the LTER network to the rest of the scientific community and to the broader society is accomplished via several mechanisms. The LTER Network Office (LNO) funds synthesis working groups via a competitive process, and the LTER Science Council conducts synthesis efforts during its annual meetings. The three-day Science Council meetings are attended by the lead principal investigators at each site as well as a second site representative with expertise in the synthetic topic of the meeting. Beginning in 2014, each year's Science Council meeting focused on one of the LTER core research areas, and in 2016, the synthesis theme was "populations and communities." Over the course of small group discussions, it emerged that each LTER site had at least one compelling "story" about what the populations and communities at their sites would be like in 50–100 yr. We therefore decided to compile these stories as broadly applicable and relevant examples of how ecosystems across the

network are changing. As the stories were produced, themes began to emerge and the stories were grouped into five different papers along these themes—state change, connectivity, resilience, time lags, and cascading effects—and combined into this special issue.

This paper addresses the cascading effects theme and includes ecological stories from the Bonanza Creek (Boreal), Kellogg Biological Station (agricultural and freshwater), Palmer (Antarctica), and Harvard Forest (temperate forest) LTER sites. We define cascading effects very broadly to include a wide array of unforeseen chains of events that result from a variety of actions or changes in a system. Cascading effects are one of the most challenging aspects of predicting the future state of ecosystems in the face of global environmental change. As noted by Kominoski et al. (2018a), interactions among ecosystem attributes and the emergent properties of ecosystems lead to nonequilibrium trajectories of ecosystem change (Peters et al. 2011, Grimm et al. 2017, Kominoski et al. 2018a). Cascading effects should therefore be viewed in a framework of alternate ecosystem development trajectories that produce a wide range of ecosystem structure, function, and services (Carpenter et al. 2006, Chapin et al. 2010).

Much previous work has addressed how changes at higher trophic levels produce cascading effects down food webs, that is, trophic cascades (e.g., Pace et al. 1999, Scheffer et al. 2005), as well as how nutrient additions produce cascading effects up food webs (e.g., Galloway et al. 2003, Slavik et al. 2004, Gaiser et al. 2005, Davis et al. 2010, Rosemond et al. 2015, Kominoski et al. 2018b). Here, we take a broader view to include a wide array of unforeseen chains of events that result from a variety of actions or changes in a system. Examples include how fire and climate interactions drive cascading impacts on Alaskan boreal ecosystems; how exotic lady beetle invasions influence native insect communities and ecosystem services; how interactions between climate, zebra mussels, and cyanobacteria affect lake ecosystems; interactions between climate, sea ice, and penguins; and how long-term land-use legacies affect northeastern forests. The stories presented here illustrate the expanding scope of thinking about cascades within the LTER network, highlight the need for long-term

studies to address these complex dynamics, and illustrate how the diversity of sites within the LTER network facilitates the emergence of overarching concepts about important drivers of ecosystem structure, function, services, and futures.

The case studies and lead authors for the different sections are as follows:

1. Fire and Climate Interactions Drive Cascading Impacts on Alaskan Boreal Ecosystems: Roger W. Ruess, Todd J. Brinkman, Hélène Genet, Knut Kielland, Jill F. Johnstone, and Michelle C. Mack
2. Exotic Lady Beetle Invasions Influence Native Insect Communities and Ecosystem Services: Christie A. Bahlai and Douglas A. Landis
3. Climate Change Can Affect Species in Complex and Unanticipated Ways: an Example with Zebra Mussels and Cyanobacteria in Lakes: Jeffrey D. White, Stephen K. Hamilton, and Orlando Sarnelle
4. Climate, Sea Ice, and Penguins in Antarctica: Maria T. Kavanaugh, William R. Fraser, and Hugh W. Ducklow
5. Past and Present Land Use Are Primary Drivers of Forest Change in Southern New England: Jonathan R. Thompson, Clarisse Hart, and David R. Foster

Fire and Climate Interactions Drive Cascading Impacts on Alaskan Boreal Ecosystems

Long-term research at the Bonanza Creek (BNZ) boreal LTER site shows how changes in the nature and extent of fire cause a cascade of changes in soil, vegetation, and vertebrates resulting in highly altered trajectories of ecosystem development. Over the past century, Alaska has warmed more than twice as rapidly as the contiguous United States, with some of the largest increases in annual air temperature occurring in interior boreal forests (Bieniek et al. 2014, Chapin et al. 2014). Warming has been driven primarily by anthropogenic emissions of greenhouse gases at the global scale, but is amplified at high latitudes by energy and trace gas feedbacks resulting from wildfire, melting of sea ice

and glaciers, lengthening of the snow-free season, and atmospheric losses of previously frozen permafrost carbon (C) as carbon dioxide (CO_2) and methane (CH_4) (Schuur et al. 2015). Because temperature is the primary driver of ecosystem dynamics in cold regions (e.g., permafrost, vegetation productivity, snow/rain regimes, wildfire risk), warming in Arctic and Antarctic regions has the potential to cause cascading effects with global repercussions (e.g., McGuire et al. 2016).

A pronounced consequence of climate warming has been increased fire activity in interior Alaska, altering historic patterns of fire size, seasonality, severity, and return interval (Calef et al. 2015). Many fires burn in highly flammable black spruce stands, which dominate the forested landscape and are often characterized by deep organic layers underlain with permafrost. Impeded drainage typically maintains high moisture levels in surface organic layers, preventing deep burning and enabling recovery of vascular and non-vascular plants that either survive the fire or are able to establish from seed on high organic soils (Hollingsworth et al. 2013). However, warmer early-season temperatures coupled with prolonged late summer drought are leading to larger fires that burn later in the fire season and into deeper soil organic layers (Turetsky et al. 2011, Barrett and Kasischke 2013). Combustion of surface organic layers and exposure of mineral soil seedbeds favors seedling recruitment of deciduous trees, such as aspen and birch, which do not establish on organic soil, thus shifting post-fire vegetation from spruce- to deciduous-dominated successional trajectories (Johnstone et al. 2010*b*) (Fig. 1). Rapid decay of deciduous litter and the absence of an insulating moss layer entrain plant–soil–microbial feedbacks within these newly established deciduous vegetation types to influence long-term trajectories of nutrient cycling and carbon (C) storage (Chapin et al. 2006, Johnstone et al. 2010*a*, Melvin et al. 2015, Alexander and Mack 2016) (Fig. 2).

Although past periods of high fire activity were associated with an expansion of deciduous forests, current rates of charcoal deposition in lake sediments indicate that recent fire activity in interior Alaska exceeds levels observed over the past 10,000 yr (Kelly et al. 2013). Strong links between climate and fire activity mean that we can anticipate continued high rates of burning in

Alaskan forests throughout the 21st century (Balshi et al. 2009). Model projections suggest that Alaskan forests may soon cross a tipping point to a new domain, where recent increases in fire activity have made deciduous stands more abundant than spruce stands on the landscape (Mann et al. 2012, Rupp et al. 2016) (Fig. 3A). Increased annual area burned has substantially increased total C emissions from Alaska black spruce forests (Genet et al. 2013, 2018), with C loss from large fire years representing up to 10 yr of statewide C accumulation (Fig. 3B). These C losses may offset enhanced vegetation productivity associated with warming and CO_2 fertilization, weaken the C sink in the boreal biome, and ultimately lead to a C source to the atmosphere beyond 2100 (Genet et al. 2013, Kelly et al. 2015, Genet et al. 2018).

Research from the BNZ LTER has identified the potential for synergistic effects of warming and increased fire to have multiple cascading impacts on ecosystem function in boreal forests across local to regional to global scales. Combustion of surface organic layers reduces ground insulation, warming permafrost soils, and exposing organic matter that has been frozen for hundreds to thousands of years to microbial decomposition, mineralization, and atmospheric release of greenhouse gases (Shur and Jorgenson 2007, Schuur et al. 2008). Globally, permafrost constitutes a C pool that is approximately twice that of the atmosphere, a significant fraction of which is vulnerable to microbial decomposition over decades to centuries as northern regions continue to warm (Schaefer et al. 2014, Schuur et al. 2015). Models incorporating the role of snow, soil organic layer thickness, water saturation, and thermal properties in controlling thaw vulnerabilities predict that the vulnerability of permafrost to climate warming will be influenced strongly by fire severity (Jafarov et al. 2013, Brown et al. 2015*b*). This has the potential to strongly impact soil C stocks (Koven et al. 2015, Genet et al. 2018). Landscape heterogeneity (topography, vegetation, drainage, permafrost ice content) exerts substantial control on the sensitivity of permafrost to warming and fire, complicating our ability to predict the nature and magnitude of ecosystem responses to thaw (Genet et al. 2013, Jorgenson et al. 2013). For example, abrupt permafrost thaw following

Fig. 1. During 2004, over 7 million acres of boreal forest burned across interior Alaska. Many of these were high-severity fires that combusted deep organic layers, exposing mineral soil and favoring the invasion of hardwoods. Within the BNZ LTER Regional Site Network, many sites that were dominated by black spruce prior to burning in 2004 (upper picture) are now converted to dense birch stands with very different vegetation and ecosystem characteristics (lower picture). Photo credit: Roger Ruess.

high-severity fires in ice-rich lowlands can trigger the formation of thermokarst bogs and wetland succession (Lara et al. 2015, Turetsky et al. 2015, Brown et al. 2015*b*), while thaw in well-drained areas with lower ice content can lead to surface drying and lake drainage (Jorgenson et al. 2013, Roach et al. 2013). In uplands, stream hydrology and chemistry are tightly coupled to vegetation, fire frequency and severity, and the distribution of permafrost. Streams draining watersheds with extensive permafrost have flashier and greater variation in stream flow than streams draining watersheds lacking permafrost (Jones and Rinehart 2010). Based on stream flow data collected from BNZ LTER watersheds since 1978, stream flows have become less responsive

to rain storms, presumably due to loss of permafrost and the effects on water routing to streams.

Vegetation changes resulting from warming and altered fire activity affect the population size and distributions of many vertebrate herbivores, including caribou (Joly et al. 2011), moose (Lord and Kielland 2015), ptarmigan (Christie et al. 2014), and snowshoe hares (Tape et al. 2015). In turn, plant–herbivore interactions strongly influence plant growth and community composition (Bryant et al. 2014, Christie et al. 2015, Olnes and Kielland 2016), and feedback to control herbivore fecundity through impacts on forage quality and abundance (Seaton et al. 2011, Paragi et al. 2015). Moose movement and browsing patterns are
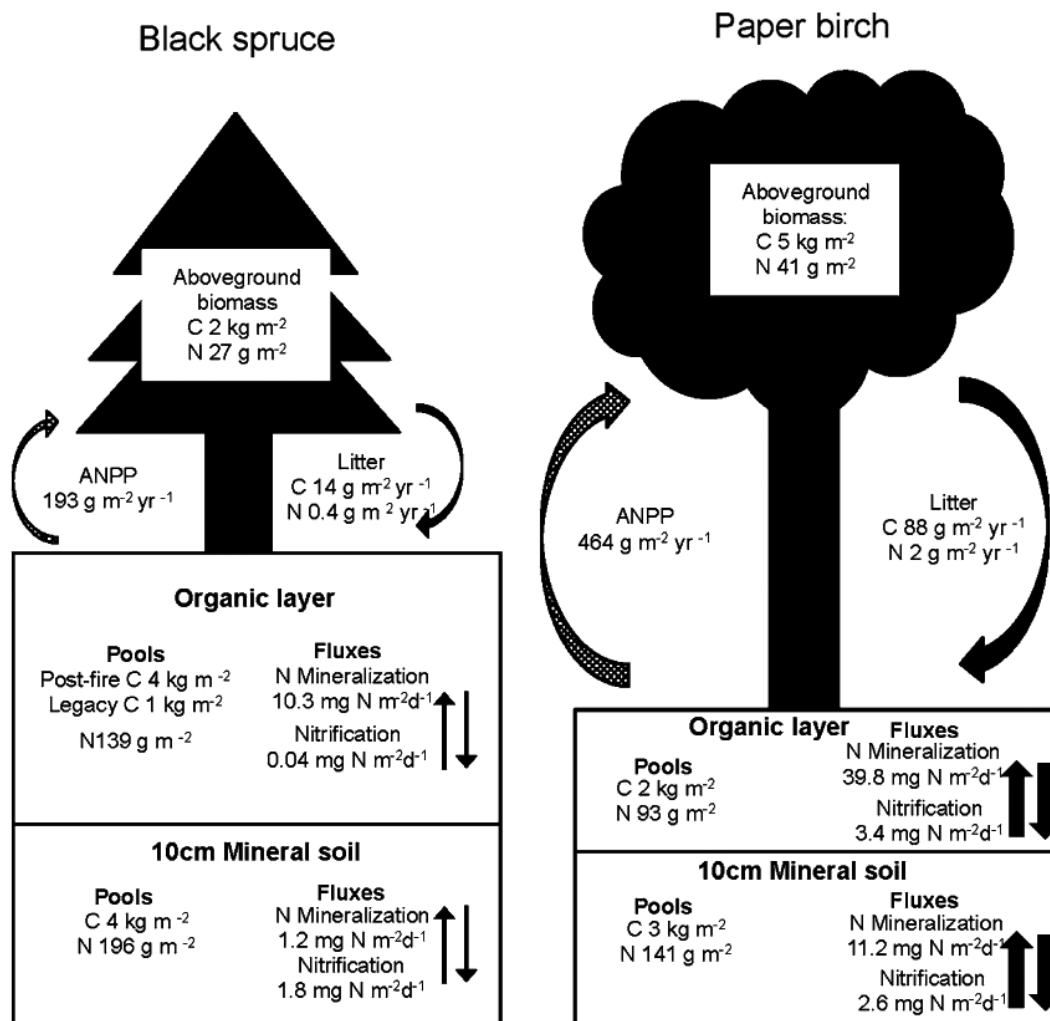
Fig. 2. High-severity fires in black spruce forests can lead to hardwood tree dominance with high aboveground net primary productivity (AGNPP). These stands accumulate little carbon (C) in soils, compared to black spruce, because high litter quality and soil conditions favor rapid decomposition rates. Low severity fires promote dominance by black spruce and mosses, resulting in low AGNPP, low litter quality, and slow decomposition rates. The net result is similar C stocks in hardwood s black spruce stands, but aboveground pools dominate in hardwoods while belowground pools dominate in black spruce. Graph shows observed differences in mean C and nitrogen (N) pools (boxes) and fluxes (arrows) measured in aboveground live tree biomass and soils for mid-successional black spruce and Alaska paper birch forests in the 1958 Murphy Dome fire scar near Fairbanks, Alaska (Melvin et al. 2015).

highly responsive to the degree of deciduousness (trees and shrubs) following fire (Brown et al. 2017), while aspen height growth during early succession is controlled by an interaction between fire severity and browsing intensity (Conway and Johnstone 2017). Moose responses to fire are important to wildlife management because many Alaskan residents rely on moose as a food source (Brown et al. 2015a). Climate-driven changes in the environment (including fires and weather) have challenged hunters' ability to access traditional hunting areas during times that would optimize harvest opportunity (Brinkman et al. 2013, Carothers et al. 2014).
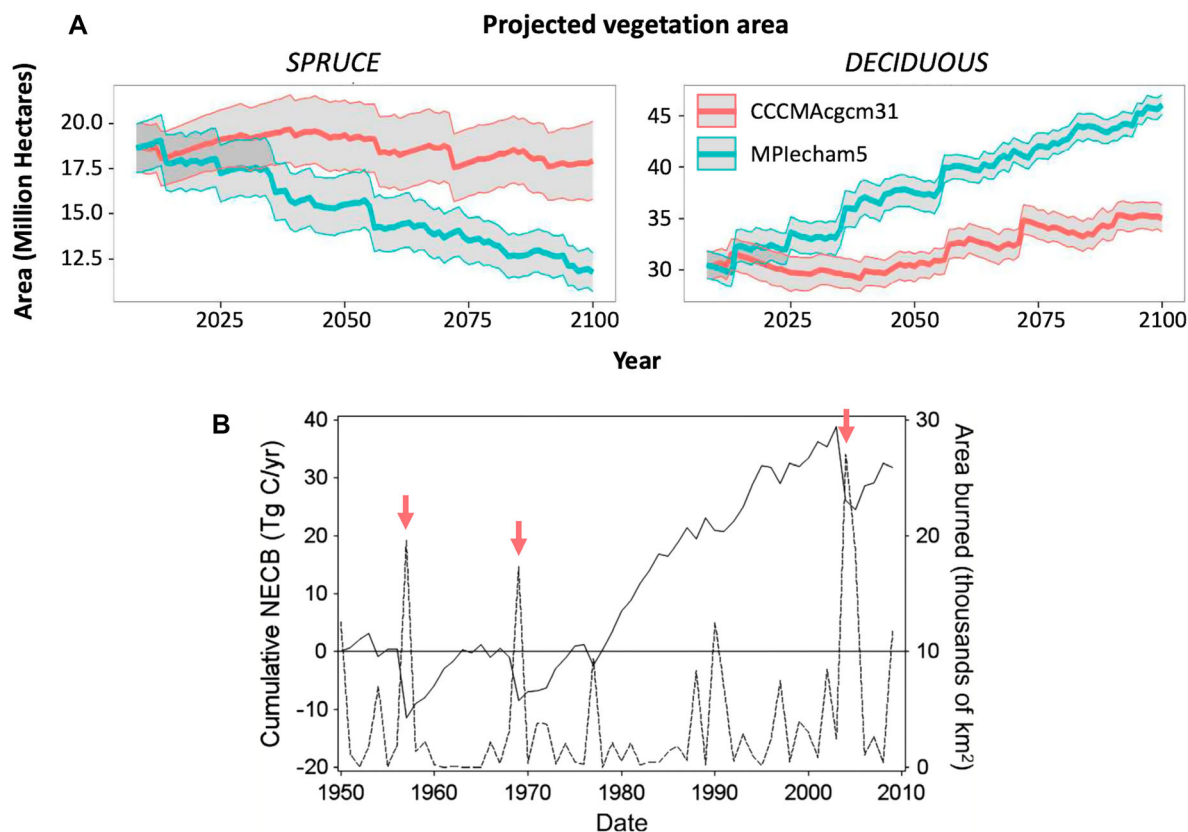
Fig. 3. (A) Projected (2010–2099) areal extent (hectares) of major forest types in the Alaska boreal forest using the ALFRESCO model for the CCCMA 3.1 (red) and the MPI-ECHAM5 (blue) climate scenarios under the A1B emission scenario, showing a 8-44% reduction in late-successional spruce forests and an 25-113% increase in deciduous forests (Pastick et al. 2017). Note the difference in *y*-axis scales between panels. (B) Statewide cumulative annual Net Ecosystem Carbon Balance (NECB; solid line) and total annual area burned (dotted line), from 1950 to 2009, for upland ecosystems in Alaska. Losses of carbon from large fire years such as 1957, 1969, and 2004 were equivalent to about 10 yr of statewide C accumulation. (From Genet et al. 2018.)

Alaskan communities differ in their exposure, sensitivity, and capacity to adapt to environmental and socioeconomic change (Trainor et al. 2009). Alaska Native communities are particularly vulnerable given the high cost of living in remote villages off the road system and the high reliance on cultural traditions, lifestyles, and economies that depend on ecosystem services (Kofinas et al. 2010, Brinkman et al. 2014).

As mentioned above, the cascading effects associated with wildfire regime in boreal Alaska will have crucial impacts on ecosystem structure, function, and services at local to regional and global scales, now and for the centuries to come. To assess these impacts affecting ecosystems beyond the spatio-temporal frame of the LTER

network, research and monitoring data collected in the field are integrated in a suite of ecosystem models specifically parameterized to represent the heterogeneity and dynamic of boreal landscapes. These improved models can serve as tools to assess the influence of social–ecological change on ecosystem services, and how management scenarios can affect adaptive responses of Alaskan communities.

Exotic Lady Beetle Invasions Influence Native Insect Communities and Ecosystem Services

Long-term research at the Kellogg Biological Station (KBS) agricultural LTER site has

characterized classical trophic cascade effects where changes in a predator cause a series of effects at lower trophic levels. The case study presented here shows how the arrival of invasive predators caused changes in native and exotic predator and prey communities, in a highly relevant pest control context.

Invasive species are one of the main drivers of global change and have the potential to reshape interactions among entire communities, influencing ecosystem function and ecosystem services (Tylianakis et al. 2008). Like shifting climate patterns, the movement of species outside their native ranges can have profound consequences on biodiversity and the functioning of communities in the invaded areas. In agricultural ecosystems of the north-central United States, successive invasions of exotic lady beetle predators have influenced community structure and ecosystem processes with wide-ranging impacts on both natural and managed ecosystems. Nearly 30 yr of observations at the KBS LTER site have allowed us the unique opportunity to detect multiple invasions and to understand their implications for insect community structure and function (Landis and Gage 2015).

Insects play profound roles in the functioning of most terrestrial ecosystems, as herbivores, predators, pollinators, and decomposers (Losey and Vaughn 2006). Lady beetles (Coleoptera: Coccinellidae) are a common group of predatory insects which shape plant biomass production by regulating population growth of herbivores. The lady beetles are considered an important ecosystem service provider in agricultural systems where they consume aphids and other small soft-bodied prey. Given the global importance of aphids as crop pests, lady beetles have been well studied within agroecosystems; however, long-term studies are rare. Beginning in 1989, entomologists associated with the KBS LTER began long-term data collection on the abundance and diversity of Coccinellidae within agricultural crops and surrounding non-crop habitats (Maredia et al. 1992b, c). Weekly observations of 13 species of lady beetles in 10 habitats during the growing season over nearly three decades provide an unparalleled view of how native insect communities respond to exotic invasions.

The initial observations of lady beetles at the KBS LTER began just three years after the detection of the exotic European seven-spotted lady beetle (Coccinella septempuncata) in southern Michigan (Maredia et al. 1992a). Even at this early stage of invasion, it already comprised nearly 80% of the total lady beetle capture in 1989 (Fig. 4). Since then, three additional species of exotic lady beetles have been detected at the site. The multicolored Asian lady beetle (Harmonia axyridis), a native of eastern Asia, was first captured in 1993 (Colunga-Garcia and Gage 1998), followed by two Eurasian species, the variegated lady beetle (Hippodamia variegata) and the fourteen-spotted lady beetle (Propylea quatuordecimpuncata) in 1997 and 2006, respectively (Gardiner and Parsons 2005, Gardiner et al. 2009a). Of these species, C. septempuncata and H. axyridis rapidly increased in abundance to become the dominant lady beetles in the community (Gardiner et al. 2009b). Although several native species could be described as co-dominant at the outset of the study, now only one native species, the pink lady beetle (Coleomegilla maculata) routinely reaches abundances greater than 25% of the community (Bahlai et al. 2013). Abundance peaks of C. maculata are primarily associated with the presence of maize (Colunga-Garcia et al. 1997) (which occurs every three years in the LTER crop rotation) and provide abundant pollen that C. maculata thrives on. The ability of C. maculata to persist in crop fields is likely due to this incomplete dietary niche overlap with its exotic competitors.

In addition to a variable coccinellid community, the abundance of aphid prey at the KBS LTER has also shifted over time, most dramatically by the invasion of the soybean aphid (Aphis glycines). The soybean aphid was first detected in the U.S. Midwest in 2000 (Ragsdale et al. 2011) and underwent dramatic boom-bust cycling until 2005 when widespread insecticide use largely damped this dynamic (Bahlai et al. 2015b). During this time, the soybean aphid provided unprecedented abundance of highly palatable prey that were differentially utilized by the lady beetle community, affecting dynamics between individual species depending on their foraging traits. The invasion of soybean aphid was particularly favorable to H. axyridis (Fig. 5) (Knapp et al. 2012), which as part of the entire predator community can provide top-down control of the soybean aphid (Costamagna and Landis 2006)
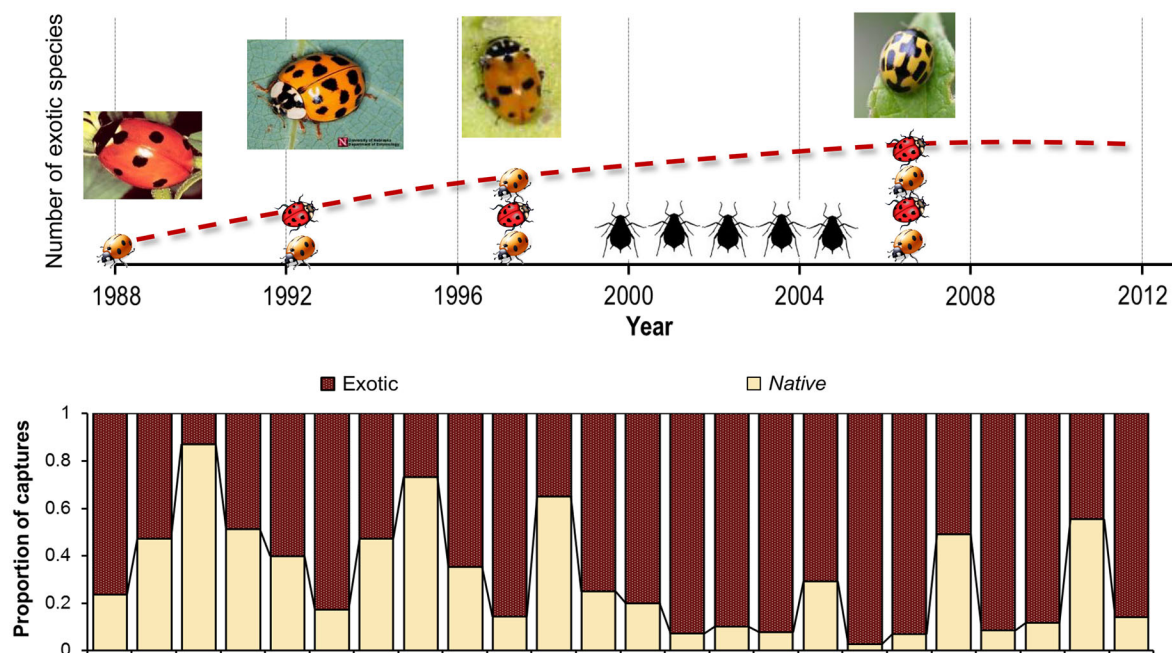
Fig. 4. Number of exotic lady beetles in the KBS LTER community and soybean aphid outbreak years (top) and long-term trends in native vs. exotic lady beetle abundance at the KBS LTER, 1989-2012. (Modified from Bahlai et al. 2013.)

resulting in a trophic cascade which protects crop yield (Costamagna et al. 2007).

Yet, although the Coccinellid community structure at the KBS LTER has changed dramatically over the study period, it appears no one invasion can completely explain the changes observed. An early analysis of site-wide population trends by species immediately before and after the arrival of *H. axyridis* found conflicting trends among population patterns in native lady beetle species: Two species declined, one species increased, and the remaining species maintained former levels (Colunga-Garcia and Gage 1998). However, a later analysis after the invasion of soybean aphid and which accounted for habitat use patterns found that as *H. axyridis* reached very high numbers in agricultural habitats, several native species both declined in abundance and dramatically shifted their habitat use patterns (Bahlai et al. 2015*a*). This result aligned directly with the predictions of the "habitat compression" hypothesis (Evans 2000) that suggests that with agricultural land-use change, native lady beetles expanded from their natural habitats (e.g., woodlands) to exploit aphids in crop fields.

However, with the introduction of superior competitors like *C. septempunctata,* which effectively reduced crop aphid abundance, crop habitats were no longer attractive to native species, which then "retreated" to their ancestral habitats. This suggests that if exotics are effective at replacing mortality previously provided by the natives, then overall pest suppression in croplands may be relatively unaffected. Indeed, we have observed no disruption to the community's overall ability to deliver biocontrol services in the landscape, despite near-complete lack of pest suppression by native species in crop habitats (Bahlai et al. 2013) (Fig. 6).

Invasions of exotic coccinellid species have caused dramatic shifts in the species composition, but not the function of the coccinellid community at our site, and this effect was further exacerbated by the arrival of an exotic prey species. Yet, the future of pest suppression at our site is uncertain. Lower diversity coccinellid communities dominated by exotic species may be less resilient to disturbance, or because of founder effects on genotypic variation, more susceptible to pathogens. Additionally, shifting weather and
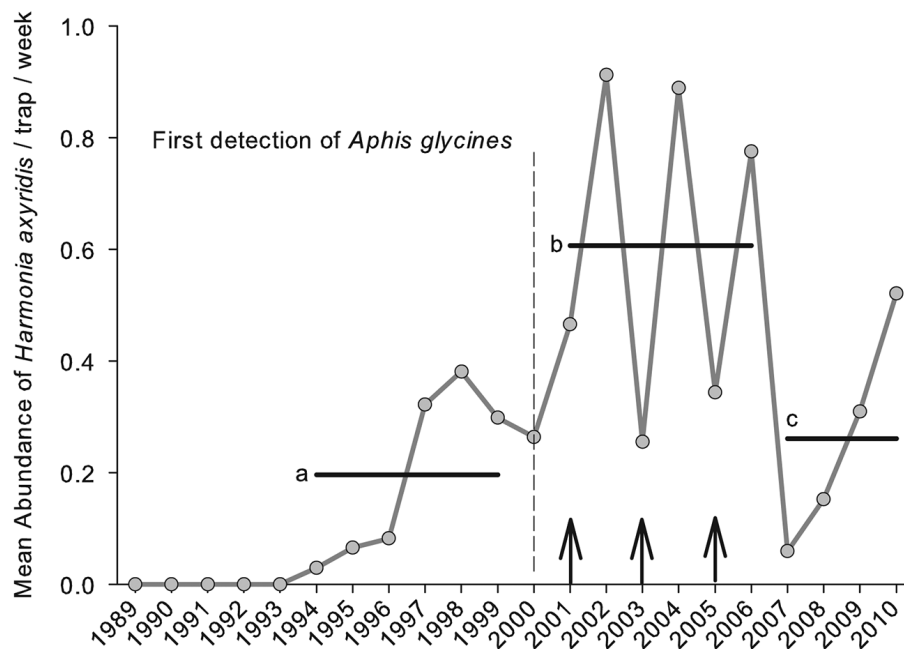
Fig. 5. Abundance of adult multicolored Asian lady beetles (*Harmonia axyridis*) at the KBS LTER from 1989 to 2010. This invasive species was first detected in 1994 and until 1999, mean abundance (marked by line a) was approximately 0.2 adults per trap/week. Following the arrival (dashed vertical line) of the soybean aphid (*Aphis glycines*), major aphid outbreaks (arrows) occurred every other year from 2001-2005, prompting strong numerical responses by *Harmonia* in the subsequent years and overall greater mean abundance (marked by line b). Since 2007, no aphid outbreaks have occurred and a new pattern of intermediate *Harmonia* abundance (marked by line c) is establishing. (Reproduced from Knapp et al. 2012.)

climate patterns may affect the phenological niche partitioning that allows certain native coccinellid species to coexist with the exotics, exacerbating native species loss. Finally, because native species may be more reliant on high-quality undisturbed habitat fragments, continued habitat loss will likely further exacerbate exotic species dominance in this community. Continued study will determine if, and by what mechanisms, native lady beetles may be able to persist in the increasingly exotic-dominated insect landscape of the KBS LTER.

CLIMATE CHANGE CAN AFFECT SPECIES IN COMPLEX AND UNANTICIPATED WAYS: AN EXAMPLE WITH ZEBRA MUSSELS AND CYANOBACTERIA IN LAKES

A second trophic cascade example from the KBS site shows how long-term data are essential for sorting out interactions between climate, the

invasive zebra mussel, and harmful cyanobacterial blooms. As in the lady beetle example, these cascades take place in a highly relevant human use context.

Each species in a community potentially responds to climate change and variability differently, and this can sometimes disrupt ecological relationships between species in unanticipated ways. These disruptions to species interactions can include mismatches in spatial distributions and phenologies, as well as extirpations, in response to both gradual and punctuated climatic variation (Memmott et al. 2007, Chen et al. 2011, Wernberg et al. 2013). Long-term data are requisite to understand community responses to climatic variation in order to distinguish actual trends from background noise and to document the short-term and protracted effects of extreme events, which can be highly stochastic and episodic in nature. Here, we present an example from freshwater habitats based on >15 yr of
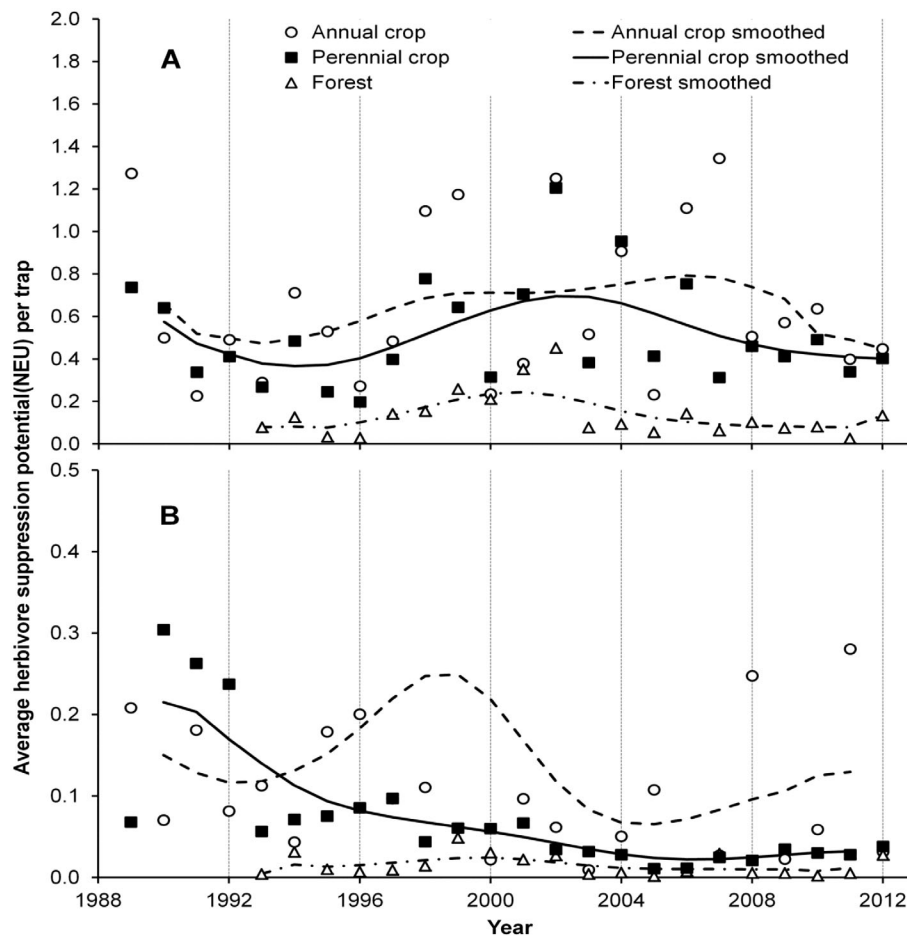
Fig. 6. Herbivore suppression potential (in natural enemy units, NEU) of aphidophagous coccinellid community by habitat type at Kellogg Biological Station, Hickory Corners, MI, 1989-2012, showing observed values (symbols) and 3 yr. smoothed (lines) data. (A) Herbivore suppression potential of all species. (B) Herbivore suppression potential due to native species only. Note that the scale of the chart excludes one outlier: a value of 0.95 NEU in annual crops in 1999. (Reproduced from Bahlai et al. 2013.)

observations of invasive zebra mussels (*Dreissena polymorpha*) and harmful cyanobacteria (*Microcystis aeruginosa*) in Gull Lake, adjacent to the Kellogg Biological Station (KBS) LTER site in southwestern Michigan.

Dreissena polymorpha is a widespread aquatic invasive species in North America that causes considerable economic and ecological damage from biofouling of water infrastructure, declines in native species (particularly bivalve mollusks), and shifts in habitat productivity and phytoplankton community composition (Strayer 2008, Higgins and Vander Zanden 2010). Since their inadvertent introduction into the Great Lakes

system beginning in the 1980s (probably through the ballast water of transatlantic ships), zebra mussels have spread to hundreds of smaller inland lakes, most likely via recreational boating (Johnson and Padilla 1996).

Zebra mussels arrived in Gull Lake, a low-nutrient inland lake, in the early 1990s. Soon after we observed surprising summer blooms of a toxic cyanobacterium—*Microcystis aeruginosa*—a species that is usually associated with more eutrophic, nutrient-rich waters. This observation stimulated more than a decade of research at KBS to determine whether the introduction of zebra mussels may have caused the shift in

phytoplankton composition toward this undesirable species.

A series of experiments in large enclosures suspended within Gull Lake, microcosm experiments in the laboratory, and lake surveys conducted across Michigan have now established a clear causal link between invasion by zebra mussels and increased dominance of the late summer phytoplankton community by *Microcystis* (Raikow et al. 2004, Sarnelle et al. 2005, Sarnelle et al. 2012) (Figs. 7, 8). This link is strongest in lakes where there is an expectation for *Microcystis* to be rare because of low phosphorus concentrations. Such lakes are the most common kind in Michigan. At higher nutrient availability (i.e., in eutrophic lakes), zebra mussels can have a negative effect on *Microcystis* (Sarnelle et al. 2012). Furthermore, we found that the concentration of toxin (microcystin) produced by *Microcystis* also increased in lakes colonized by zebra mussels (Knoll et al. 2008), particularly when nitrogen is relatively abundant (Horst et al. 2014).

The mechanism whereby zebra mussels promote *Microcystis* is still not known with certainty.
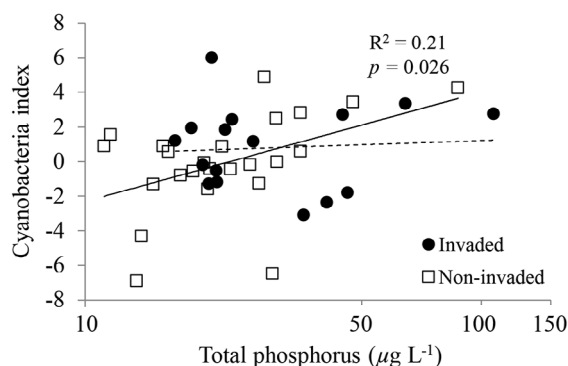

Fig. 7. Influence of zebra mussels (*Dreissena polymorpha*) on total cyanobacterial dominance in Michigan inland lakes surveyed in 1998–1999, expressed as a relative abundance index. Regression lines are as follows: lakes without zebra mussels (solid line, squares), $y = 6.338x - 8.6594$, $R^2 = 0.21$, $P = 0.026$; and lakes with zebra mussels (dotted line, circles), not significant ($P = 0.79$). Cyanobacteria, including *Microcystis*, increase with total phosphorus (TP) in Michigan inland lakes except when *D. polymorpha* are present, as a result of their promotion of *Microcystis* at lower TP. (Reproduced from Raikow et al. 2004.)

Most likely, it involves some degree of selective feeding by the mussels, in which they egest the *Microcystis* as pseudofeces while digesting most other phytoplankton species, which may also enhance nutrient uptake by *Microcystis* (Vanderploeg et al. 2001). Another hypothesis, which is not mutually exclusive, involves the excretion of nitrogen and phosphorus by the mussels in forms or ratios that somehow favor *Microcystis* (Vanderploeg et al. 2017). In addition, the ability of *Microcystis* to regulate its buoyancy could allow it to access nutrient-rich bottom waters around zebra mussel colonies.

The influence of climate change on the zebra mussel-*Microcystis* interaction centers on the impact of increasing water temperature. Elevated temperatures during the summer will increasingly bring lakes into the optimum ranges for cyanobacterial growth, and along with associated increases in water-column stability (thermal stratification), limnologists have predicted that cyanobacterial blooms will generally increase with warming temperatures (Paerl and Huisman 2008, Carey et al. 2012, Kosten et al. 2012).

Records of ice cover are one of the longest series of data available to indicate whether lakes are becoming warmer overall. Like many other north-temperate lakes with long-term ice cover records (Magnuson et al. 2000, Jensen et al. 2007), Gull Lake exhibits a response consistent with a warming climate. The Gull Lake ice cover record, which dates back to 1924 and continues to be maintained as a KBS LTER data set, shows a significant decrease in winter ice cover of 0.22 d/yr, such that the ice season is now 20 d shorter than when record keeping began (Fig. 9A). In Gull Lake, this is driven by a significant trend toward later freeze dates, although there is also a tendency toward earlier thaw dates (Fig. 9B). In the absence of a sufficiently long water temperature record, these ice cover data reflect an overall, long-term warming trend of the lake and its surroundings.

The distribution of zebra mussels is known to be limited by high water temperatures, and laboratory experiments suggest an acute lethal temperature threshold of 30 °C (Nalepa and Schloesser 2013). Mussel die-offs have been associated with warm-water temperatures (~30°C) at the southernmost limits of their range (Allen et al. 1999, Boeckman and Bidwell 2014,

Michigan Lake Surveys
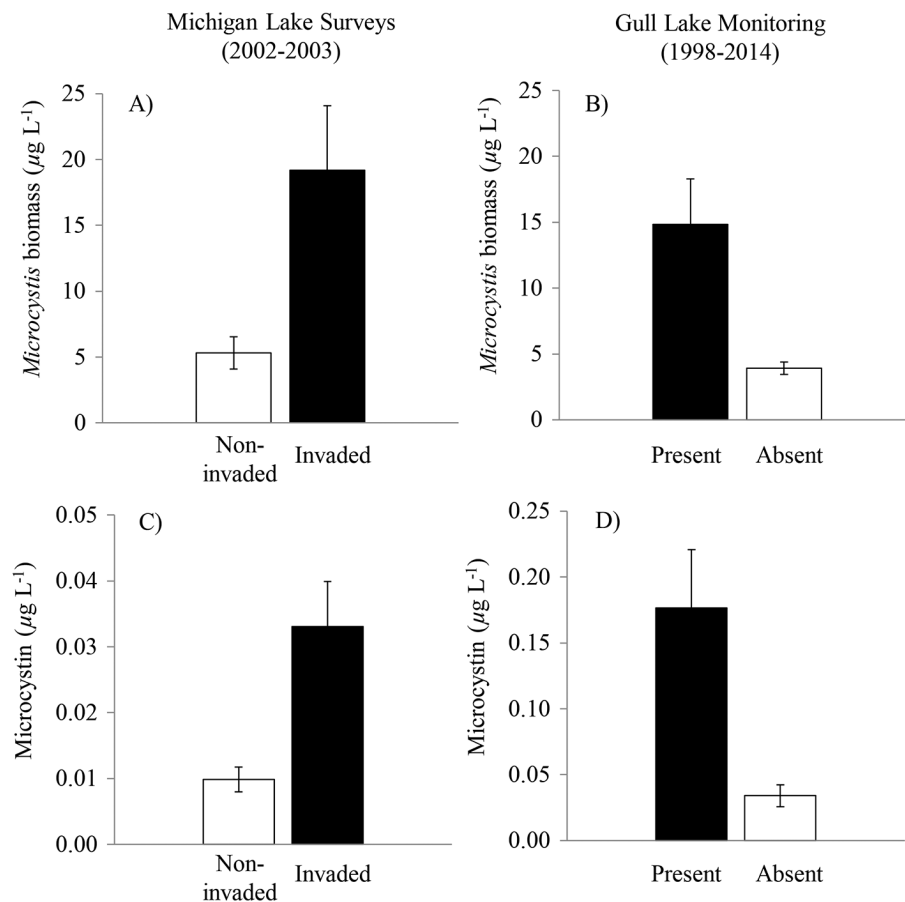(2002-2003)

Gull Lake Monitoring
(1998-2014)

Fig. 8. Influence of *Dreissena polymorpha* presence (solid bars) or absence (open bars) on *Microcystis* biomass (A, B) and microcystin toxin (C, D) in Michigan inland lakes. A comparison is made between invaded ($n = 20$) and non-invaded ($n = 19$) low-nutrient (TP ≤ 20 μg/L) lakes distributed across Michigan that were surveyed in 2002–2003 (A, C) and Gull Lake during years mussels were either present ($n = 10$) on the mixed layer sediments or absent ($n = 3$) as a result of heat-induced mass mortality (B, D). Error bars are ± SE. The magnitudes of change in both *Microcystis* biomass (3.6× vs. 3.8×) and microcystin (3.3× vs. 5.2×) are highly congruent between the lake surveys and Gull Lake long-term monitoring, respectively. Note the difference in scale between the microcystin panels. Data in (A) and (C) are from Knoll et al. (2008); data in (B) and (D) are from White et al. (2017).

Churchill et al. 2017). Compared to shallower inland lakes of Michigan, Gull Lake is deep and cool but its surface waters can approach 30°C in the warmest summers. Nevertheless, in monitoring zebra mussel populations since 1998, we never observed mass mortality of the mussels until one week in 2010.

In that week of relatively warm weather (August 2010), maximum water temperatures in Gull Lake reached 29°C and nearly all of the mussels died abruptly in waters down to about 4 m depth (Fig. 10). Mussels did not re-establish

in the shallow waters until 2013, as a result of continued high mortality (mean: ~84%) and failed recruitment during the two summers following the initial die-off, when surface water temperatures exceeded 30°C. Zebra mussel populations in Gull Lake subsequently recovered by 2014, presumably by reproduction of surviving mussels in cooler waters below the summer thermocline. Interestingly, water temperature records over 13 yr showed that previous years without mussel die-offs had reached similar maximum temperatures to those when high mortality was
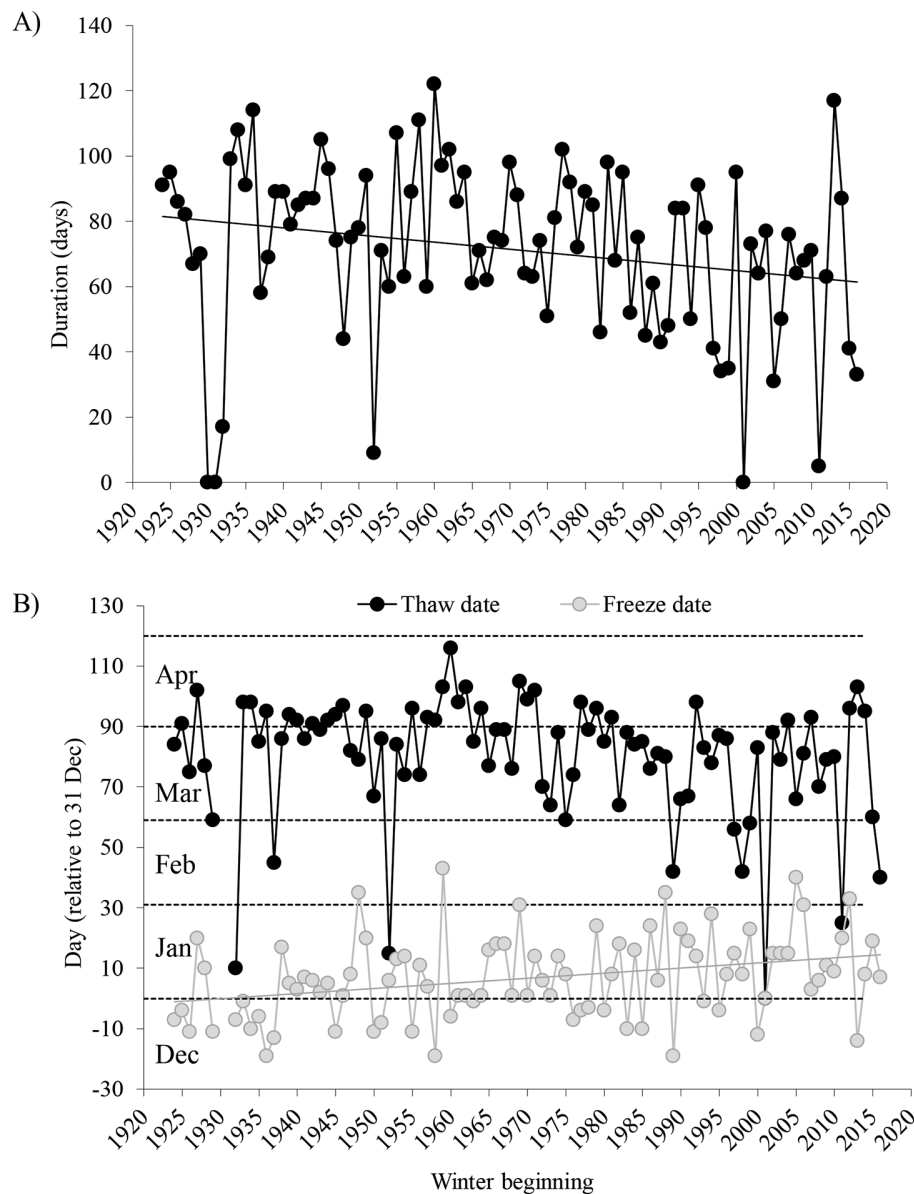
Fig. 9. Gull Lake ice cover trends, 1924–2016. (A) Ice cover duration in days (linear regression, $y = -0.218x + 501.5$, $R^2 = 0.05$, $P = 0.034$). (B) Freeze date (gray circles; linear regression, $y = 0.174x - 3367.0$, $R^2 = 0.11$, $P = 0.001$) and thaw date (black circles; linear regression, $P > 0.05$); dates are day of year relative to 31 December. The lake is considered frozen if more than half of the surface is ice-covered for more than 1 d.

observed, suggesting that the mussel mortality we observed was not a simple function of maximum water temperature.

We followed up these observations by deploying caged mussels and temperature loggers across a depth–temperature gradient in Gull Lake over four summers. Observations of *in situ* mortality as well as laboratory incubation experiments led us to conclude that it was not the absolute maximum temperature but rather the accumulated time (i.e., degree hours) in water >25°C that resulted in mass mortality (White et al. 2015) (Fig. 11A). This lethal threshold is considerably lower than many previous
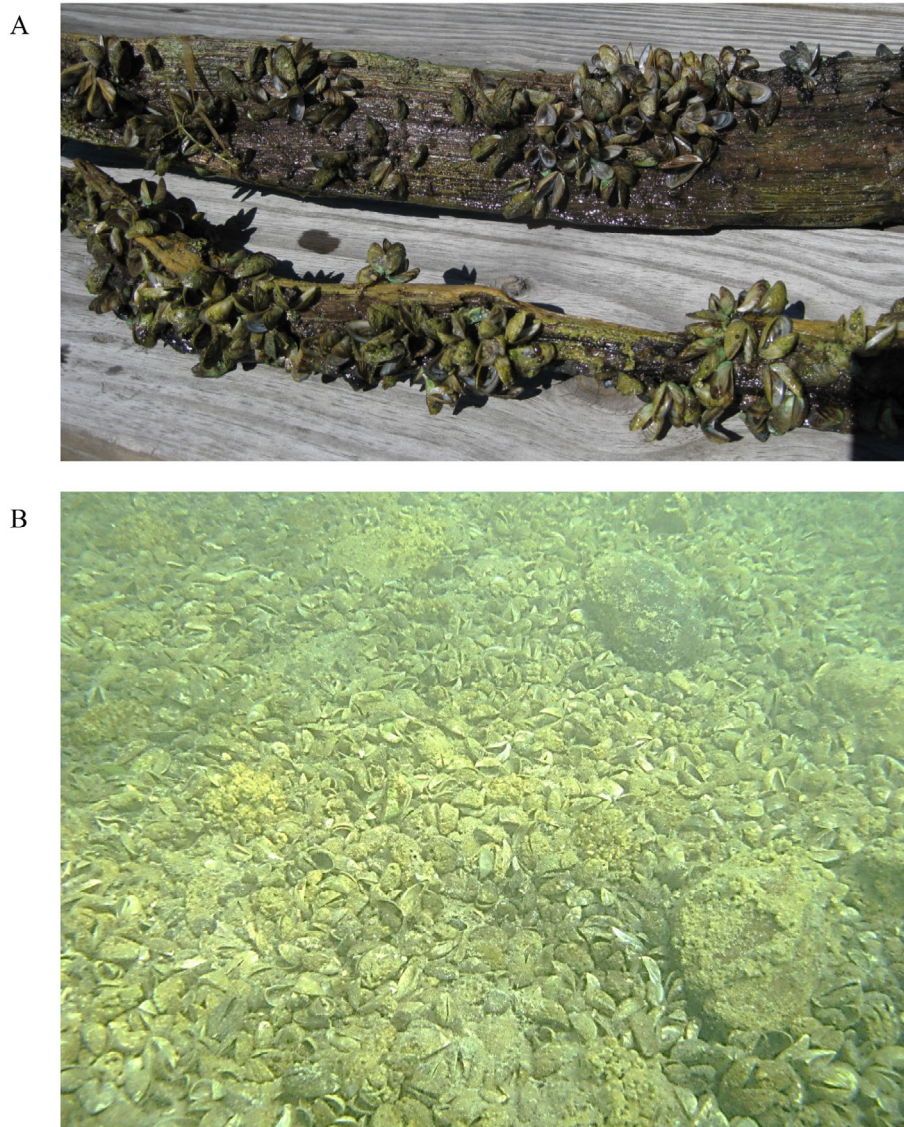
Fig. 10. (A) Recently expired *Dreissena polymorpha* retrieved from the nearshore area of Gull Lake immediately following the 2010 mass mortality event on mixed layer sediments. (B) Shells of dead *D. polymorpha* cover the bottom of Gull Lake at a depth of 2 m in 2011, following the 2010 mass mortality event. (Reproduced from White et al. 2015.)

experimentally derived estimates for *Dreissena*. Much attention has focused on the acute, maximum temperature tolerance of a focal organism, but we found that chronic exposure to warm but sublethal temperatures is also critical. Climate change scenarios project increases in not only maximum temperatures but also the duration of warm temperatures, so we may expect more of these warm-water episodes and associated

stresses for the biota of north-temperate lakes in the future.

Of particular interest with regard to our previous research was the observation that during summers when zebra mussel density on the sediments in contact with the mixed layer was drastically reduced by heat-induced mortality, *Microcystis* abundance and microcystin concentration declined by an average of 71% and 81%,
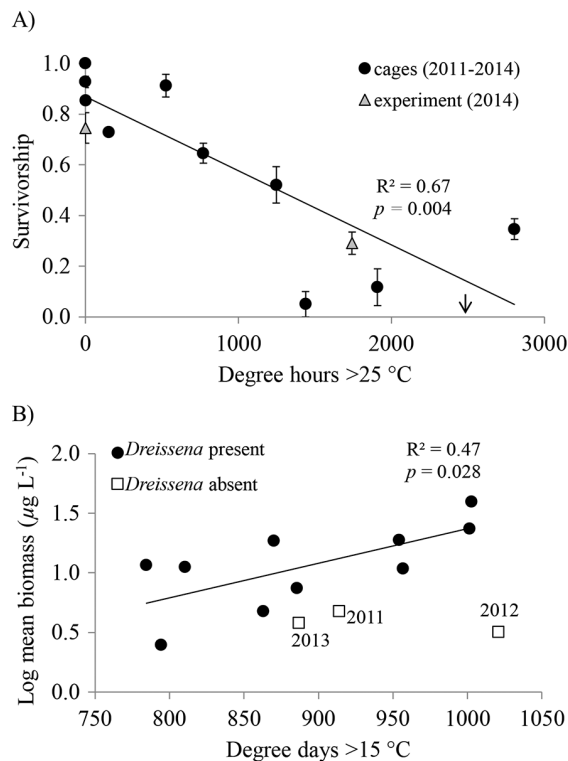
A)

B)

Fig. 11. Inverse responses of *Microcystis* and *Dreissena polymorpha* to natural temperature variation in Gull Lake. (A) Survivorship of caged *Dreissena polymorpha* (16–30 mm shell length) in Gull Lake (May–October 2011-2014) as a function of lake degree hours >25°C. Results from a 2014 laboratory experiment assessing the chronic temperature tolerance of Gull Lake *D. polymorpha* are included for comparison (triangles). Survivorship is given as the proportion of remaining live individuals. Error bars are ± SE. The regression line (significant at $P < 0.05$) is for caged *D. polymorpha* only. The arrow denotes accumulated degree hours in Gull Lake during the initial mass mortality event in 2010. (B) Gull Lake *Microcystis* dry biomass as a function of interannual variation in lake degree days >15°C. Note the log scale. Years with abundant zebra mussels (*D. polymorpha*) on mixed layer sediments (circles, $n = 10$) are differentiated from years (2011-2013; $n = 3$, squares) during which they were largely absent as a result of heat-induced mass mortality. The regression line (significant at $P < 0.05$) is for years with *D. polymorpha* only. Data in (A) modified from White et al. (2015); data in (B) from White et al. (2017). Note the difference in metrics between the *x*-axes.

respectively, in Gull Lake (White et al. 2017). This included 2012, the warmest summer of the 13-yr period of record, when *Microcystis* biomass was nearly an order of magnitude lower than would be predicted from water temperature alone. In contrast, for years when *Dreissena* were abundant on mixed layer sediments, we found a significant, positive relationship between summer mean water temperature and *Microcystis* biomass in Gull Lake ($n = 10$ yr), with biomass varying nearly 16-fold across this period (White et al. 2017) (Fig. 11B). This supports our previous conclusions from field experiments and lake surveys regarding *Dreissena's* role as a strong facilitator of *Microcystis* in low-nutrient lakes (Fig. 8) and represented a "natural experiment" that we could never have conducted intentionally.

Generally, the forecast for cyanobacteria is to increase with warming temperatures, but in this particular example, the complex interaction between zebra mussels, nutrient availability, and *Microcystis* may actually result in a decrease in blooms in low-nutrient Michigan lakes as water temperatures warm. We were able to identify this complex interaction only through multiple years of observations in Gull Lake—which enabled us to recognize unusual events—in combination with hypothesis testing through experimentation. The combined complexity of ecological networks and stochasticity of climatic variation—particularly statistically extreme, episodic events—is difficult to understand and disentangle in short-term studies. The fortuitous observation of a mass die-off of *Dreissena* during our long-term monitoring served as an additional line of evidence to support our earlier findings and revealed an example of how climate change may affect ecological interactions in complex and unpredictable ways.

CLIMATE, SEA ICE, AND PENGUINS IN ANTARCTICA

Long-term research at the Palmer (PAL) Antarctica LTER site has characterized a cascade of effects catalyzed by changes in sea ice that have led to declines and increases in different species of penguins in the region. These changes appear to be influenced by multiple, interacting mechanisms that lead to diverse and unexpected ecosystem states.

Palmer Station is one of three research bases operated by the U.S. Antarctic Program. It is located on the western side of the Antarctic Peninsula (WAP, 64.8° S, 64.1° W), about 800 miles south of Punta Arenas, Chile. The Palmer Station region has been a region of rapid climate warming and conspicuous ecosystem response, making it an ideal region for an LTER site and for studying environmental change. The Palmer LTER project has been investigating the marine pelagic ecosystem in the WAP region since 1992, based on a rich body of preceding observations, especially on Adélie penguin populations, a critical data set for detecting and assessing change in the Antarctic marine ecosystem. Here, we review changes observed in the region and their probable drivers, assess the problem of attributing ecological changes to long-term climate change, and finally discuss the challenge of detecting change at ecologically relevant scales in an area of great climate and biological variability.

The marine ecosystem over the continental shelf in the northern WAP has experienced significant changes at the bottom and top of the food web. The changes in Adélie and related local Pygoscelid penguin populations provided the first clear evidence of ongoing environmental change in the Palmer region (Fig. 12; Fraser et al. 1992). Adèlies had already declined by about 30% before the first documented increases in air temperature in the mid-1990s. Gentoo penguins, well-established farther north along the Peninsula and on the subantarctic islands, first started to immigrate to the Palmer region in low numbers in the mid-70s and subsequently increased rapidly via successful local breeding and continued immigration.

The primary producers in the WAP ecosystem are unicellular phytoplankton, with generation times on the order of 1–10 ds, and corresponding space (patch) scales of 10–100 km. Their great temporal variability and spatial variability confound trend detection by traditional discrete shipboard sampling. The PAL LTER detected a significant (ca. 50%) decline in phytoplankton stocks over 1978–2006 from satellite ocean color data (Montes-Hugo et al. 2009). More recent data show the trend continuing through 2012 (Fig. 13A). Phytoplankton are not merely declining in numbers; they are also getting smaller. In Antarctic coastal and shelf environments, phytoplankton communities tend to be dominated by large diatoms, the preferred food of Antarctic krill. However, phytoplankton >20 μm in size (diatoms) are decreasing in the shelf environment in the northern WAP (Fig. 13B) and being replaced by smaller forms (e.g., cryptophytes) that cannot be grazed efficiently by krill. These changes have large implications for Antarctic krill, the critical link between primary producers
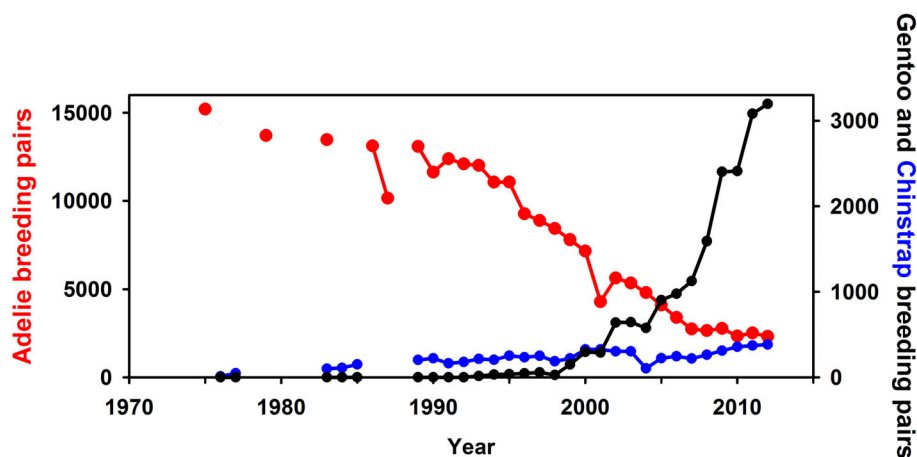

Fig. 12. Changes in Pygoscelid penguin populations near Palmer Station 1975–2015. The zero entries (Gentoo, 1976–1992) are observations while an absence of symbols indicates no data. Red arrow: abrupt change in nonlinear response to sea ice change in 1993. Data courtesy W. R. Fraser; available from http://oceaninformatics.ucsd.edu/datazoo/data/pallter/datasets: What will Palmer look like in the future ver 2.3.docx.
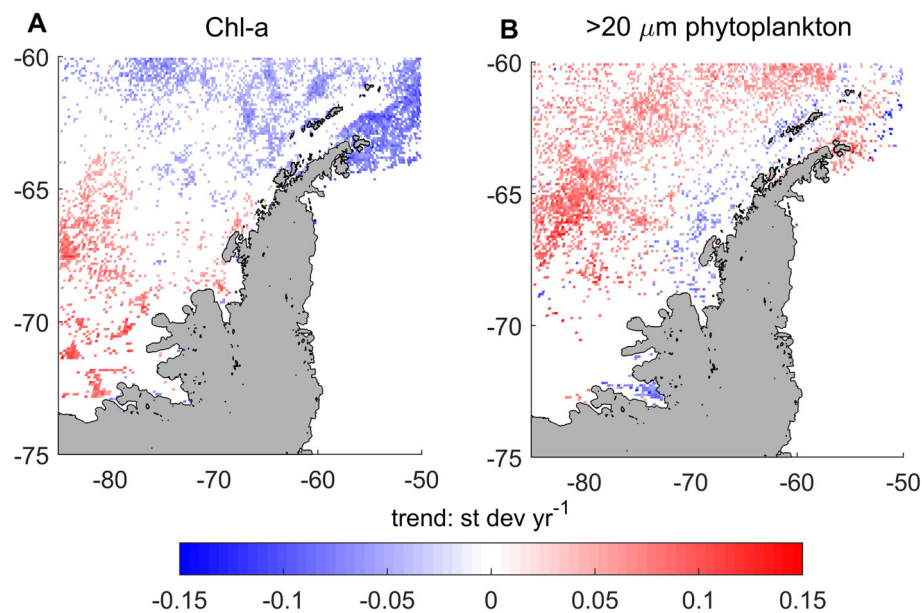
Fig. 13. Standardized trends (SD/yr) of phytoplankton properties along the western Antarctic Peninsula from 1997 to 2014. (A) Phytoplankton biomass ([chl-a] mg/m^3; Dierssen and Smith 2000); (B) cell size (fraction [chl-a] > 20 μm; Montes-Hugo et al. 2009). Each color pixel indicates a significant trend ($P < 0.05$), calculated from the seasonally detrended anomalies over the period.

and large predators in the Antarctic marine food web.

Most Antarctic marine populations are critically dependent on the spatial extent and duration of sea ice cover (pagophily). Long-term sea ice decline is the principal driver of ecological change in the WAP region (Bestelmeyer et al. 2011). At interannual scales, sea ice variability is driven by 3–6-yr cycles of the Southern Annular Mode and ENSO-related atmospheric forcing. Sea ice has been linked to interannual variability of phytoplankton bloom magnitude and krill breeding success through variations in water-column stratification and mixing (Saba et al. 2014). In this context, Adélie penguins crossed a threshold in response to declining sea ice in 1993 (Fig. 12), exhibiting an abrupt transition in population trajectory associated with an apparent regime shift. However, mechanistically linking a sea ice decline to this transition presents a complicated picture that is not necessarily attributable to changes in krill abundance. For example, a direct linear relationship does not explain why other krill predators such as Gentoo and

Chinstrap penguins are increasing. Indeed, changes in penguin populations are likely influenced by multiple, interacting mechanisms, some of which are likely yet to be discovered, and may include processes unrelated to marine food web dynamics such as the effects of colony exposure to prevailing winds and snow accumulation (Fraser et al. 2013). The case of krill is examined further below.

Antarctic krill (*Euphausia superba*) present an apparently clear case of long-term ecological change correlated with sea ice decline. Krill are crustacean zooplankton (adult size 6 cm, 2 g wet weight), the dominant prey item of penguins, seals, and whales. They are highly variable in space and time and difficult to capture in their preferred habitat, the sea ice zone. Krill density can range from zero to vast swarms covering hundreds of kilometers. These factors complicate establishing trends. Meta-analysis of circumpolar summertime krill data from 1926 to 2004 showed a significant long-term, basin-scale decline in the Southwest Atlantic sector (50-70° S, 30-70° W, including the northern WAP), and comprising

50–70% of the total Southern Ocean krill population (Atkinson et al. 2004). There was a significant correlation between temporal changes in krill stocks over the SW Atlantic sector and sea ice extent and duration. However, change in midsummer *E. superba* stocks within the 700 × 200 km LTER sampling grid (1993–2013, 20–100 km resolution) did not reflect the larger trend of krill decline related to sea ice change in the SW Atlantic (Steinberg et al. 2015). Antarctic krill in the LTER region did not change over the study period, although their variability was related to measured rates of primary production lagged by two years. This relationship suggests that regional, interannual variations of larval recruitment to adult krill populations are related to sea ice-mediated changes in food availability. However, as outlined above, the types of food preferred by the krill are changing.

What the ecosystem looks like moving forward will depend on the future mean state and associated variance of the system's environmental drivers (sea ice, winds, and atmospheric/oceanic warming in particular). Although the WAP environment is changing rapidly, it remains challenging to discern some ecological (phytoplankton, zooplankton) trends at local to regional scales in less than a few decades. This highlights the importance of repeated surveys over spatial scales relevant to key processes in order to document and understand food web responses to climate change. Trends in the Palmer region suggest a future ecosystem dominated by microbial primary producers and the absence of some of the iconic species typifying Antarctic seas. This forecast, based on the simplistic assumption that current forcing will continue, is always uncertain (Turner et al. 2016), especially in ecological systems prone to nonlinear regime change (Bestelmeyer et al. 2011).

Past and Present Land Use are Primary Drivers of Forest Change in Southern New England

For over a century, Harvard Forest (HFR) researchers have studied the cascading effects wrought by centuries of human land use in southern New England. A history of extensive land clearance and timber harvesting for agriculture well into the 19th century, followed by farm abandonment and forest succession, initiated a lengthy trajectory for the region's forests as they continue to develop in structure, composition, and function. Modern global change dynamics, including climate change and natural and human disturbances, are thus overlaid on an inherently dynamic system. Thirty years of research in Harvard Forest's Long-Term Ecological Research program has allowed scientists to disentangle past and present drivers of change and to understand better their interactions and implications for the future.

The legacy of colonial-era land use continues to drive changes to New England's forests in three distinct ways: (1) forest area, (2) structure and biomass, and (3) species composition. Modern global change drivers alter those trajectories in ways that are sometimes subtractive (e.g., modern land-use converting forests to other uses), sometimes additive (e.g., growing seasons lengthened by climate change enhance tree growth), and often unprecedented (e.g., invasive insects selectively eliminating foundation tree species). HFR's long-term observational studies, experiments, measurements, and modeling have begun to separate the legacies of past and modern forces. They show a surprising endurance of history that would not have been predicted from dominant theory or short-term studies.

Prior to European colonization, New England was almost completely forested. By the mid-19th century, at the peak of colonial agriculture, only about half of southern New England's forests remained. Since then, in a globally relevant example of ecosystem resilience, forest cover has expanded across >80%t of the landscape (Fig. 14). After more than 150 yr of expansion, the extent of forest area peaked in the 1980s and has been followed by a steady decline of forest cover in every New England state, as conversion to developed uses eliminated an average of 24,000 acres of forest each year regionally from 1990 to 2010 (Olofsson et al. 2016, Foster et al. 2017). If recent trends in land development persist, over the next 50 yr, human land use is poised to exert an even greater influence on the extent of Northeast U.S. forests than climate change (Thompson et al. 2011, Duveneck and Thompson 2019).

Like much of New England's forests, the dominant canopy trees at HFR are over a century old.
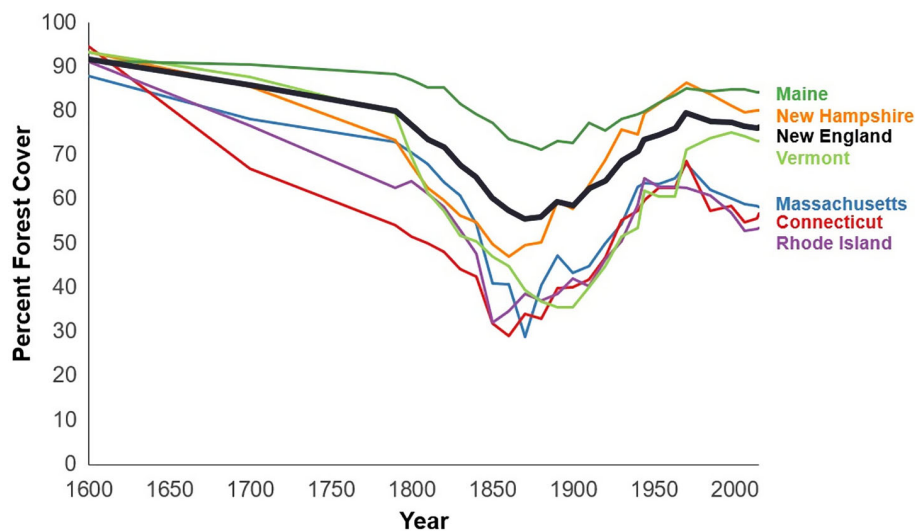
Fig. 14. Forest cover in New England declined from ca. 1600 to 1865 as European colonists converted much of the landscape for agricultural uses. In the mid-nineteenth century, widespread farm abandonment initiated more than 150 yr reforestation. Since the mid-1980s forest cover has been declining as forests are converted for residential development and other developed uses. (Adapted from Foster and Aber 2004.)

As the forest matures, theories of forest ecosystem development (e.g., Bormann and Likens 1979, Kominoski et al. 2018a) predict a transition from strong biomass aggradation to slowing biomass growth and stochastic mortality forming canopy gaps. But that is not what's happening at HFR. Thirty years of eddy covariance and plot measurements show little canopy mortality, and the rate of biomass accrual is increasing due to continued post-colonial forest development and anthropogenic changes to climate and atmospheric chemistry. A continual measure of forest growth has been recorded since 1990 by HFR's EMS eddy-flux tower, which is the world's longest continuous record of forest ecosystem carbon, water, and energy exchanges with the atmosphere (Fig. 15; Barford et al. 2001, Urbanski et al. 2007). Biometric inventory plots within the tower's footprint provide an estimate of aboveground productivity as an independent constraint on the annual C balance from the eddy covariance measurements. HFR scientists have brought together hundreds of thousands of observations on the C cycle at HFR, derived from a wide range of temporal and spatial scales and collectively describing the mixture of conifer- and hardwood-dominated forests as active C sinks with soils and tree biomass having nearly equal contributions to C storage (Finzi et al. 2020).

Perspectives from dendroecology and paleoecology records gathered by HFR scientists across New England reveal a specific pattern of forest change over centuries and millennia. This pattern was driven largely by climate change and accompanied by gradual (although occasionally abrupt) shifts in compositional structure (e.g., range-wide collapse of eastern hemlock loss 5500 yr bp). These records underscore the resilience of the region's forests and the tight coupling between climate and forest structure and composition—until European settlers arrived.

Shifts in the forces governing forest change during European settlement can best be seen in archival land-survey records. By assembling a comprehensive database of records describing hundreds of thousands of "witness trees," once used as property markers, HFR has developed a robust understanding of pre-colonial forest composition. Long-lived and shade-tolerant species, such as beech, oak, and hemlock dominated these forests. Save for the chestnut, which was eliminated as a canopy tree by a fungal blight early in the twentieth century, all native tree species remain part of the modern forest despite dramatic shifts in community composition (Fig. 16).
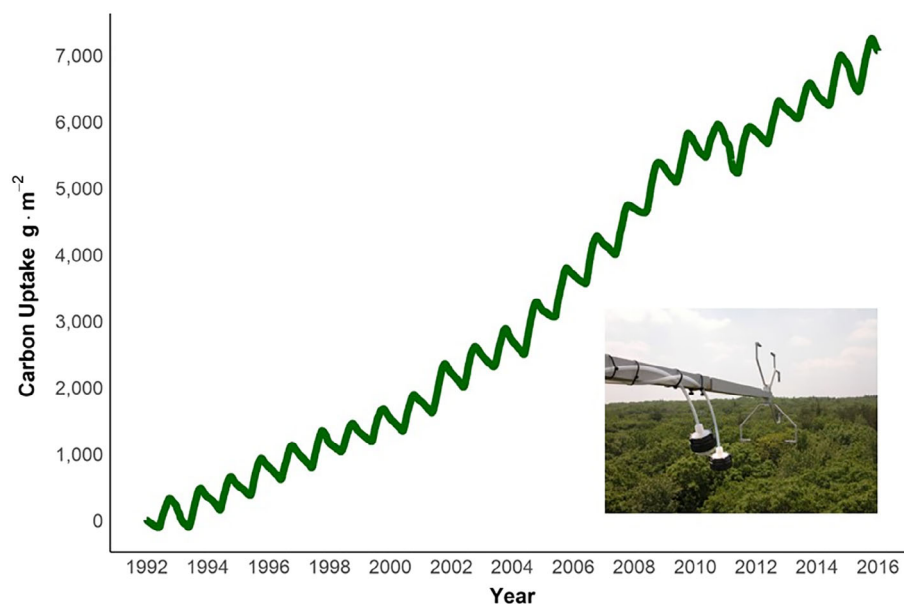
Fig. 15. Cumulative ecosystem uptake of carbon (C, i.e., net ecosystem production) as measured at the Harvard Forest Environmental Measurement Site flux tower. The area surrounding the tower is dominated by red oak (*Quercus rubra*) and red maple (*Acer rubrum*) trees that are between 100 and 120 yr old; their continuous uptake of C is testament to the ongoing recovery of forests from colonial land use. Data from Harvard Forest Data Archive (Munger and Wofsy 2019).
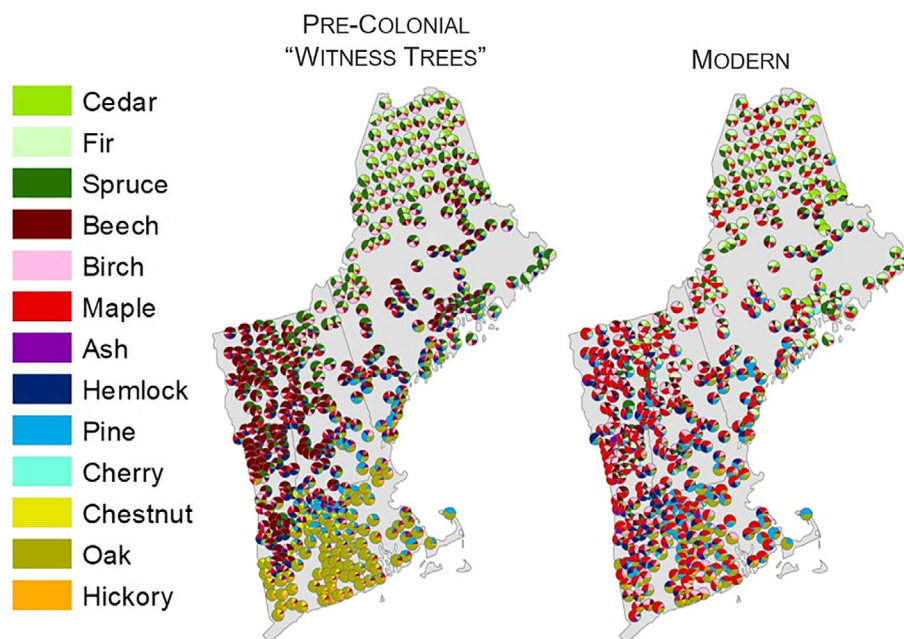

Fig. 16. The relative composition of New England's forests between pre-colonial era Witness Trees (*n* = 133,551) and modern inventory trees (*n* = 79,315) has changed substantially. While native trees continue to dominate the landscape, the community composition has shifted dramatically; late-successional species have declined in favor of early-successional species. (From Thompson et al. 2013.)

Modern forests have a much higher proportion of red maple, cherry, and other pioneer species. Further, the tree composition is more homogeneous and less coupled to local climatic controls (Foster et al. 1998, Fuller et al. 1998). The witness tree records strongly associate the magnitude of colonial land use with the degree of compositional change in the modern forest (Thompson et al. 2013).

Permanent plot studies at the Harvard Forest —ranging in size from 400 m^2 to 35 ha, and in temporal depth from <10 to >80 yr—also reveals the slow compositional shift as recovering forests continue to grow and trend toward mature, late-successional, long-lived, and shade-tolerant species (Eisen and Barker Plotkin 2015). On many HFR forest plots, red oak is slowly overtopping and succeeding red maple. The dominance and greater photosynthetic capacity of oaks is one reason for the increased C uptake observed at the EMS flux tower (Urbanski et al. 2007).

Long-term data from HFR have been used extensively to formalize theory and parameterize models of ecosystem development (e.g., Aber et al. 1992, Albani et al. 2006). These models have recently been coupled to models of land use and forest management to help scale site-based data to the region (Duveneck and Thompson 2019). Simulations suggest that future land use, not climate change, will have the greatest influence on forest dynamics in New England over the next 50 yr. Today, the region's forests are mostly (i.e., >80%), controlled by private landowners, including >800,000 family-owned woodlots and many large, corporate-owned timberlands. Public land —a few large, federally managed forests and many state and municipal forests—is also important components of the landscape. The modern forest land-use regime includes variable rates, patterns, and intensities of forest conversion, harvesting, and land protection. The ownership mosaic explains much of the variation in regional scale land use (Foster et al. 2017, Thompson et al. 2017*a*, *b*). Forest loss to development is concentrated around urban areas while timber harvesting remains the dominant ecological disturbance in the rural landscape (Kittredge et al. 2017). A continuation of the recent land-use trends will result in a large and spatially heterogeneous difference between the potential and realized C

stocks. If recent trends continue, simulations suggest that forest C would be reduced by 16%, below potential levels (Duveneck and Thompson 2019).

However, recent land-use change is not necessarily predictive of the future. To better envision the range of potential land-use futures, HFR has led a major participatory scenario project, called New England Landscape Futures (NELF), to examine the socio-ecological implications of alternative land-use trajectories. The scenarios were co-designed with more than 200 stakeholders from throughout the region (McBride et al. 2017, 2019). Through a multi-year structured process, NELF produced four divergent narrative scenarios that contrast with a recent trends scenario. The qualitative scenarios were translated to quantitative representations of land-use and land cover (LULC) change that, in turn, were used to simulate the future forest impacts in a physiologically based forest landscape model calibrated and validated using long-term data from HFR. The simulations yielded strongly divergent representations of the future New England landscape that differ in terms of the amount, type, intensity, and spatial pattern of change.

Today, HFR researchers are using these scenarios and simulations to understand better the range of human and natural impacts—past, present, and future—driving ecosystem processes and services, from C storage, to wildlife habitat, to stream flows. They are working closely with land managers and policymakers to forge a sustainable future for the landscape at local to national scales.

CONCLUSIONS

Cascading effects, which we have defined very broadly to include a wide array of unforeseen chains of events that result from a variety of actions or changes in a system, will continue to be an important challenge in analysis of future ecosystem structure, function, services, and trajectories. The case studies presented here support the idea that interactions among ecosystem attributes and the emergent properties of ecosystems lead to nonequilibrium trajectories of ecosystem change (Peters et al. 2011, Grimm et al. 2017,

Kominoski et al. 2018a). Cascading effects should therefore be viewed in a framework of alternate ecosystem development trajectories that produce a wide range of ecosystem structure, function, and services (Carpenter et al. 2006, Chapin et al. 2010).

For example, although climate change is having important direct effects on boreal forests, its effects on fire activity—severity, size, and return interval—are likely to have cascading effects on multiple aspects of these ecosystems that will be much more profound than the direct effects over the long term. In the temperate forests of the northeast, legacies of a long history of human management and disturbance strongly affect the composition of current forests, which creates a cascade of effects as the new tree species are decimated by the climate-facilitated invasion of an exotic pest. In Antarctica, declining sea ice creates a cascade of effects including declines in Adèlie and increases in Gentoo penguins, and changes in phytoplankton and then zooplankton populations. In the face of complex environmental change, it is important to recognize that cascading effects can catalyze multiple changes in ecosystems that can lead to markedly different outcomes.

In addition to expanding the range of cascading effects and possible outcomes of these effects, our stories also shed light on new types of trophic cascades in ecosystems. Changes in lady beetle populations due to exotic species invasion are likely to have important future effects on pest control in agricultural ecosystems, as well as the conservation of native species. Zebra mussels have been a well-studied invader, but long-term experiments and surveys have established links between climate, the presence of the mussels, and harmful algal blooms. Again, recognition that ecosystems are changing and that trophic cascades driven by invasive species can produce a wide range of ecosystem responses, is critical for understanding and managing these species and their impacts.

These stories highlight the need for long-term studies to sort out the complexities of different types of cascades. The diversity of sites within the LTER network facilitates the emergence of overarching concepts about trophic interactions as an important driver of ecosystem structure, function, services, and futures.

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