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SPECIAL FEATURE:
FORECASTING EARTH'S ECOSYSTEMS WITH LONG-TERM ECOLOGICAL RESEARCH

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

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Abstract. Ecosystems are changing in complex and unpredictable ways, and analysis of these changes is facilitated by coordinated, long-term research. Meeting diverse societal needs requires an understanding of what populations and communities will be dominant in 20, 50, and 100 yr. 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 or 100 yr. As the stories were prepared, themes emerged, and the stories were grouped into papers along five themes for this special issue: state change, connectivity, resilience, time lags, and cascading effects. This paper addresses the resilience theme and includes stories from the Baltimore (urban), Hubbard Brook (northern hardwood forest), Andrews (temperate rain forest), Moorea (coral reef), Cedar Creek (grassland), and North Temperate Lakes (lakes) sites. The concept of resilience (the capacity of a system to maintain structure and processes in the face of disturbance) is an old topic that has seen a resurgence of interest as the nature and extent of global environmental change have intensified. The stories we present here show the power of long-term manipulation experiments (Cedar Creek), the value of long-term monitoring of forests in both natural (Andrews, Hubbard Brook) and urban settings (Baltimore), and insights that can be gained from modeling and/or experimental approaches paired with long-term observations (North Temperate Lakes, Moorea). Three main conclusions emerge from the analysis: (1) Resilience research has matured

over the past 40 yr of the LTER program; (2) there are many examples of high resilience among the ecosystems in the LTER network; (3) there are also many warning signs of declining resilience of the ecosystems we study. These stories highlight the need for long-term studies to address this complex topic and show how the diversity of sites within the LTER network facilitates the emergence of overarching concepts about this important driver of ecosystem structure, function, services, and futures.

Key words: coral reefs; experimental manipulations; grasslands; northern hardwood forest; rain forest; Special Feature: Forecasting Earth's Ecosystems with Long-term Ecological Research; temperature; urban forest.

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Introduction

Ecosystems across the world are changing in complex and unpredictable ways (Grimm et al. 2013), and the challenge of studying 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, agricultural intensification, and species movement (Steffen et al. 2015). The needs of diverse components of society to know how ecosystems are changing present a fundamental challenge to ecological science. What populations and communities will be dominant in 20, 50, and 100 yr? How will these communities interact with changing environmental conditions to assemble into ecosystem units? What functions and services will these ecosystems support?

The capacity of ecological science to provide societally relevant information on ecosystem change is greatly facilitated by the presence of research and monitoring networks, and coordinated, long-term studies and networks of sites date back to the 1960s (Golley 1996). One of the longest running networks, the U.S. National Science Foundation (NSF) funded Long-Term Ecological Research (LTER) network, is a group of long-term site-based research projects aimed at understanding ecological processes in 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). LTER sites were chosen in a competitive process based on fundamental ecological questions requiring the ideas, investigators, and sites to study long-term phenomena using a blend of experiments, monitoring, modeling, and comparative studies, as opposed to being selected to cover the range of major ecosystem types or natural biomes, or to collect a synchronized set of monitoring data. LTER sites do carry out integrative, cross-site, network-wide research, and data collection at each site is organized around five core research areas: primary production, population studies, movement of organic matter, movement of inorganic matter, and disturbance patterns.

The focus on five core research areas across diverse systems has created opportunities for synthetic analyses that offer unique insight into how environmental changes affect communities and ecosystems. For this special issue of *Ecosphere,* we provide an assessment of how populations, communities, and ecosystems in the network are changing across five general themes: state change, connectivity, resilience, time lags, and cascading effects. The topic of this paper is "resilience" and we include stories from the Baltimore (urban), Hubbard Brook (northern hardwood forest), Andrews (temperate rain forest), Moorea (coral reef), Cedar Creek (grassland), and North Temperate Lakes (lakes) sites. The concept of resilience (the capacity of an ecosystem to maintain structure and processes in the face of disturbance) (Peterson et al. 1998) is an old topic (Holling 1973) that has seen a resurgence of interest as the nature and extent of global environmental change have intensified (Ogden et al. 2013, Pace et al. 2015). Understanding resilience is essential

for developing a capacity for predicting future structure, function, and services of ecosystems. The stories we present here show the power of long-term manipulation experiments (Cedar Creek), the value of long-term monitoring of forests in both natural (Andrews, Hubbard Brook) and urban settings (Baltimore), and insights that can be gained from modeling and/or experimental approaches paired with long-term observations (North Temperate Lakes, Moorea). These stories illustrate that resilience research has matured over the past 40 yr of the LTER program. It has moved from relatively simple assessments of responses to single major disturbance events, for example, a big fire, clear-cutting, a hurricane, to evaluation of how interactions between multiple disturbances affect diverse aspects of ecosystem structure, function, and services. Our analysis also shows that while there are many examples of high resilience among the ecosystems in the LTER network, there are also many warning signs of declining resilience within these ecosystems. The expanding scope of thinking about resilience within the LTER network highlights the need for long-term studies to address this complex topic. It shows how the diversity of sites within the LTER network facilitates the emergence of overarching concepts about this important driver of ecosystem structure, function, services, and futures.

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

1. Baltimore Urban LTER: Resilience in the Face of Environmental and Species Change in Urban Forests: Laura Templeton, Peter M. Groffman, Maile C. Neel and Joe H. Sullivan
2. Cedar Creek (Grassland) LTER: Observing the Unobservable—Long-term Experiments Provide Early Insights into Future Climate Change: Jane Cowles, Eric W. Seabloom, Sarah Hobbie and Clare E. Kazanski
3. Hubbard Brook (Forest) LTER: Anticipating the Impact of Climate Change on the Forest Community in the Year 2070: John J. Battles, Natalie L. Cleavitt, Natalie S. van Doorn and Timothy J. Fahey
4. What is the Future for the Coral Reefs of Moorea LTER? Peter J. Edmunds, Robert C. Carpenter, Sally J. Holbrook, and Russell J. Schmitt
5. Eroding Resilience of Northern Wisconsin Cool-Water Fisheries: Climate and Habitat: Stephen R. Carpenter, Gretchen J.A. Hansen, Jake M. Vander Zanden and Emily H. Stanley
6. Responding to Change: Lessons Learned from an Ancient Forest at the Andrews LTER: Michael Paul Nelson and Alan J. Tepley (with input from Ivan Arismendi, Matt Betts, Bryan Black, Stan Gregory, Mark Harmon, Sherri Johnson, Julia Jones, Mark Schulze, Tom Spies, Fred Swanson, and Christoph Thomas—collectively, this represents >250 yr of experience at the Andrews Forest).

Baltimore Urban LTER: Resilience in the Face of Environmental and Species Change in Urban Forests

The novel disturbance regimes of urban ecosystems provide unique opportunities for addressing basic questions about resilience. Here, long-term data on relict natural forests studied as part of the Baltimore urban LTER (BES) site reveal how interactions between changes in climate, herbivory, and invasive species influence resilience in urban forests, with relevance to forests across the Eastern United States.

Human-induced disturbances have dramatically shaped forest communities surrounding the Chesapeake Bay on the eastern coast of the United States since the arrival of European colonizers (Sprague et al. 2006, Brush 2009). More recently, city development has produced a patchy distribution of forests juxtaposed with larger urban ecosystems (Pickett et al. 2008). Forest patches embedded in the urban matrix are exposed to higher air temperatures, increased nitrogen deposition, altered hydrology, and higher atmospheric carbon dioxide levels (Oke 1982, Brazel et al. 2000, Savva et al. 2010). The assembly of plant communities within urban forests is also influenced by human manipulation of the landscape, including choice in species planted (Swan et al. 2011). Fragmentation and isolation alter seed source availability, dispersal, and seedling establishment in urban forests (Williams et al. 2009, Trentanovi et al. 2013). Such anthropogenic factors have caused divergences

between the plant community structures of urban and rural forests.

In 1998, the Baltimore Ecosystem Study (BES) established eight permanent forest plots with the intention of investigating the long-term impacts of urbanization on natural ecosystems (Groffman et al. 2006). Half the plots were located in urban forest patches and half were in rural forests. In 2015, we revisited these plots to investigate ecological change (Templeton et al. 2019).

Few differences were found in the tree layer between 1998 and 2015, with *Quercus* spp. (oaks) and *Liriodendron tulipifera*. (tulip poplar) the most abundant tree species. In addition to presenting a structural barrier for deer browsing, mature trees are generally long-lived and more resilient to disturbance than understory species. In the sapling layer, however, mortality exceeded recruitment in both the urban and rural plots (Fig. 1a, b). More than 50% of all species present in each urban plot and 33% of all species present in each rural plot experienced a greater than 50% loss of individuals (Fig. 1a, b). In the rural plots, *Nyssa sylvatica*, *Carya glabra*, and *C. tomentosa* were the most retained sapling species, while *Acer rubrum, N. sylvatica*, and *Fagus grandifolia* were the most retained sapling species in the urban plots (Fig. 1a). *N. sylvatica* and *A. rubrum* have had particular success in expanding their ranges and abundances in the eastern United States because they are adapted to understory environments, are habitat generalists, and are not preferred by deer (Abrams 1990, Nowacki and Abrams 2008, McGarvey et al. 2013, Desprez et al. 2014).

Canopy cover remained relatively unchanged (at ~85%) in all the plots between 1998 and 2015 (data not shown). When canopy disturbance is low, the opportunity for the many understory species that rely on periodic breaks in the canopy to survive is reduced (Runkle 1982, Brokaw 1987). Limited canopy openness coincided with the absence of *Quercus* spp. and

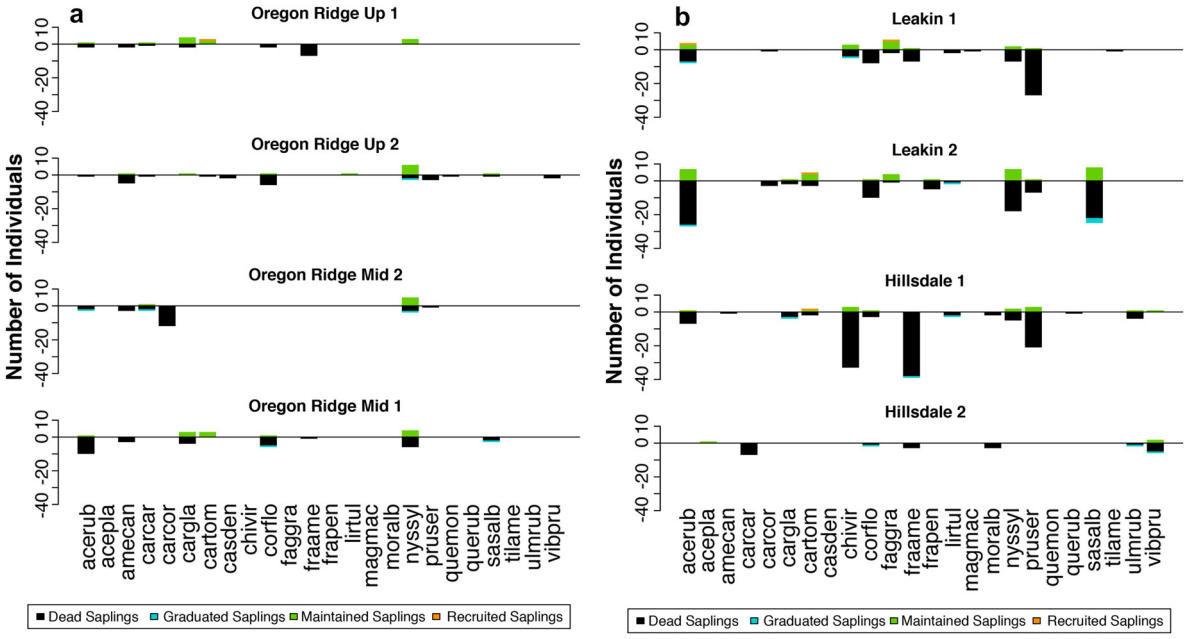

Fig. 1. Diagram illustrating the distribution of death, graduation, retention, and recruitment of saplings within rural (a) and urban (b) forest plots in the Baltimore metropolitan area. Individuals that died between the 1998 and 2015 surveys were considered losses. Individuals recruited since 1998 were considered gains. Species that were counted as saplings in both the 1998 and 2015 surveys were considered retained. Each bar represents the gain or loss of individuals of a species. Bars are organized vertically with loss below the horizontal axis and presence above. Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. (From Templeton et al. 2019.)

L. tulipifera individuals in the sapling layer (Fig. 1a, b). *Quercus* spp. and *L. tulipifera* are considered shade-intolerant (Burns and Honkala 1990), suggesting that a relatively closed-canopy environment may have contributed to their decline. However, Cowell et al. (2010) reported that canopy gaps were only marginally associated with oak survival, implying that light availability alone was not enough to maintain oak dominance. If canopy cover were the primary driver of understory plant composition in the plots, we would expect to see higher relative abundances of shade-tolerant species. Instead, we observed reductions of nearly every species except those that are structurally large or unpalatable to deer. Regardless of the cause, the absence of *Quercus* spp. and *L. tulipifera* from the sapling layer indicates that Baltimore-area forests may look quite different in the next century.

Another finding highlighting the importance of deer herbivory was a marked decline in shrub cover from 1998 to 2015 in the rural plots, a time period that saw no significant change in shrub cover in the urban plots (Fig. 2). Notably, the rural plots experienced huge reductions of *Viburnum acerifolium*, a species preferentially browsed by deer (Kribel et al. 2011). The resilience of shrub cover in the urban plots is explained by the proliferation of *Lindera benzoin* (Fig. 3b, d), a species avoided by deer due to the biochemical defenses of its leaves and twigs (Rawinski 2008). Stromayer and Warren (1997) proposed that deer browsing shifts understory vegetation to an alternative stable state that is resistant to the regeneration of previously reported dominant

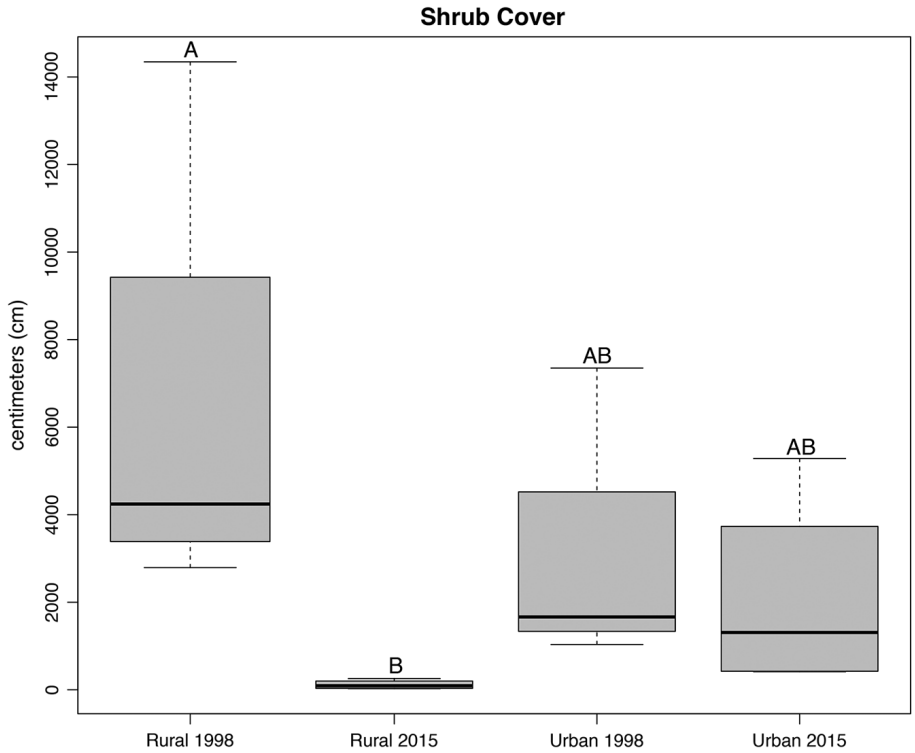

Fig. 2. Box and whisker diagram of shrub cover in urban and rural forest plots in the Baltimore metropolitan area in 1998 and 2015. The upper and lower limits of each box indicate the 75th and 25th percentiles, respectively. The bar dissecting each box is the median value of that group (n = 4). The upper and lower limits of the whiskers indicate the maximum and minimum values for that group. The same letters above each box and whisker plot represent no difference whereas distinct letters represent a statistically significant difference as determined by Welch-ANOVA with the Games-Howell post hoc test ($P < 0.05$). $F = 11.855$, $P = 0.005$. (Data from Templeton et al. 2019.)

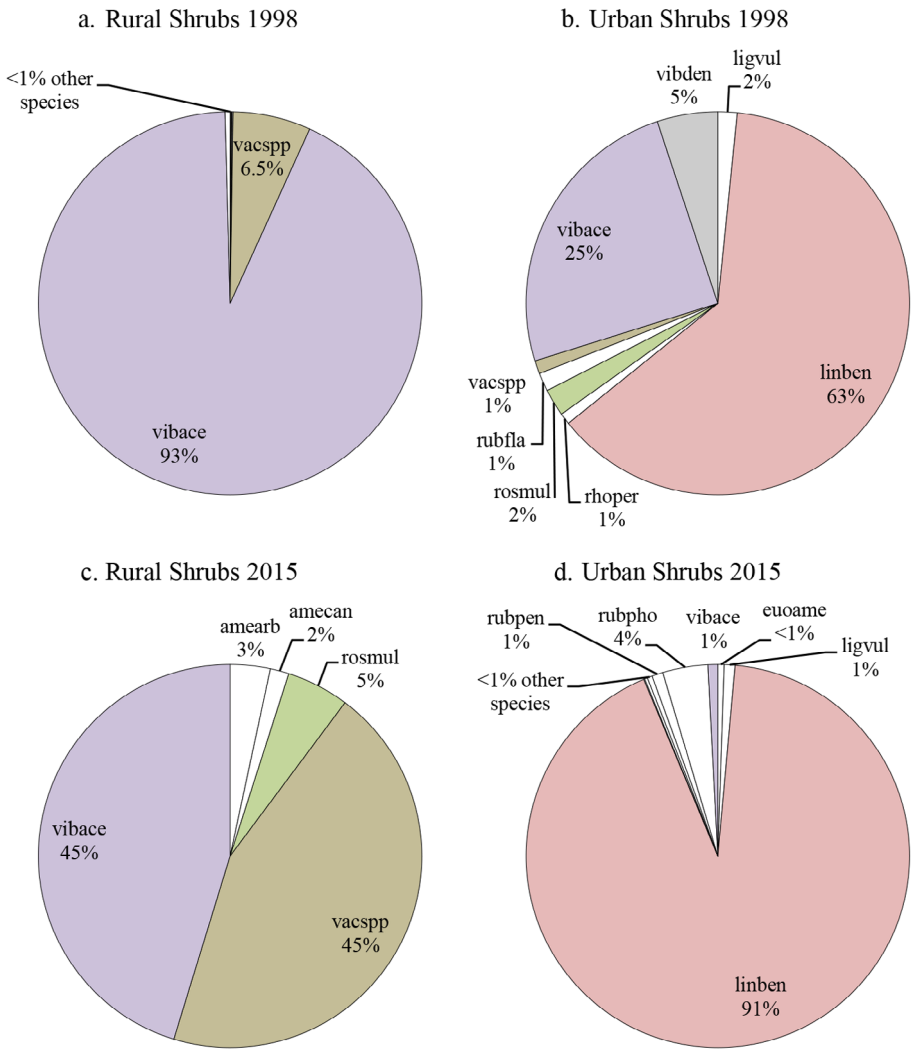

Fig. 3. Relative proportion of shrub species in urban and rural forest plots in the Baltimore metropolitan area in 1998 and 2015. Percentages were calculated as the proportion of a species measured in cm of cover. Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. (Data from Templeton et al. 2019.)

species. As such, overbrowsing results in forest stands devoid of understory plants and overrepresented by mature trees (Tilghman 1989, Stromayer and Warren 1997, Côté et al. 2004, McGarvey et al. 2013).

Urban forests often experience naturalization of escaped exotic species (Kowarik 2003, McDonnell and Hahs 2008), which commonly increases alpha diversity (species richness) (Schwartz et al. 2006, McKinney 2008, Socolar et al. 2016). Indeed, alpha diversity was comparatively higher in the urban plots in both survey years (Table 1). As non-native species were a minimal proportion of the total plant community sampled (data not shown), higher urban alpha diversities could alternatively be explained by a widespread loss of species from the rural plots rather than by an increase of new species in the urban plots. Loss of species in the rural plots was likely due primarily to deer browsing and canopy closure concomitant with limited exposure to novel species. Interestingly, alpha diversity in the urban

Table 1. Diversity metrics for all species in urban and rural forest plots in the Baltimore metropolitan area.

Plot group	Total no. species (γ)	Alpha diversity (α)	Beta diversity (β)	No. species lost since 1998	No. species gained since 1998	Turnover since 1998 ($\beta\tau$)
Urban 1998	73	41 ± 3.08^{A}	0.42 ± 0.06^{A}			
Rural 1998	46	30.75 ± 0.63^{B}	0.57 ± 0.03^{B}			
Urban 2015	69	39.5 ± 2.87^{A}	0.42 ± 0.03^{A}	20	16	0.44
Rural 2015	40	21.75 ± 2.39^{B}	0.43 ± 0.03^{A}	11	5	0.26

Notes: Total species (γ) is the sum total of all species within a group (n = 4). Alpha diversity (α) is the mean species richness per group. Beta diversity (β) is the average pairwise comparison of the inverse of the Jaccard similarity index within each group. Species lost and species gained were summed per group. Turnover since 1998 ($\beta\tau$) is the absolute value of species lost and gained divided by the product of alpha and two (McCune & Grace 2002). The same letters for values in the columns of alpha and beta diversity represent no difference whereas distinct letters represent a statistically significant difference as determined by ANOVA with Tukey's post hoc test ($P < 0.05$). Alpha diversity, $P = 0.0003$ ($F = 15.15$) and beta diversity, $P = 0.013$, ($F = 4.652$). Adapted from Templeton et al. (2019).

plots did not decline between 1998 and 2015 despite having comparable canopy cover to the rural plots. Thus, we conclude that the high alpha diversity in the urban plots is likely due to a combination of deer herbivory in the rural plots and species introductions in the urban plots.

Beta diversity (community dissimilarity) significantly declined in the rural plots (Table 1). These findings suggest that a species lost in the rural plots was unique to an individual plot, whereas a species gained or retained was similar across all rural plots. Although many species were lost in the urban plots, species introduction was high (Table 1). We argue that turnover (species replacement) maintained alpha and beta diversities in the urban plots. In other words, species were unanimously lost or gained in the urban plots resulting in compositional change, without changes to alpha or beta diversity. Our findings may provide evidence that urban forests are more dynamic and therefore more resilient compared to rural forests.

It has been proposed that small isolated forest fragments may have particularly high species turnover due to high rates of species loss coupled with influxes of species migrating from forest edges (Laurance 2002). We suggest that a similar, highly dynamic pattern occurred in the urban plots. Other studies have also shown that moderate levels of urbanization can facilitate biodiversity loss as well as gain (Schwartz et al. 2006, McKinney 2008, Socolar et al. 2016). The ability of an ecosystem to be structurally resilient due to high turnover suggests a functional role for diversity (Folke et al. 2004).

Our long-term data showed that species turnover in the urban plots was nearly twice that of the rural plots. Turnover has important implications for the resilience of ecosystems (Allen et al. 2005). When species are lost and turnover is low, plant communities may become homogenized both locally and regionally (Groffman et al. 2014, La Sorte et al. 2014). We suggest that higher exposure to novel species, as is common in urban areas, may allow urban forests to maintain diversity. Apart from saplings, plant biomass was also more stable in the urban plots. These results suggest that high rates of species turnover may help urban forests adapt to environmental stress.

Cedar Creek (Grassland) LTER: Observing the Unobservable—Long-Term Experiments Provide Early Insights into Future Climate Change

At the Cedar Creek Ecosystem Science Reserve (CDR) LTER site in Minnesota, long-term experiments and theory have complemented long-term observational data to address fundamental questions about resilience. The CDR site lies at the intersection of three of the largest biomes in North America—tallgrass prairie, eastern deciduous forest, and northern coniferous forest—where human-driven changes in fire regime, herbivory, nutrient supply rates, and climate have and will continue to affect plant communities and ecosystem processes (Frelich and Reich 2010).

Understanding how concurrent changes in climate and other local and global factors impact ecosystem processes is vital to predict future ecosystem resiliency, functioning, and services. Here, we describe key ecological insights that have emerged from use of long-term experiments at CDR that inform how ecosystem structure and

function may respond to future global change. Achieving such understanding is facilitated by long-term observations, as no experiment or model can perfectly recreate natural systems. However, there are limitations to what we can learn from observations alone. An observational approach relies on analyzing response to natural variability and requires waiting for rare events to occur (e.g., multiple droughts) to inform predictions about a future that is likely to be characterized by increased occurrence of extreme events. In addition, it is challenging to isolate the effects of correlated factors, such as temperature, carbon dioxide (CO_2,) and nutrient deposition using observational data. Furthermore, historical data are just that ... historical. If future climate is expected to be novel in ways we have yet to observe, the historical record can only tell us so much. Long-term experiments and theory can complement long-term observational data to address these limitations, by creating conditions, such as a string of droughts or hot summers, which would be very unlikely in historical data. Experiments also can provide unique mechanistic insight by creating novel combinations of global change factors that are highly correlated in historical data (e.g., precipitation, CO_2, and temperature).

Since the early 1980s, the Cedar Creek LTER program has conducted experimental nutrient addition and cessation experiments contemporaneous with an increase in anthropogenic nitrogen deposition in the region. This work has revealed how nitrogen addition reduces plant species richness (Clark and Tilman 2008) and has shown that communities do not necessarily recover after nitrogen addition stops (Isbell et al. 2013). A major drought in 1988 offered an opportunity to examine how climate, nutrients, and plant species diversity have coupled effects on ecosystem dynamics and resiliency. For instance, the experimental addition of nutrients caused local plant species extinctions, and the plots that had lost the most species were the most severely affected by drought (Tilman and Downing 1994), suggesting that communities that are more diverse might be more resilient to extreme droughts. This initial result catalyzed the first large-scale biodiversity experiment in the world (BioDiv), which confirmed that productivity in diverse communities was indeed more resilient in the face of normal climate fluctuations (Tilman et al. 2006). Twenty years later, the importance of diversity in buffering ecosystems from climate fluctuations or other perturbations has been demonstrated in many other experiments and natural systems around the world (Hautier et al. 2014, 2015, Isbell et al. 2015).

As a variety of anthropogenic changes are occurring simultaneously, identifying the singular effects of one global change factor is nearly impossible; the planetary climate change "experiment" was not set up with the scientific method in mind. Experimental manipulations at Cedar Creek, however, have allowed for parsing the impacts of co-occurring factors, and their interactions, on plant communities and processes. In 1997, researchers at Cedar Creek established one of the first experiments to disarticulate the correlated effects of biodiversity loss and CO_2 and nitrogen enrichment arising from human activities (BioCON). These experiments demonstrated the interactive impacts of CO_2 and nitrogen on biodiversity loss. Similar to the long-term nitrogen addition plots mentioned above, nitrogen led to a reduction of species richness by 16% at ambient CO_2, yet this was cut in half in the elevated CO_2 plots (Reich 2009).

The long-term nitrogen addition, plant diversity, and global change experiments at Cedar Creek make it possible to isolate the impacts of biodiversity from other co-occurring factors and to understand how the effects of global changes can compound or change over time (e.g., Reich et al. 2012). These experiments highlight that short-term studies may not always accurately predict long-term outcomes. However, these experiments still rely on natural climate variation to assess how biodiversity affects stability in the face of climate change. Ironically, there has not been a severe drought during the more than 20 yr since BioDiv and similar experiments at Cedar Creek were established (Fig. 4a), and this has limited the potential to resolve the ways in which plant diversity can buffer against major climate perturbations. Fortunately, experimental climate manipulations at a small scale create the opportunity to study the potential impacts of predicted climate change (Figs. 4b, 5).

More recently, direct manipulations of temperature and precipitation have been layered onto BioCON to assess impacts of additional interacting global changes (TeRaCON). TeRaCON

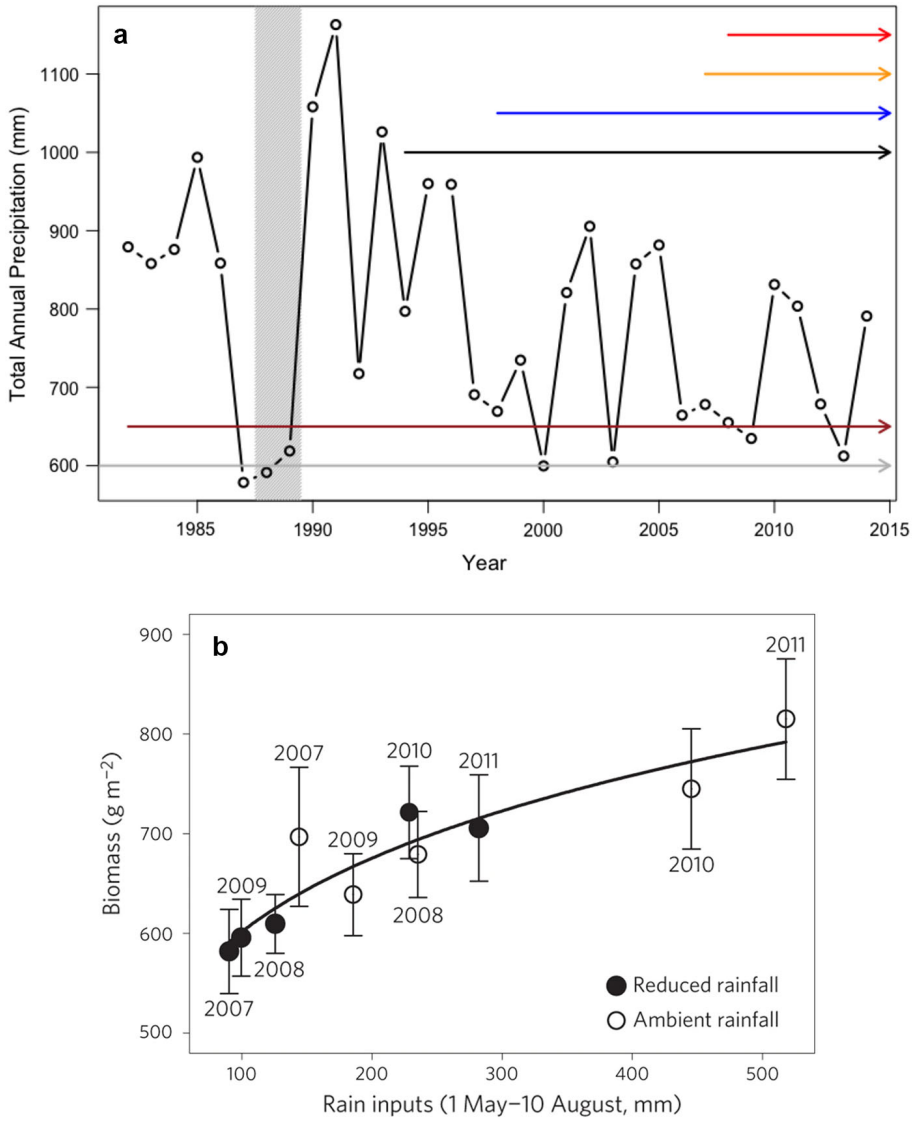

Fig. 4. (a) Annual precipitation patterns at the Cedar Creek LTER site in Minnesota. Our biodiversity experiments (black and blue arrows), designed originally to corroborate findings that biodiversity provides resilience in the face of drought (seen in nitrogen addition experiment, brown arrow), have yet to experience a major drought despite having run 23 and 20 ys, respectively. As such, we can experimentally manipulate drought and temperature (orange and red arrows) to create rare but potential environmental conditions to strengthen and confirm observational findings. (b) The effect of experimental drought manipulations on biomass production fall in line with natural variation yet can create conditions unobserved historically (Fig. 4b from Reich et al. 2014.)

manipulates temperature, rainfall, CO_2, and nitrogen and has yielded multiple insights into how belowground resources constrain plant response to elevated CO_2. For instance, when nitrogen and water inputs were both at their lowest levels (drought treatment, no nitrogen addition), the otherwise observed positive impact of CO_2 on plant productivity was absent (Reich et al. 2014). More generally, low levels of any two resources constrained the response to the third.

An important and often unexamined factor in the study of climate change is the role plant

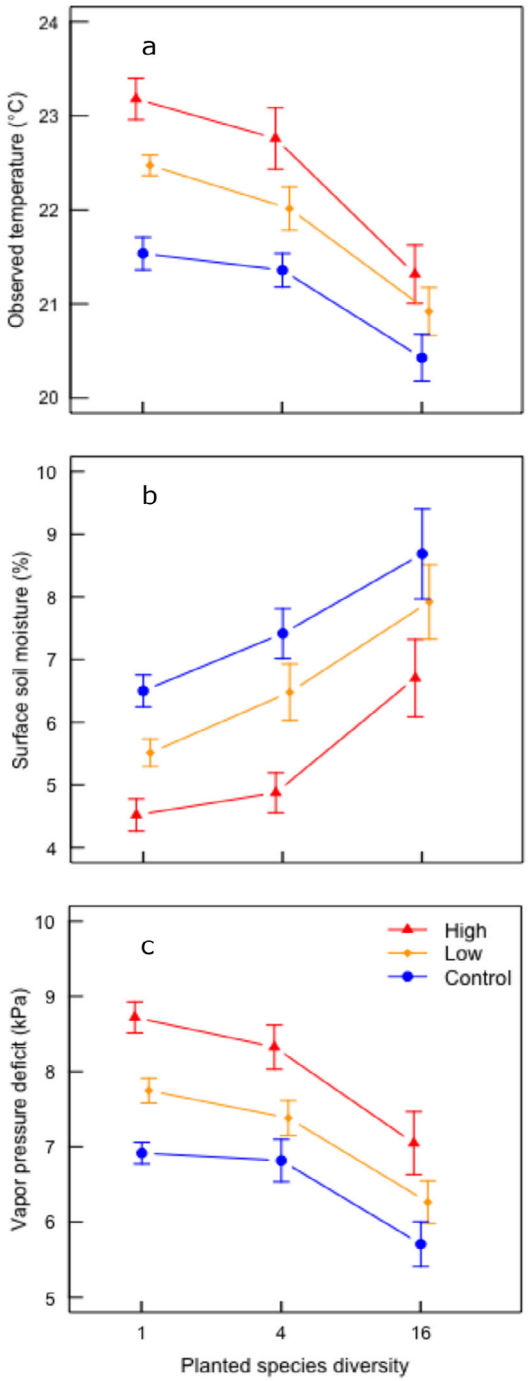

Fig. 5. Biodiversity (planted species richness) at the Cedar Creek LTER site effectively counteracts the warming and drying effects of experimental warming via microclimate amelioration and thus should not be ignored in studying multi-faceted global changes. (Figure adapted from Cowles et al. 2016.)

communities can play in ameliorating the negative effects of harsh climatic conditions by affecting their microclimates. A factorial biodiversity and warming (BAC) experiment within the larger BioDiv experiment revealed that the combination of warming and higher plant species richness, and therefore greater biomass, effectively creates conditions similar to those in unwarmed, low diversity plots (Fig. 5, Cowles et al. 2016). Similarly, in the neighboring BioCON experiment (non-warmed), high diversity plots were 2 °C cooler than monocultures (Wright et al. 2014). As such, the diversity of a community not only is impacted by global climate change, but it can also (at least partially) mitigate its effects. To come full circle, we have now added a drought treatment to these plots, crossed with biodiversity and warming, enabling us to return to the original ideas about how biodiversity influences response to drought that emerged from the nitrogen addition experiments.

In sum, long-term experiments such as those at Cedar Creek are an important complement to observational studies in developing an understanding of community and ecosystem resilience to climate change. The experiments on interacting elements of global change at Cedar Creek have highlighted the moderating effect of biodiversity on resilience in the face of nutrient additions, warming, and drought. These insights arise both from experiments that manipulate climate directly (e.g., warming and drought treatments) or that manipulate other global change factors that are occurring concurrently with climate (e.g., nutrient addition and biodiversity loss) to test how these factors interact with natural climate variability. Long-term ecological research programs that combine observational evidence, experimental results, and theory are particularly powerful in developing an understanding of how ecosystems respond to the many ways in which humans are impacting the globe.

Hubbard Brook (Forest) LTER: Anticipating the Impact of Climate Change on the Forest Community in the Year 2070

Beginning in the 1960s, field experiments at the Hubbard Brook Experimental Forest (HBR)

LTER site have tested fundamental ideas about ecosystem recovery from disturbance. These results have informed understanding of the dimensions of resilience in northeastern forests. Here, a 53-yr record of forest composition and structure is used to show the slow degradation of resilience caused by the interactions of a warming climate, the legacy of acid rain, and the progression of an exotic forest pathogen complex.

A defining characteristic of the forest at HBR in particular, and the northern hardwood forest in general, is its capacity to resist minor disturbances and to recover from major disturbances. An early insight from the first decade of ecosystem research at HBR noted the rapid re-establishment of the vegetation following a catastrophic event (i.e., deforestation, Likens et al. 1978). Further work outlined an orderly pattern whereby the forest returns to dominance by shade-tolerant, mature forest tree species and total ecosystem biomass is maintained (Bormann and Likens 1979). In other words, the forests at HBR have been resilient ecosystems.

This contemporary observation of resilience at HBR reflects the historic, regional pattern. Forests returned to New England in the last century following widespread intensive logging and after 19th-century farms were abandoned as agriculture migrated west. Today, trees dominate 80% of the New England landscape. Northern hardwood forests, like those studied at HBR (Fig. 6), are the most common forest type in the region accounting for more than 4.4 million hectares (36% of all New England forests, FIA 2017). A key question regarding the future of the northern hardwood forest in New England is: Do the lessons learned from past research hold given unprecedented changes in the environment and in biota?

Results from the HBR record challenge an expectation of resilience in the face of the cumulative effects of multiple anthropogenic perturbations over the last 50 yr, which have had negative impacts on tree populations. For example, since the first inventory of the reference watershed (Watershed 6) in 1965 (Fig. 7), mean annual air temperature rose approximately 1°C (Hamburg et al. 2013), acidic deposition peaked and then decreased (Driscoll et al. 2001), and a beech bark disease complex progressed through the three phases of expansion, aftermath, and accommodation (sensu Huston 1994). The effects on tree populations that dominate the northern hardwood forest have been profound. The decrease in soil fertility due to acid leaching of base cations has clearly limited the growth rate and reproduction of sugar maple trees (*Acer saccharum),* especially on inherently low fertility soils (Battles et al. 2014, Cleavitt et al. 2017). At the same time, beech bark disease has transformed the population structure of American beech (*Fagus grandifolia*). The disease has gradually increased the mortality of the largest trees while releasing saplings in the understory. The result is a substantially smaller and younger population of trees. This transformation is also apparent in the shift of productivity over time—smaller beech trees now account for proportionally more of the biomass accumulation (Fig. 8).

Together these changes in the demography of the dominant tree species have contributed to a marked decline in the productivity of the HBR forest, but the degree is less than would be expected, given the stressors on these two dominant species. Understanding the reasons why remains a focus of ongoing research but the explanation includes the following: (1) the historically strong competitive interaction between sugar maple and beech, and (2) the fact that at HBR, sugar maple and beech are in the heart of their range. We predict that these same mitigating forces will constrain the consequences of climate change over the next 50 yr.

Recent efforts to understand the impact of global warming on forest communities have emphasized the need to consider the joint response of constituent tree populations to abiotic and biotic changes (Clark et al. 2014, Rollinson et al. 2016). One argument is that shifts in the competitive hierarchy can offset reductions in vigor caused by higher temperatures, air pollution, or exotic pests. At HBR, coincident declines of sugar maple and beech have largely canceled each other and retained the fundamental dynamics of the northern hardwood forest where these two mature forest species with different life histories compete for dominance. This competitive balance lends stability to the ecosystem. It is important to note that population responses to the perturbation while negative have not been catastrophic. For example, the reduction of sugar

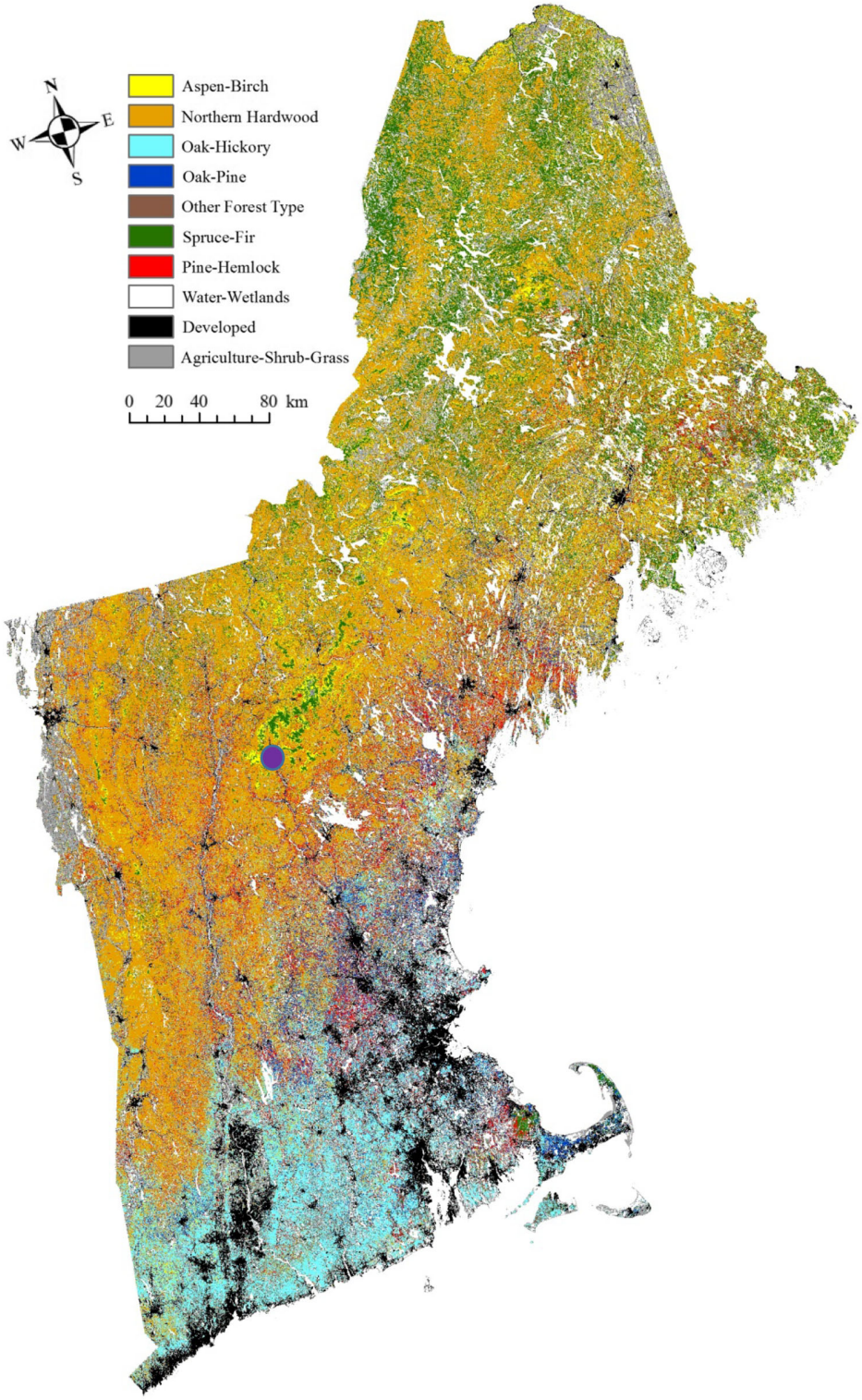

Fig. 6. Imputed forest composition map for New England (Duveneck et al. 2017). Purple dot denotes the location of the Hubbard Brook Experimental Forest.

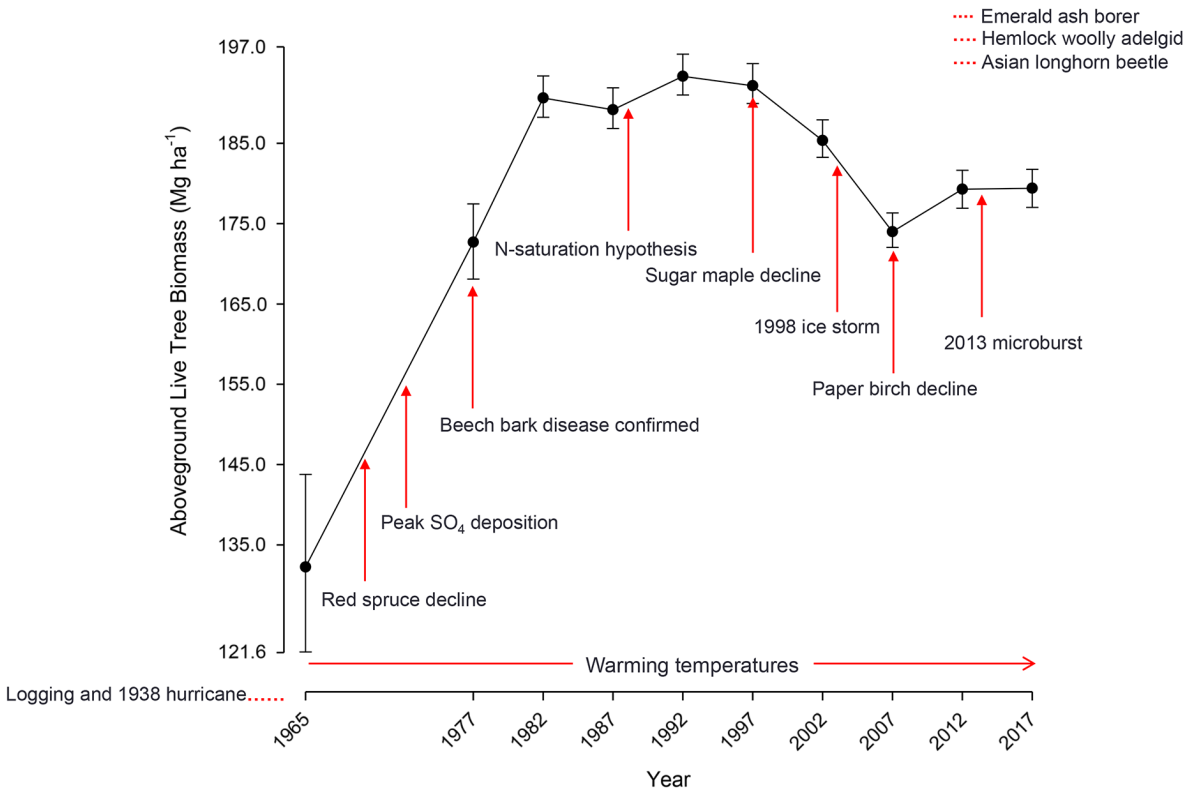

Fig. 7. Biomass accumulation in the reference watershed at the Hubbard Brook Experimental Forest. Historical events, perturbations, and likely future changes are noted along the timeline.

maple growth has not translated into sustained increases in canopy tree mortality at large scales across the entire 30 km^2 Hubbard Brook Valley (van Doorn et al. 2011). However, our perception of forest resilience also depends upon the spatial scale of observation. At finer spatial scales, especially on more infertile local sites, maple decline has been more severe. In the long-term reference watershed (13.2 ha), the mortality of adult sugar maple has outpaced recruitment (Juice et al. 2006, Battles et al. 2014) suggesting that the future composition and structure of the forest in the watershed will fundamentally change. Such scale dependency of resilience reflects the spatial heterogeneity of the biophysical environment.

The projected changes in climate over the next 50 yr are unlikely to have immediate impacts on sugar maple or beech populations. At HBR, both species are near their optimal climatic regimes (Canham and Murphy 2016*a*, 2017). The degree of the expected changes, namely increases in mean annual air temperature on the order of 0.2°C/decade and in annual precipitation of 2%/decade (Hayhoe et al. 2007, Groffman et al. 2012), is predicted to have a negligible impact on tree survival and growth. On the other hand, the warming climate may have already begun to shift tree recruitment. The sentinel monitoring program at HBR has documented the establishment of climate migrants, like red oak (*Quercus rubra*) and white pine (*Pinus strobus*), in the lower elevations of the experimental forest. Moreover, the warming climate may also be contributing to the observed but gradual shift in dominance between sugar maple and beech (Fig. 9). Considering the direction and magnitude of warming, the effects are likely to be more negative for sugar maple regeneration than beech (Canham and Murphy 2016*b*).

In 2070, the northern hardwood forest at Hubbard Brook will likely still resemble the community first measured in 1965. In terms of species

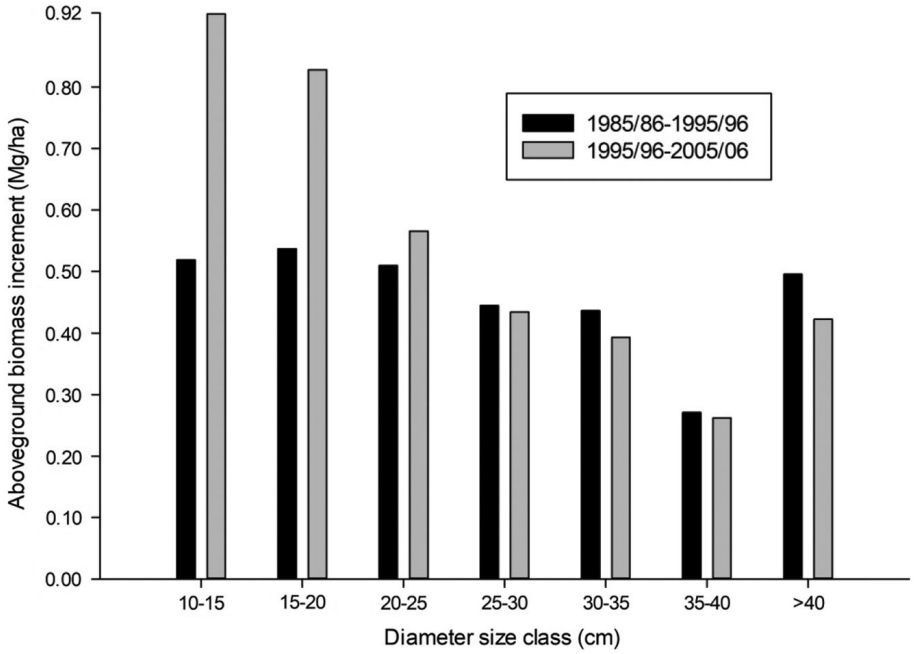

Fig. 8. Trends in aboveground biomass accumulation by size class for American beech in the Hubbard Brook Valley.

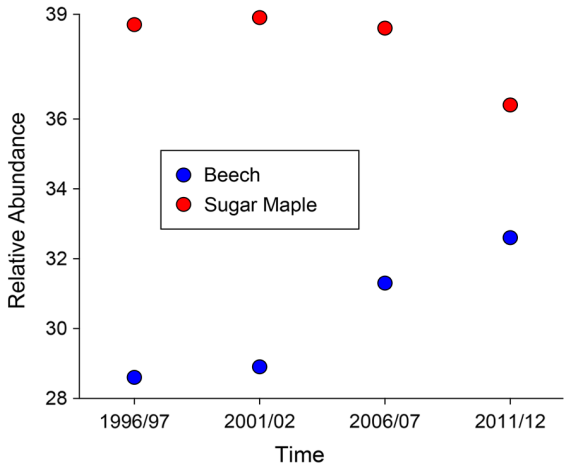

Fig. 9. Recent changes in the relative abundance of beech and sugar maple trees in the reference watershed at the Hubbard Brook Experimental Forest. Relative abundance calculated from the density of stems ≥10 cm in diameter at breast height (measured at 1.37 m above ground).

composition and structure, resilience will prevail. Sugar maple and beech will dominate a closed-canopy forest where canopy turnover is governed by fine-scale disturbances. However, closer inspection of productivity trends, tree demography, and understory composition suggests impending changes that may overwhelm the resilience of the northern hardwood forest and transform the ecosystem toward the end of the 21st century.

What is the Future for the Coral Reefs of Moorea LTER?

Long-term observations at the Moorea Coral Reef (MCR) LTER site show remarkable resilience to major disturbance events that occurred about a decade ago and reveal the complex biological interactions that underlie that resilience. However, it is unclear whether (or how long) the capacity for high coral community resilience will continue in a future characterized by increasing seawater temperatures and declining seawater pH.

The MCR LTER program was established in 2004 and seeks to understand patterns and drivers of community and ecosystem dynamics. Time-series data are collected from three coral habitats—fringing reefs (closest to land), back reefs (behind the reef crest), and fore reef on the outer slope—on the three shores of this triangular island (Fig. 10). With a perimeter of 50 km, Moorea is small enough to study as a discrete entity, but large enough to be ecologically relevant to coral reefs throughout the region. Wide-scale coral bleaching in 2019 substantially depleted coral cover on the fore reefs of Moorea, but despite mortality of up to 50% of the coral, the fore reefs of Moorea still have a greater cover of live corals than many reefs throughout the world. The MCR LTER site has been testing key hypotheses addressing the mechanisms of coral resilience, and it can leverage nearly two decades of time-series data to generate hypotheses and inform the conclusions drawn from long-term experiments.

The negative effects of human development can be seen in every biome, yet not all

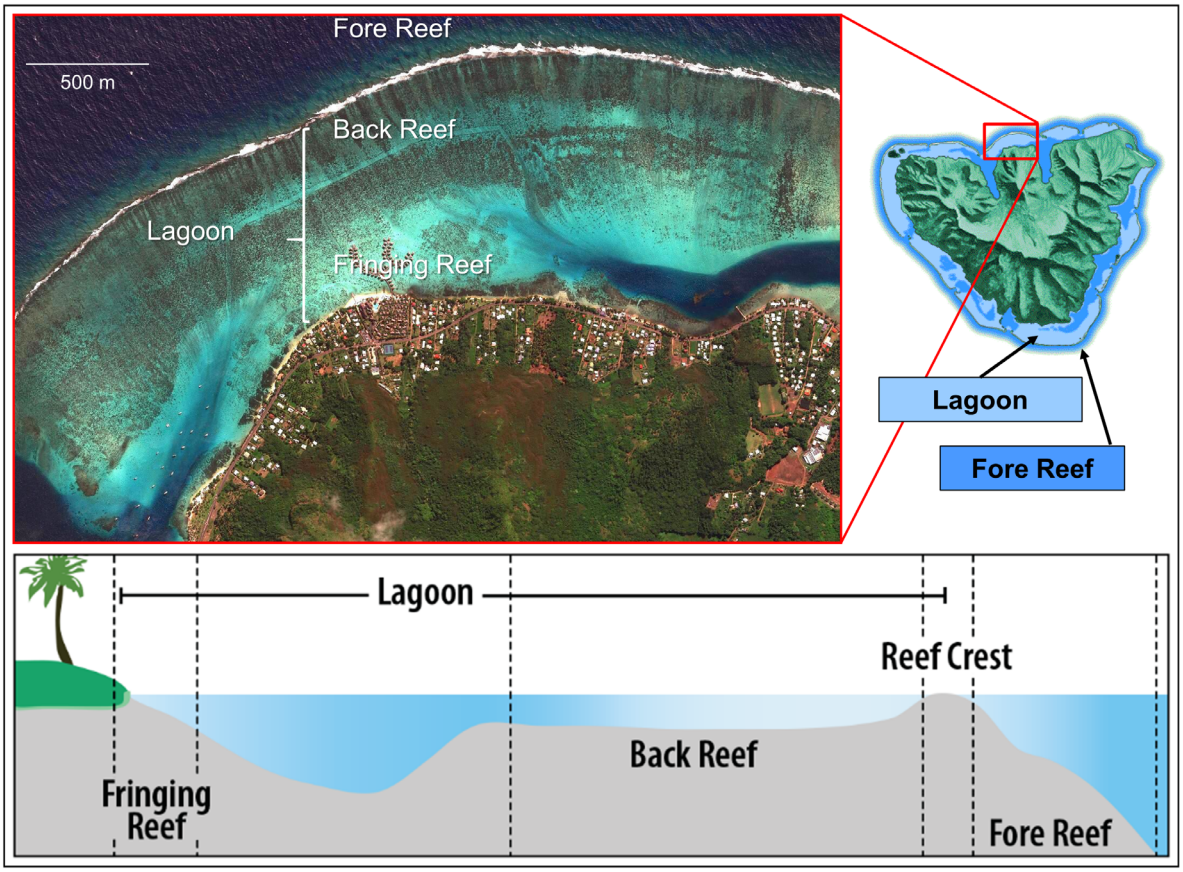

Fig. 10. The Moorea Coral Reef LTER site encompasses the coral habitats surrounding Moorea, French Polynesia including the fringing reef closest to shore, the back reef in the lagoon behind the reef crest, and the outer fore reef. The lower inset shows a cross section of the reef topography.

ecosystems are equally affected. Tropical coral reefs are among the most threatened ecosystems, and they are faced with severe disturbances of local and global extent (Hughes et al. 2003). This, plus evidence of catastrophic and repeated mortality of scleractinian (stony, or hard) corals (Bruno and Selig 2007, Edmunds and Elahi 2007, Mumby et al. 2007, De'ath et al. 2012, Edmunds et al. 2014*a*), has led some to suggest that coral reefs could be faced with ecological extinction within the current century (Pandolfi et al. 2003, 2005). Coral reefs support a tremendous biodiversity, believed to be the most of any ecosystem on Earth, and losses of corals—the foundation species—threaten much of the associated community (Munday 2004, Holbrook et al. 2008, 2015, Adam et al. 2014). Thus, the question to ask about the reefs of Moorea arguably is not what they will look like in the future, but whether they have a future at all? After more than a decade of comprehensive time-series analyses of the reefs and ocean environment of Moorea in French Polynesia, the Moorea Coral Reef Long-Term Ecological Research (MCR LTER) site is in a unique position to address this question.

Fifteen years ago when the MCR LTER site was first established, it seemed clear that the largest threats to coral reefs were posed by global climate change (Hoegh-Guldberg 1999, Hughes et al. 2003), and already the dark clouds of ocean acidification were gathering (Langdon et al. 2000). The first LTER proposal for this site addressed the risks to reefs of a wide range of ongoing and impending threats. Overall, in 2004 it seemed likely that in the longer term, dynamics of these reef communities would be shaped by coral bleaching driven by rising seawater temperature, the implications of declining seawater pH for the ability of reef calcifiers to deposit calcium carbonate, and the decline in community resilience favoring macroalgae over scleractinian corals (Hoegh-Guldberg 1999, Hughes et al. 2003, Hoegh-Guldberg et al. 2007, Carpenter et al. 2008). The results of the first decade of time-series analyses revealed how limited our ability was to accurately project how the reefs of Moorea would change.

In 2005, mean coral cover was ~35–45% in the three coral habitats of Moorea (fringing reef, back reef, fore reef (Adam et al. 2011), but as early as 2006 we started to observe feeding scars of the corallivous Crown-of-Thorns Seastar (COTS, *Acanthaster planci*) at >20 m depth on the fore reef. Within 5 yr, a massive population outbreak of this coral predator consumed virtually all of the corals on the fore reef and caused localized damage in the back- and fringing reefs (Adam et al. 2011). This dramatic, landscape-scale death of coral tissue was punctuated by Cyclone Oli (February 2010), which removed many of the dead-in-place coral skeletons, especially on the north shore (Fig. 11). Together these disturbances resulted in dramatic changes in the reef community, particularly the assemblage of fishes (Adam et al. 2014, Han et al. 2016).

Thus, within the first 6 yr of establishment of our site, we witnessed what we had feared might happen to the reefs of Moorea through more slowly acting global drivers of reef destruction (i.e., climate change and ocean acidification) and increasing human population growth, yet this outcome was caused by disturbances (COTS outbreaks, cyclones) that actually are routine occurrences on Pacific coral reefs. Faced with such a large scale of coral mortality, our expectations for the future of the denuded fore reef of Moorea were strongly affected by the widespread death of corals seen throughout the Caribbean (Edmunds and Elahi 2007, Mumby et al. 2007) and Indo-Pacific (Bruno and Selig 2007, De'ath et al. 2012). Based on observed responses elsewhere, we thought there was a reasonable likelihood that the reefs of Moorea would show a shift to macroalgal dominance (Hughes 1994), which might represent a community state governed by a different set of stabilizing feedbacks (Mumby et al. 2013, Schmitt et al. 2019). As a projection for the future of reefs in Moorea, these scenarios proved to be incorrect, especially for the COTS-ravaged fore reef.

In 2011, we recorded two events that set the stage for recovery of the fore reef at a rapid pace. First, grazing by fish herbivores prevented the establishment of macroalgae and maintained open surfaces suitable for the settlement of coral larvae (Adam et al. 2011, Holbrook et al. 2016). Second, coral recruitment dramatically increased relative to the rates recorded over the previous years (Bramanti and Edmunds 2016, Tsounis and Edmunds 2016), initially fueled by pocilloporid corals (Bramanti and Edmunds 2016, Holbrook et al. 2018). Pocilloporids are among the most

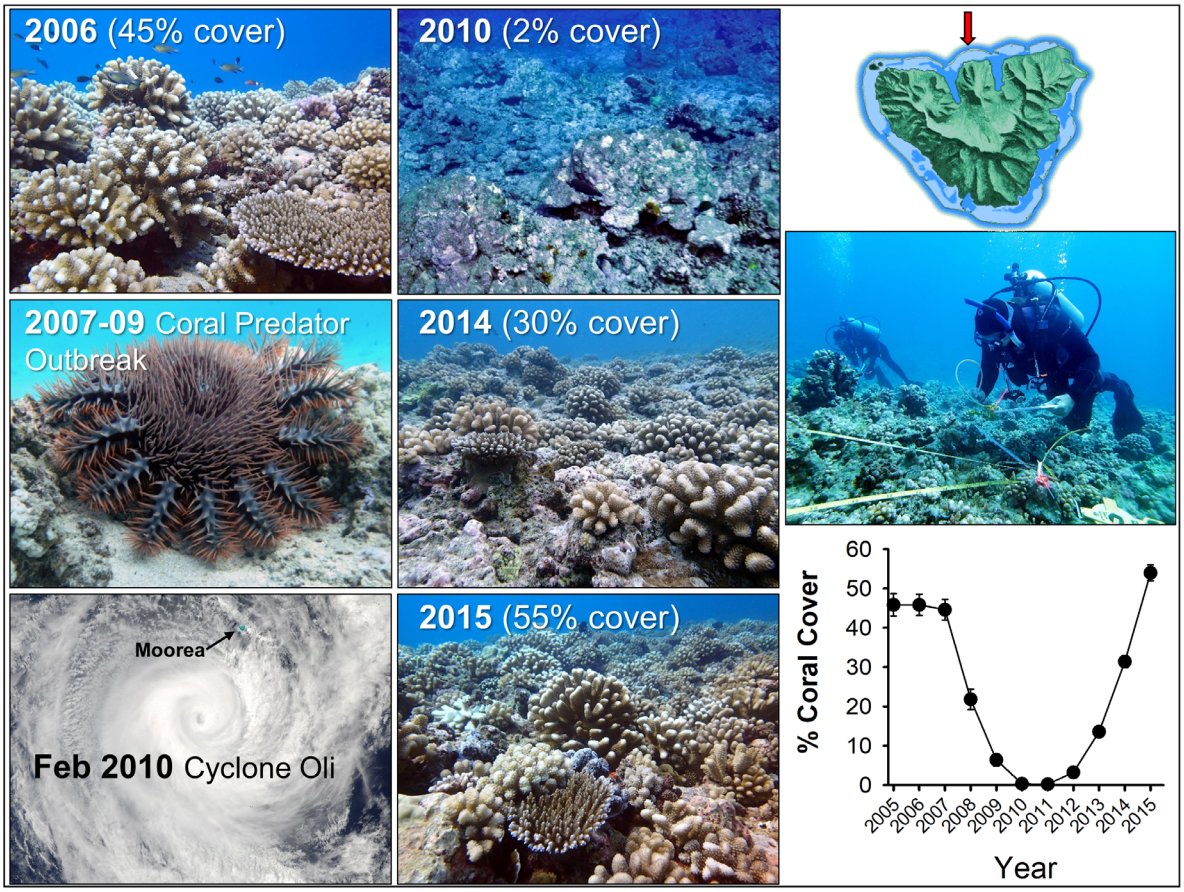

Fig. 11. Photographic series of corals and disturbance events at a permanent Moorea Coral Reefs (MCR) LTER study site at a north shore fore reef location (left photographs). The location of the study site is indicated by the arrow on the map of Moorea (top right). Time-series data for the percent cover (± 1 SE) of live coral (bottom right), as estimated from permanent photoquadrats, show the abrupt loss of coral due mostly to consumption by corallivorous Crown-of-Thorns Seastars (middle left; photo credit: M.H. Schmitt, MCR), followed by a rapid return to high coral cover. Middle right photograph (photo credit: A.J. Brooks, MCR) shows MCR LTER Principal Investigators Sally J. Holbrook (left) and Russell J. Schmitt (right) collecting time-series data on recruitment of corals to the fore reef. (Photo credit for landscape photos of fore reef coral: R. J. Schmitt, MCR; NASA Cyclone Oli image by Jeff Schmaltz, MODIS Rapid Response Team, Goddard Space Flight Center, with labels added by the authors.)

common scleractinians on Pacific reefs (Forsman et al. 2013), and they have featured prominently in the ecology of Moorea's reefs for decades. Genetic evidence suggests that the source of young corals that re-colonized the fore reef likely was mostly from local adults (Forsman et al. 2013, Edmunds et al. 2016*a*), again emphasizing the importance of local patterns of habitat connectivity which are driven by physical oceanographic forcing (Hench et al. 2008, Leichter et al. 2013, Edmunds et al. 2018). As a consequence of these two ecological events—suppression of macroalgae by fish herbivores and robust coral recruitment due to strong (and possibly, within-island) larval connectivity—cover of coral on the fore reef of the north shore returned to pre-COTS levels in less than one decade (Fig. 11). Further, multivariate analyses reveal that community structure at these locations is now very similar to that prevailing before the COTS outbreak,

indicating that the coral community on the fore reef of Moorea remains remarkably resilient (Holbrook et al. 2018). However, the threats of longer-term drivers have not dissipated, and a program of microcosm-to-mesocosm-to-*in situ* experiments has been ongoing in the MCR research program to quantity these effects and reveal underlying mechanisms (Holbrook et al. 2008, Comeau et al. 2014, 2015, Edmunds et al. 2014*b*, 2016*b*).

The baseball playing philosopher Yogi Berra has been credited with the pronouncement that "It's tough to make predictions, especially about the future," an adage that rings true in ecology in general and for the coral reefs of Moorea in particular. However, the growing quantity of biological and physical data from the MCR LTER is reducing the error in projections of the future state of the coral reefs (Kayal et al. 2018), although we are circumspect as to the time horizon over which such projection can apply. Focusing on a half-century time scale, and the coarsest level of resolution, nearly a decade and a half of observations leaves us optimistic that coral reefs will remain around Moorea, but it is unlikely that the goods and services they deliver, or their ecological attributes will remain the same. Specifically, MCR LTER data support three projections regarding the state of future reefs:

1. Selective pressures posed by rising seawater temperature and declining pH will favor population increases for a small number of coral species (winners), and dramatic population declines (and potential ecological extinction) for many others (losers). Associated shifts in the functional groups of corals represented by winning species—for example, the extent to which they produce massive vs. branching colonies, or the extent to which they display weedy life history traits—will modify community structure and dynamics.
2. The ecosystem integrity of these reefs will change as seawater pH declines, particularly through impaired net accretion that will threaten the structural integrity of the wave-resistant reef framework, and its capacity to keep pace with sea level rise.
3. Ecosystem resilience, the capacity of the system to recover following disturbances, will likely decline as the frequency of storm disturbances increases and the regional coral population declines in size, thus diminishing the capacity for source–sink dynamics of coral larvae within a meta-population construct. Quantification of the extent to which the coral reefs of Moorea are genetically connected with one another, and with nearby islands, is required to sharpen this projection, but it is likely that impaired connectivity will reduce the likelihood of repeated recovery dynamics similar that we observed between 2010 and 2016.

Eroding Resilience of Northern Wisconsin Cool-Water Fisheries: Climate and Habitat

Long-term research at the North Temperate Lakes (NTL) LTER site has shed light on how climate, habitat, predation, and fishing practices influence the resilience of fisheries. This work is done in a management context where data and models have been used to evaluate the possibility of a "safe operating space" to support resilient fisheries in the region. The safe operating space of a recreational fishery is bounded by levels of harvest, habitat, predation, and other environmental factors that allow the fishery to maintain its current species composition and production into the future despite environmental shocks, that is, remain resilient (Carpenter et al. 2017). Crossing any of these boundaries can allow the fishery to lose resilience and shift into a state of reduced production and altered species dominance. A resilient fishery is managed to maintain a large safe operating space that allows the fishery to fluctuate and undergo environmental disturbances, yet avoid crossing boundaries that lead to loss of production or loss of high-value species. Climate change and habitat alteration can interact to decrease the size of the safe operating space for many recreational fisheries, leaving managers no alternative but reduced harvest to sustain the fishery (Carpenter et al. 2017, Hansen et al. 2019).

Recreation and tourism are the backbone of Northern Wisconsin's economy, and walleye (*Sander vitreus*) are an especially important fishery across this region. This iconic species is

harvested for consumption by both recreational and tribal subsistence fishers. Following the imposition of a court-mandated management system in the 1980s for managing recreational and tribal harvest, the walleye fishery was stable for approximately 20 yr (Nesper 2002). Since the mid-2000s, however, walleye populations in many northern Wisconsin lakes have declined, and the underlying causes are just emerging from current research (Hansen et al. 2015*b*). Potential causes include changes in climate, habitat, predation, and fishing practices. In the face of this loss of resilience, researchers and managers are seeking a combination of fishing, predator, and habitat management that could build resilience of walleye fisheries despite changes in climate and socioeconomic factors that are not controllable by regional fisheries agencies (Carpenter et al. 2017).

Against the backdrop of the shifting walleye fishery, Wisconsin lakes have been responding to changes in the regional climate in a variety of ways. Ice duration is declining (Magnuson et al. 2000, Ghanbari et al. 2009) and summertime surface waters are warming in most lakes (Winslow et al. 2017). In turn, these shifts have led to increases in the duration of thermal stratification by ca.1 month over the last century (Magee et al. 2016). Precipitation has also been declining in northern Wisconsin (Kucharik et al. 2010), and a decadal-scale oscillation in lake levels that has been present for at least 75 yr now appears to be shifting in frequency and magnitude due to record-low water levels (Fig. 12a; Watras et al. 2014). During dry years, lowering of lake levels exposes fallen trees, or coarse woody habitat, that normally provides essential habitat for fishes (Fig. 12b). Declines in coarse woody habitat are associated with fish community changes including extirpation of yellow perch (Sass et al. 2006) and reductions in growth rate of sunfish (*Lepomis* spp.) and largemouth bass (*Micropterus salmoides*) (Schindler et al. 2000, Gaeta et al. 2014).

Walleye are known as a cool-water fish because of their temperature preferences. They also rely on dim light conditions for feeding, and these combined requirements can be defined in terms of thermal–optical habitat area—the area of lake bottom in which both temperature and light conditions are at optimal levels for this species (Lester et al. 2004). Water clarity can increase during drought periods (Fig. 12c), as water residence time is prolonged and inputs of nutrients and colored dissolved organic matter decrease, thereby reducing light absorption by phytoplankton and colored dissolved organic matter. Although the effects of drought on water clarity can vary among lakes (Lisi and Hein 2019), decreases in walleye habitat associated with surface warming and increased clarity have consequences for walleye populations (Hansen et al. 2019).

A key indicator of the status of the walleye fishery is recruitment, measured in Wisconsin lakes as the number of young-of-year individuals per mile of shoreline that survive to their first autumn. Increasing numbers of Northern Wisconsin lakes are exhibiting recruitment declines (Fig. 12d), and this poor recruitment may be attributable to drought, loss of shoreline habitat, high water clarity, or warm temperatures (Hansen et al. 2015*a*, Hansen et al. 2017). Adult walleye densities (Fig. 12e) as well as walleye production, biomass, and turnover, P/B (Rypel et al. 2018) are also declining, though at a slower rate than recruitment. Slow declines of adult breeding stock warn of fishery "invisible collapse" (Post et al. 2002), as these long-lived predators gradually succumb to mortality and harvest and are not replaced by recruitment. Stocking can and does supplement natural recruitment to some degree, but stocked walleye populations do not support the same densities of adult fish as do naturally recruiting populations (Nate et al. 2000).

Coincident with the walleye decline, largemouth bass population densities are increasing in Northern Wisconsin lakes (Hansen et al. 2015*c*). Harvest regulations (bag limits and season length) for this species have been liberalized but have not increased harvest. Only a small percentage of the individuals caught by anglers are retained, and most are released (Gaeta et al. 2013, Hansen et al. 2015*c*), reflecting the trend of angler preferences toward a catch-and-release bass fishery (Gaeta et al. 2013, Hansen et al. 2015*c*). Largemouth bass populations are now essentially unmanaged in Northern Wisconsin because the primary tool of management—harvest regulation—is not impacting bass populations. It is possible that largemouth bass are important competitors or predators of young-of-year walleye and thereby are playing a role in the walleye decline (Hansen et al. 2015*c*, Tunney et al. 2017), although examination of largemouth

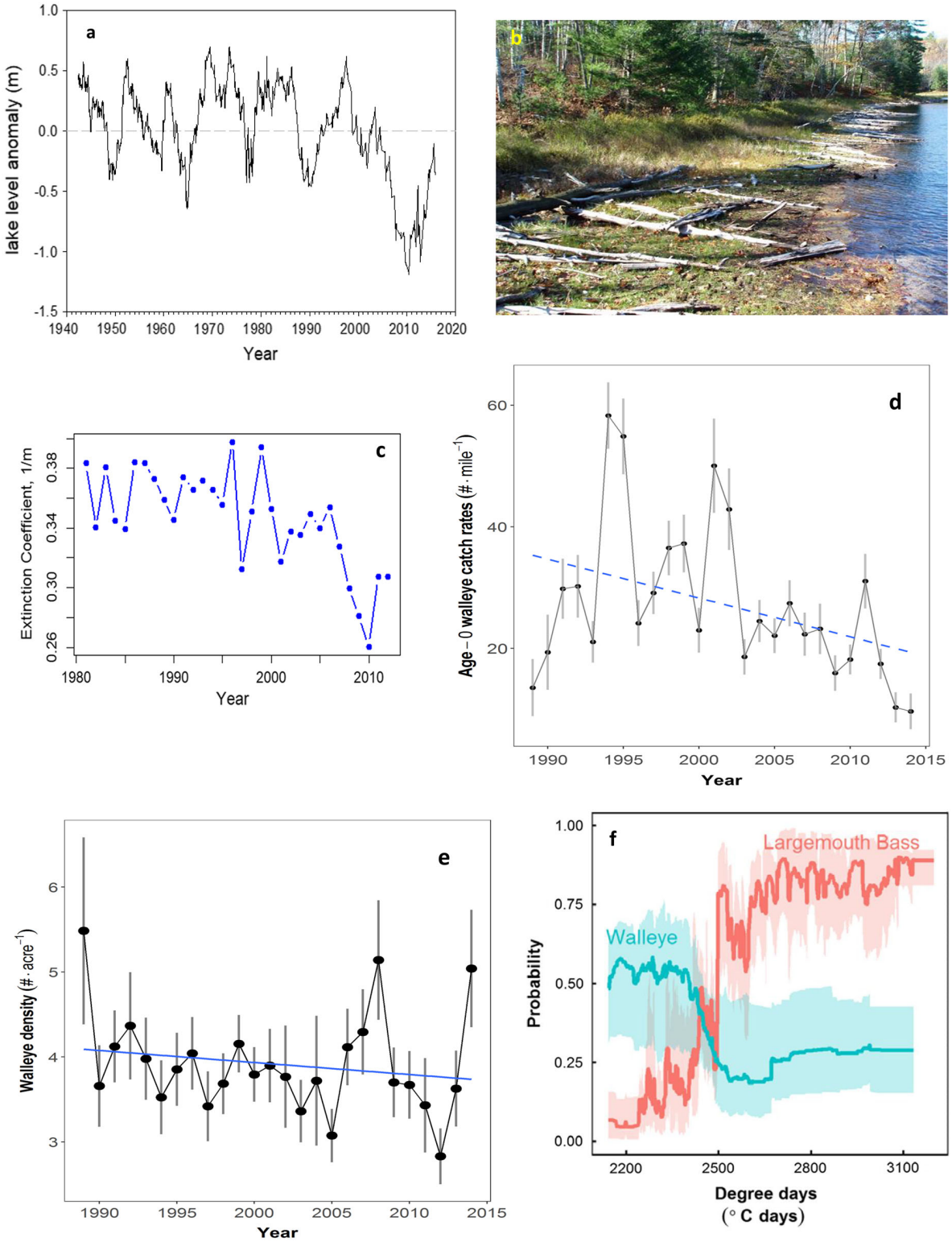

Fig. 12. (a) Lake level departures (anomalies) from the long-term mean at the North Temperate Lakes (NTL)

(Fig. 12. *Continued*)

LTER site. The time series is an aggregation from Buffalo Lake (1942–1989) and Crystal Lake (1981–2014). (Modified from Watras et al. 2014.) (b) Previously submerged woody habitat stranded along the receding shoreline of Little Rock Lake in 2007. Photo credit: J. Gaeta. (c) Long-term trend of light extinction coefficient (m^{-1}, inverse of water clarity) for Trout Lake. Values are averages of monthly measurements made in June, July, and August. (d) Long-term trend of walleye recruits (young-of-year at the end of growing season) for northern Wisconsin lakes (n = 36–160 lakes per year, mean 100 lakes), including NTL lakes (means ± 1 SE). Decline rate is 6.6%/yr. (e) Long-term trend of adult walleye density in northern Wisconsin lakes (average of 36 lakes per year, range = 26–56 lakes), including NTL lakes. Decline rate is 2%/yr (means ± SE). (f) Probability of successful walleye recruitment (blue line) and relative abundance of largemouth bass (red line) vs. growing degree days (5°C basis) in northern Wisconsin projected from empirical model for Wisconsin lakes, including NTL lakes (Hansen et al. 2015*a*).

bass diets does not support this hypothesis (Kelling et al. 2016).

Climate warming may play a role in both declining walleye and increasing largemouth bass populations in northern Wisconsin lakes. To test this hypothesis, coupled physical and fish population models were developed and calibrated for 2148 Northern Wisconsin lakes, including NTL LTER study lakes, under contemporary (1989–2014) climate and then applied to future (2040–2089) climate projections (Hansen et al. 2017). Water temperature degree days (5°C base) was predictive of both walleye recruitment and largemouth bass abundance. A degree day threshold separating walleye-dominated from largemouth bass-dominated lakes was identified; when degree days exceeded about 2500°C•days, a sharp decline in the probability of successful walleye recruitment was mirrored by a steep rise in the probability of largemouth bass dominance (Fig. 12f). However, the negative effects of water temperature were negligible in Wisconsin's largest lakes, suggesting that warming negatively affects walleye not through direct physiological mechanisms, but possibly through indirect food web effects (Hansen et al. 2017). Regardless of the mechanism, this analysis suggests that warm-water fishes such as largemouth bass will replace Northern Wisconsin's cool-water walleye stocks in many lakes if observed and projected climate trends continue. Should this scenario develop in coming decades, recreational anglers will encounter fewer opportunities to fish for cool-water fish such as walleye and perch, and more opportunities to fish for bass and sunfish.

Warming water temperatures and drought in Northern Wisconsin challenge the resilience of walleye, the most popular and economically important cool-water fishery in the state. Declining recruitment and loss of reproductive potential as adult walleye decline suggest that losses of individual lake walleye fisheries could become widespread if drought cycles continue to deepen and lakes continue to warm. Nonetheless, current long-term research and modeling will provide managers with the information they need to build the resilience of walleye fisheries in at least some lakes (Hansen et al. 2015*b*, Carpenter et al. 2017). Resilience of this socio-ecological system may be viewed on the landscape scale, where some lakes continue to support walleye and others do not, and anglers and managers must adjust their behavior and expectations accordingly (Carpenter and Brock 2004). In contrast to the situation for walleye, climate trends appear to be increasing the resilience and spatial distribution of warm-water fishes such as largemouth bass and sunfish in Northern Wisconsin.

Will these trends continue in Northern Wisconsin? Will shifts between cool- and warm-water fisheries be gradual and continuous, or sharp and abrupt? Will Northern Wisconsin's larger cooler lakes prove to be refugia for cool-water fisheries, and if so for how long? Will fishers adapt to growing opportunity for harvest of warm-water species? Or will they preferentially seek dwindling cool-water fishes and thereby accelerate the decline of walleye and perch in the region? Will invasive species alter food web dynamics with unexpected consequences for the walleye- largemouth bass interactions? As the outcomes unfold, ongoing and future NTL LTER research will answer these fundamental questions about fisheries and recreational traditions

that underpin livelihoods and lifestyles in Northern Wisconsin.

Responding to Change: Lessons Learned from an Ancient Forest at the Andrews LTER

Long-term research at the HJ. Andrews Forest (AND) LTER site has investigated how natural drivers of ecological change—such as fire, air temperature, and precipitation—which vary in timing and severity, interact with anthropogenic drivers of change—fire suppression, forest harvest, and plantations—that may enhance or diminish resilience. Research at AND has revealed how these drivers of change have interacted and influenced forest ecosystems of the Pacific Northwest over the past millennium, and how these processes may shape ecosystems in the coming century.

The HJ Andrews Experimental Forest is part of the forests that make up North America's Cascadia mountain landscape of the Pacific Northwest. The Andrews Forest and neighboring areas are representative of Douglas-fir forests of the larger Cascadian landscape in terms of having tens of percent of the landscape in forest plantations established from 1950 to 1990, within a matrix of mature (100- to 200-yr-old) and old (>200-yr and commonly 400 to 500 yr-old) forests established after wildfire. Western Oregon tree-ring chronologies suggest the past century has been relatively calm in comparison with apparently dramatic variability from the mid-1600s through about 1800 (Weisberg and Swanson 2003, Tepley 2010), when periods of relatively frequent fire were interspersed with periods of relatively infrequent fire (Fig. 13). In total, these growth and recruitment histories speak to the tremendous variability forests in the region of the Andrews Forest have witnessed over the past 800 yr, and their resilience to these perturbations. Anthropogenic drivers of change have imposed by far the greatest effects on the landscape over the period of observation (past 70 yr), and the ecosystem has demonstrated resilience to both natural and anthropogenic disturbance. However, future anthropogenic climate change and other, more difficult to predict social changes, may transform the future ecosystem in unanticipated ways.

In the coming century, anthropogenic global climate change may push this ecosystem into non-analog conditions outside the historical envelope. Climate models project an increase in air temperature of up to 3°C by the 2080s, with little change in precipitation; projected warming rates range from 0.1° to 0.6°C per decade (Mote and Salathe 2010). Forests throughout the region have faced warming temperatures and declining snowpacks over the past century, with rates of warming of 0.05°C per decade before 1950, rising to 0.2°C per decade since 1950 (Abatzoglou et al. 2014, Sproles et al. 2017, Mote et al. 2018). While we believe that these regional trends are impacting the Andrews Forest, warming trends from long-term temperature records taken under the old-growth forest canopy in the Andrews Forest are at the lowest end of the observed range. In the coming century, we anticipate increasing winter floods, prolonged summer droughts, increasing risk of major fire, greater seasonal contraction of stream networks, shifts in seasonal moisture availability, and shifts in the active growing season. Biological responses to changes in the physical system thus far have been subtle and variable, but the magnitude and direction of future responses remain largely uncertain. Still, the long-term record of research at the Andrews Forest may offer some insights about what we can, and cannot, expect under changing conditions.

In many respects, our forested mountain ecosystem appears to be resilient, with processes and functions that resist and recover from major disturbances. For example, the steep topography, tall forests, and resulting cold-air drainage may create a thermal refuge in lower parts of the valley, reducing the potential for disturbance by wildfire and the effects of seasonal drought, and decoupling temperature change at low elevation from changes at high elevation (Daly et al. 2010). Structurally complex old-growth forests can be cooler than other forest types during late spring and summer, creating microclimate refugia that might buffer bird populations from negative effects of warming (Frey et al. 2016).

Although understory thermal conditions may currently be relatively immune to regional climate change, temperatures and related stresses on tree canopies may be very different. For example, thermal infrared imagery of an old-

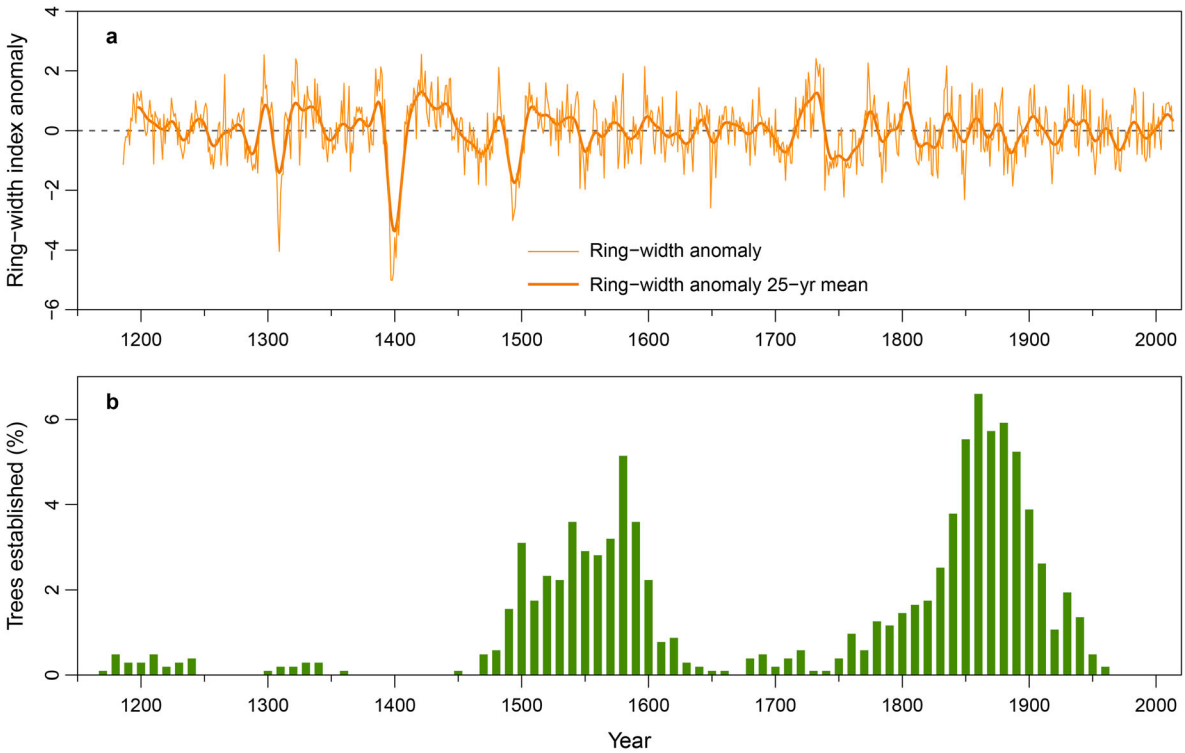

Fig. 13. (a) Anomalies of average ring width index based on tree-ring chronologies combined from five "super" old-growth Douglas-fir stands and one from an incense cedar stand in the Andrews Forest region of the western Cascade Mountains. Time series were detrended with a 100-year 50% frequency cutoff cubic spline to reduce age-related growth declines and long-term growth suppressions or releases due to stand-level disturbances. The variability captured reflects broad-scale external forcing of forest growth. Notable suppressions around 1400 and just before 1500 are likely insect outbreaks. Other notable patterns include the relatively quiescent period of relatively low variability from the late 1500s through the latter 1600s after which variability from interannual to interdecadal timescales increases, peaking in the early 1700s and at a level exceeding that of the 20th century. (b) Tree recruitment history derived from 1,030 establishment dates for Douglas-fir in the Andrews region. Major recruitment pulses in the 1500s and 1800s likely represent responses to periods of widespread burning, when several fires burned different parts of the Andrews Forest region in each century. Source: Tepley (2010) and unpublished data of Tepley and Black.

growth canopy in the summer of 2015 showed canopy skin temperatures exceeding 45°C, well above the optimum temperature of photosynthesis and approaching temperatures that damage leaf tissue (C. Still, *unpublished manuscript*). As a result, we might expect to see increased plant mortality (van Mantgem et al. 2009) and shifts in community assemblages in future years (e.g., HilleRisLambers et al. 2015).

Stream ecosystems at the Andrews Forest also demonstrate some amount of resilience to disturbance. In our 30-yr study of Cutthroat Trout and Pacific Giant Salamanders, we have been surprised to find that population sizes of these top predators have increased after major floods (Dodds et al. 2012). However, long-term records indicate an increasing synchrony between annually occurring maximum stream temperature and minimum stream flows, which may reduce the capacity of aquatic biota to recover or adapt to these annual extreme events (Arismendi et al. 2013). Resilience to these changes may require community reorganization, which may in turn depend, at least in part, upon the ability of top predators, such as fish and salamanders, to find refuges during warm dry summers.

Anthropogenic drivers have strongly influenced ecosystem properties in the past 150 yr, and their effects will continue to play out over the coming century. Timber management in the second half of the 20th century shifted the forest age distribution away from old growth toward early-seral vegetation. However, the cessation of old-growth clear-cutting on federal lands in the mid-1990s, combined with fire suppression, resulted in a pulse of young, closed canopied plantations and a decline in early-seral habitat on federal lands (Swanson et al. 2011).

Other anthropogenic drivers, especially a century of fire suppression policy, combined with climate change, may increase fire occurrence in the future. Unlike drier regions with historically frequent fire, where a century of fire suppression has led to a fuel buildup that now makes forests susceptible to high-severity fire, the effects of fire suppression are less obvious in the moist, productive forests on the west side of the Cascades. Here, it was not unusual for individual stands to historically experience fire-free intervals longer than the current period of effective fire suppression. The effects of fire suppression become apparent when considering broader landscape patterns, including a reduction in the variation of old-growth forest structures that develop in response to burning at different intervals and different severities (Tepley et al. 2013, 2018), and a loss of naturally regenerating early-seral forest (Hansen et al. 1991). Unmanaged, early-seral ecosystems developing after natural disturbances are among the most biologically diverse and under-represented ecosystems in the region (Swanson et al. 2011).

Additional anthropogenic changes, such as endangered species protection or reintroduction, or invasive species, will add uncertainty to forest change in the coming century. Gray wolves will likely soon return to our system, and Barred owls will likely soon replace iconic Northern spotted owls (Diller et al. 2016, Wiens et al. 2017). Exotic, invasive plants (especially false brome) introduced by human visitors may alter the character of the forest understory (Taylor and Cruzan 2015). We cannot predict how humans will respond to those changes, or how those changes may collide with human decision-making. For example, because prey populations in the Andrews Forest are currently sparse, the return of wolves is not expected to create trophic cascades. If, however, humans begin managing for more complex early-seral habitat and prey populations increase, the ecological trajectory of the forest might be different, a change that might in turn effect prey and predator populations.

When we consider our history, variability in human decision-making in our region seems even more fickle and unpredictable than variability in biological and ecological systems. At almost any time from the beginning of the HJ Andrews Experimental Forest in 1948 to the late 1980s, it would have been foolish to predict that we would have an effective cultural revolt against liquidating the remainder of our old-growth forests. Society engaged with the federal forestlands in the Pacific Northwest (of which the Andrews Forest is an example) with rather passive stewardship for the first half of the 20th century. The 1950s to 1980s witnessed a dramatic shift toward timber extraction (1950s–1980s), followed by another abrupt shift in the final decades of the 20th century, the era of ecosystem management and biodiversity conservation on federal forestlands (e.g., Spies and Duncan 2012, Harris 2013).

Standing in a grove of 500-yr-old trees, inspired by their impression of permanence, it is tempting to see this forest as resilient. In many ways, of course, that impression seems accurate. Not only is the forest still here after all these years, through the past 500 yr of disturbance, but we believe at least certain parts of our system possesses the ability to buffer against at least a certain amount of external change. In studying the Andrews Forest for the past 70 yr, however, we also know that the forest has repeatedly revealed an ecology of (often-unexpected) change: an ecology of surprise. Humility seems the order of the day when faced with that reality. It might be the embodiment of humility that creates the most resilience of all.

Conclusions

The case studies presented here show that resilience research at LTER sites has matured significantly over the 40 yr that the NSF LTER program has been in existence; moving from relatively simple assessments of responses to single major disturbance events, for example, a big fire, clear-

cutting, a hurricane, to evaluation of how interactions between multiple disturbances affect diverse aspects of ecosystem structure, function, and services. In Baltimore, the novel disturbance regimes of urban ecosystems have allowed for analysis of how interactions between changes in herbivory and invasive species influence resilience in urban forests, with relevance to forests across the Eastern United States. At the Cedar Creek grassland site, long-term experiments and theory have been used to address novel combinations of global change factors (precipitation, temperature, and other abiotic and biotic factors) that have no analog in historical records. At Hubbard Brook, resilience research has moved from extreme clear-cutting experiments to analysis of more subtle interactions between climate change, the legacy of acid rain, and an exotic pest. Long-term observations at the Moorea Coral Reef site show remarkable resilience to a major disturbance event and the complex biological interactions that underlie that resilience. However, this resilience is predicted to decline in the future along with increasing temperatures and declining pH of seawater. At the North Temperate Lakes site, long-term research has shed light on how climate, habitat, predation, and fishing practices influence the resilience of fisheries. The maturation of resilience research in the LTER network suggests that there is potential for addressing how resilience will affect the ecological futures of diverse ecosystems. This potential is likely to be realized if long-term data collection, experiments, and modeling activities continue to develop as they have over the past 40 yr.

Many of our stories suggest a high capacity for resilience among the ecosystems in the LTER network. The forests at Hubbard Brook and Andrews have shown resilience in the face of climate and atmospheric change, and the coral reefs of Moorea have recovered from dramatic disturbance over the course of relatively recent LTER observations. The studies in Baltimore and Cedar Creek highlight some of the mechanisms that may underlie this resilience; biodiversity increases resilience to drought and fosters microclimates that provide resilience to climate change. The urban forests of Baltimore, beset with invasive species and large herbivore populations, have shown resilience, partially due to the presence of these invasive species that colonize quickly and succeed under altered environmental conditions.

But challenges remain for many ecosystems. Fish populations and communities in north temperate lakes may not be resilient in the face of both climate change and human exploitation. And many studies hint at limits of resilience and uncertainties that will need to be examined with further long-term research. Several studies point to human decision-making as a strong and unpredictable driver of resilience in ecosystems. These stories highlight the need for long-term studies to sort out the complexities of resilience and how the diversity of sites within the LTER network facilitate the emergence of overarching concepts about this important driver of ecosystem structure, function, services, and futures.

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