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

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

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Abstract. Ecosystems across the United States are changing in complex ways that are difficult to predict. Coordinated long-term research and analysis are required to assess how these changes will affect a diverse array of ecosystem services. This paper is part of a series that is a product of a synthesis effort of the U.S. National Science Foundation's Long Term Ecological Research (LTER) network. This effort revealed that each LTER site had at least one compelling scientific case study about "what their site would look like" in 50 or 100 yr. As the site results were prepared, themes emerged, and the case studies were grouped into separate papers along five themes: state change, connectivity, resilience, time lags, and cascading effects and compiled into this special issue. This paper addresses the time lags theme with five examples from diverse biomes including tundra (Arctic), coastal upwelling (California Current Ecosystem), montane forests (Coweeta), and Everglades freshwater and coastal wetlands (Florida Coastal Everglades) LTER sites. Its objective is to demonstrate the importance of different types of time lags, in different kinds of ecosystems, as drivers of ecosystem structure and function and how these can effectively be addressed with long-term studies. The concept that slow, interactive, compounded changes can have dramatic effects on ecosystem structure, function, services, and future scenarios is apparent in many systems, but they are difficult to quantify and predict. The case studies presented here illustrate the expanding scope of thinking about time lags within the LTER network and beyond. Specifically, they examine what variables are best indicators of lagged changes in arctic tundra, how progressive ocean warming can have profound effects on zooplankton and phytoplankton in waters off the California coast, how a series of species changes over many decades can affect Eastern deciduous forests, and how infrequent, extreme cold spells and storms can have enduring effects on fish populations and wetland vegetation along the Southeast coast and the Gulf of Mexico. The case studies highlight the need for a diverse set of LTER (and other research networks) sites to sort out the multiple components of time lag effects in ecosystems.

Key words: climate change; climate change detection; climate signal filtering; ecosystem response; Special Feature: Forecasting Earth's Ecosystems with Long-Term Ecological Research.

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INTRODUCTION

It is well recognized that ecosystems across the United States are changing in complex ways that are difficult to predict (Grimm et al. 2013). It is also well established (since the 1960s) that analysis of these changes requires coordinated, long-term research (Golley 1996). The challenge of ecosystem change has only intensified in recent years along with the nature and extent of land-use change, agricultural intensification, species movement, and global environmental changes in climate, and air and water pollution (Steffen et al. 2005). Understanding the ability of ecosystems to provide services to fulfill a diverse array of societal needs requires addressing several questions: What populations and communities will be dominant in 20, 50, and 100 yr? How will biogeochemical cycles change in response to changing climate and elevated carbon dioxide (CO₂)? How will 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 long-term ecosystem change is greatly facilitated by the presence of research and monitoring networks. The U.S. National Science Foundation (NSF) funded Long term Ecological Research (LTER) network consists 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 not chosen to cover the range of major ecosystem types or natural biomes and do not collect a standardized set of monitoring data. Rather, 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. 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 and community studies, movement of organic matter, movement of inorganic matter, and disturbance patterns.

In 2014, LTER network scientists began an effort to revisit each of the five LTER core areas of research. This analysis revealed that each LTER site had at least one compelling case study about “what their site would look like” in 50 or 100 yr. As the results were prepared, themes emerged, and the studies were grouped into five separate papers along these themes: state change, connectivity, resilience, time lags, and cascading effects and compiled into this special issue. The objective of the series of papers is to show the importance of long-term basic research for addressing the hardest questions in ecology that have significant implications for environmental policy and management. This paper addresses the time lags theme with five examples from diverse biomes including tundra (Arctic), coastal upwelling (California Current Ecosystem), montane forests (Coweeta), and Everglades freshwater and coastal wetlands (Florida Coastal Everglades) LTER sites. Its objective is to demonstrate the importance of different types of time lags, in different kinds of ecosystems, as a driver of ecosystem structure and function and how this can effectively be addressed with long-term studies. Time lags have been one of the most persistent challenges in ecosystem ecology as their inherent nature greatly complicates attribution of cause and effect. Given their temporal dimension, they were one of the main motivators and justification for founding the LTER network (Magnuson 1990). The concept that slow,

interactive, compounded changes can have dramatic effects on ecosystem structure, function, services, and futures is apparent in many systems, but difficult to quantify and predict (Groffman et al. 2006, Jackson et al. 2018), especially with short-term (e.g., three-year) research projects.

The examples illustrate that time lag effects are key drivers in terrestrial, coastal, and aquatic ecosystems, from arctic to tropical latitudes. They also document how time lags effects can emerge from physical, chemical, or biological drivers. The case studies highlight the need for a diverse set of LTER biome sites and corresponding long-term studies to sort out these multiple components of time lags. More generally, the LTER network facilitates the emergence of overarching concepts, such as time lags, that address important dynamics and that may complicate the response of ecosystems to changes in the environment.

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

1. Arctic Tundra LTER: How Long Term Is Long Term Enough? Edward B. Rastetter, Gaius R. Shaver and Laura Gough
2. California Current Ecosystem LTER: Secular Changes in Marine Ecosystems: Mark D. Ohman
3. Coweeta LTER: What Can Long-Term Data Can Reveal About How Southern Appalachian Forests Will Respond to Invasive Species, Land Management, and Climate Change: Katherine J. Elliott, Chelcy F. Miniat and C. Rhett Jackson
4. Vulnerability to Extreme Climate Events: Effects of a 100-Year Cold Event on Fish Communities and Fisheries in the Florida Coastal Everglades (FCE) LTER: J.S. Rehage and R.E. Boucek
5. Mangrove Wetlands: Marking the Impact of Climate Change in the Florida Coastal Everglades LTER: Victor H. Rivera-Monroy, Tess M. Danielson and Edward Castañeda-Moya

ARCTIC TUNDRA LTER: HOW LONG TERM IS LONG TERM ENOUGH?

Researchers at the Arctic Tundra (ARC) LTER site have addressed time lag effects by using

long-term data and a simulation model to test concepts about how different features of ecosystems respond to changes in climate at different time scales and how this affects our ability to detect short- and long-term drivers of change. Trends in climate are often difficult to detect because of the inherent variability in climate data. For example, the long-term (64-yr) temperature record at Barrow Alaska indicates a warming rate of about 0.5°C per decade, roughly twice as fast as the global average ($r^2 = 0.39$, $n = 64$, $P < 0.01$; Hobbie et al. 2017; Alaska Climate Research Center, *available online*, <http://climate.gi.alaska.edu>). However, because of the variability in these data, the regression of temperature vs. time does not have a significant positive slope until the 46th year of the record ($r^2 = 0.1$, $n = 46$, $P < 0.05$). Responses of ecosystems to these changes in climate might be expected to take even longer to be detectable in the long-term record. For example, in a recent resampling of moist acidic tundra at the Arctic Tundra LTER site near Toolik Lake, Alaska (68°37'46" N, 149°34'35" W), plant biomass in control plots had not changed after 35 yr and, unlike other reports for the Arctic (Myers-Smith et al. 2011), shrub biomass had not increased significantly ($P > 0.05$; Shaver 2016).

Hobbie et al. (2017) postulated that some features of ecosystems respond so rapidly to changes in climate (and weather) that the high-frequency climate variability is fully reflected in the responses of these features (high-pass filter). Other features respond so slowly that they effectively average out the high-frequency climate variability and changes in these features only reflect long-term climate trends (low-pass filter). Still other features of ecosystems might respond slowly enough to filter out the high-frequency noise in the climate but fast enough to be useful indicators of climate change (medium-pass filter).

Here, we used the multiple element limitation (MEL) model (Rastetter et al. 2013, Jiang et al. 2015, 2016, 2017, Pearce et al. 2015) to simulate responses of moist acidic tundra to warming with the rate and variability of the Barrow temperature record described above. We used a within-year temperature record from Toolik Lake, imposed a continuous 0.05°C/yr increase, and added a normally distributed deviation to

the mean annual temperature consistent with the variability in the Barrow record (standard deviation = 1.16°C). All other climate variables, carbon dioxide (CO_2), and nutrient deposition levels were the same as those used by Pearce et al. (2015) and remained the same for each year of the simulation. We ran 10 replicate simulations beginning with 50 yr with no warming trend and then 200 yr of warming at the 0.05°C per year rate.

Cumulative annual net primary production (NPP, expressed as grams carbon [C] per year) increased each year by about $0.27 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ($\sim 0.1\%$ per yr) partly because of the stimulation of photosynthesis by warmer conditions and partly because of the warming-induced acceleration of nutrient cycles (Fig. 1). Plant biomass increased at a rate of about $1.55 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ($\sim 0.2\%$ per yr) in response to the increase in NPP and a net redistribution of nutrients from soil organic matter to vegetation. After a lag of about 20 yr, carbon stored in highly organic soil (peat) declined at a rate of about $1 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ($\sim 0.02\%$ per yr). After a lag of over 50 yr, mineral-soil organic matter also declined at a rate of about $0.9 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ($\sim 0.006\%$ per yr, data not shown). Because of the lag in peat and mineral-soil organic matter loss, there was a small net gain of total ecosystem carbon in most simulations after 200 yr of warming (range -5 to $80 \text{ g C}/\text{m}^2$; -0.025% to 0.4%).

To assess how quickly the trends in ecosystem characteristics would become detectable, we calculated correlation coefficients between each characteristic and time since warming began (Fig. 2). For the first few years, correlations varied widely among simulations and fluctuated year to year within simulations; these correlations are spurious and linked to chance associations between initial conditions and autocorrelated ecosystem characteristics. Eventually, the correlations emerged as significant and consistent with the long-term trends in the data (Fig. 2). We used the timing of this final emergence to assess how quickly the trends in ecosystem characteristics became detectable. For NPP, the correlations became significant between 50 and 90 yr after warming began. This long time before the change in NPP emerged as significant is even longer than that of the raw temperature record (46 yr), suggesting that NPP is affected by

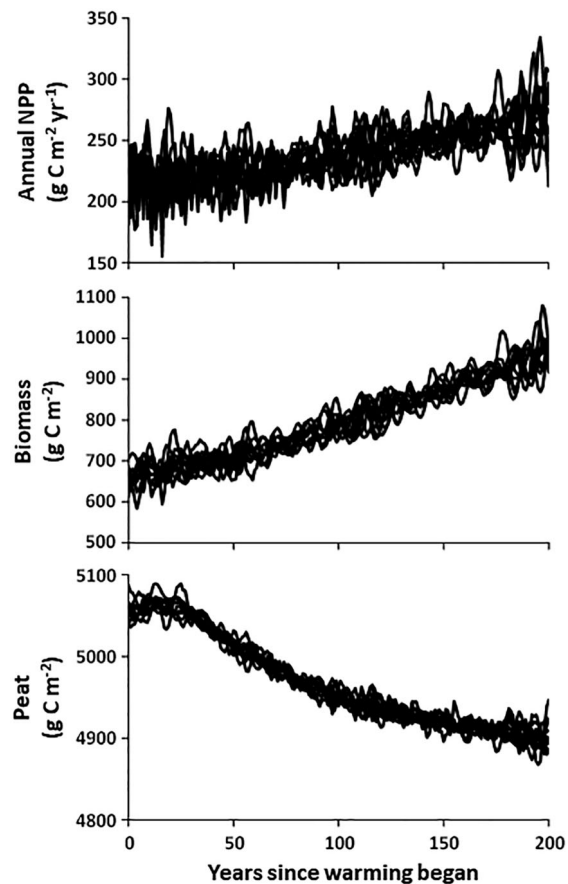


Fig. 1. Simulated response of moist acidic tundra to a 0.05°C per year warming. Data are for 10 replicate simulations with normal-random variability in the annual mean temperature (standard deviation = 1.16°C) and a warming trend of $0.05^{\circ}\text{C}/\text{yr}$. Cumulative annual net primary production (NPP) increases each year by about $0.27 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ or $5.4 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}\cdot^{\circ}\text{C}^{-1}$, plant biomass increases at a rate of about $1.55 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ or $31 \text{ g C}\cdot\text{m}^{-2}\cdot^{\circ}\text{C}^{-1}$, and, after a 20-yr lag, peat decreases by about $1 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ or $20 \text{ g C}\cdot\text{m}^{-2}\cdot^{\circ}\text{C}^{-1}$.

internally driven variability related to feedbacks associated with nutrient cycling and allometric and stoichiometric adjustments in the vegetation. The trend in plant biomass became significant between 20 and 70 yr after warming began, indicating that the year-to-year autocorrelation in biomass helps integrate and dampen variability in NPP. Nevertheless, 20–70 yr is a long time, comparable to the time needed for the raw temperature record to indicate significance. The peat integrates over an even longer period of time,

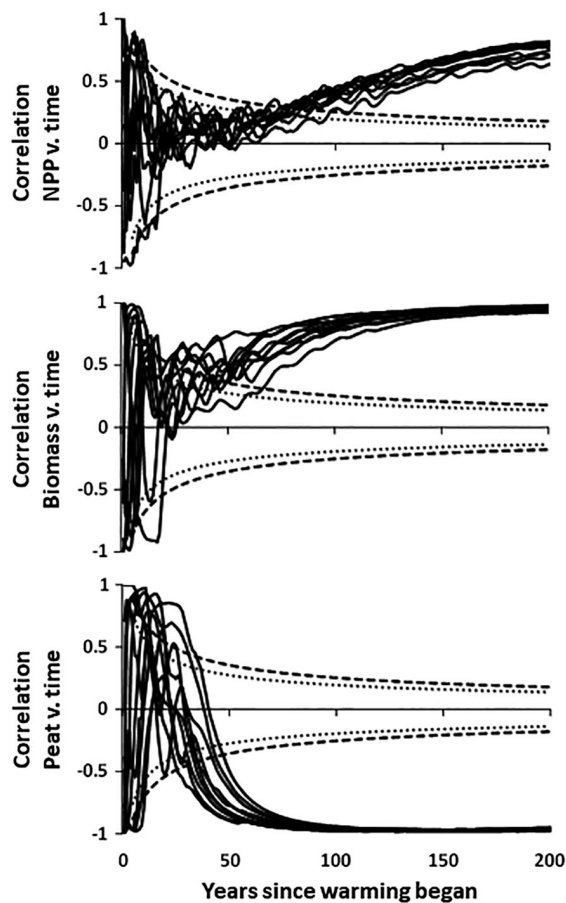


Fig. 2. Correlation of cumulative annual net primary production (NPP), plant biomass, and peat v. time for each of the 10 replicate simulations. Correlations are calculated from the beginning of warming. Dotted line is the $P = 0.05$ significance level, and dashed line is the $P = 0.01$ significance level. It takes NPP between 50 and 90 yr to emerge as a significant trend, between 20 and 70 yr for biomass to emerge as significant, and 20 and 50 yr for peat to emerge as significant.

and the correlations emerged as significant between 25 and 50 yr after warming began.

Our results indicate that fast responding ecosystem characteristics and fast turnover element pools might not be the best indicators of a response to climate change because they transfer variability in climate into their own response (high-pass filters; e.g., year-to-year variability in climate is reflected in high variability of NPP). It might therefore be difficult to detect a significant trend in such data except in very-long-term

records. Ecosystem characteristics that integrate over longer periods of time might be better indicators of a response to climate change because such characteristics can filter out the high-frequency noise in the climate data (low-pass filters; e.g., plant biomass or peat). However, other sources of variability also need to be taken into account. For example, our analysis suggests that peat loss might be the best of the three characteristics to detect responses to warming quickly. However, the spatial variability in peat abundance on the tundra would likely overwhelm the benefits detected in our analysis. Thus, a full assessment of all sources of variation is needed. In any case, our simulations indicate that detecting trends in ecosystem characteristics can take a long time, making long-term monitoring and experimentation vital.

There is a general expectation that warming in the Arctic will result in a loss of soil carbon and an increase in woody vegetation in tussock tundra. However, unlike other regions (Myers-Smith et al. 2011), those changes are not yet detectable at the Arctic Tundra LTER site and might remain difficult to detect for several decades. The reasons for this discrepancy are not clear and might take as long to unravel as it does for the vegetation signal to emerge from the background variability.

CALIFORNIA CURRENT ECOSYSTEM LTER: SECULAR CHANGES IN MARINE ECOSYSTEMS

The pelagic ecosystems that are the focus of the California Current (CCE) LTER site are dominated by short-lived organisms that respond to short-term variation in climate. However, these ecosystems are also affected by natural, low-frequency variation in climate that complicates analysis of underlying progressive secular changes and predictions of future state. Marine pelagic ecosystems are particularly sensitive to climate forcing because of direct and indirect effects of atmospheric variability on the upper ocean. Direct effects include the action of radiative forcing, wind stress, and atmosphere–ocean gas exchange on the upper ocean, while indirect effects include changes in ocean circulation, geochemical composition, ice cover, and sea level that are in turn related to atmospheric variables. Pelagic ecosystems are also strongly influenced by climate

signals because the basal organisms in pelagic food webs are unicellular algae that have rapid growth rates and short turnover times, leading to very close temporal coupling between changes in the ocean's physical-chemical environment and changes in abundances of planktonic organisms. Planktonic grazers, as well as primary producers, usually have relatively short generation times and changes in their abundance tend to reflect and even amplify changes in the physical environment (Hsieh and Ohman 2006, Di Lorenzo and Ohman 2013, Peterson et al. 2017).

In addition to long-term progressive climate change, the Northeast Pacific Ocean is influenced by strong natural variations in climate that occur on interannual (e.g., El Niño-Southern Oscillation) and multi-decadal (e.g., Pacific Decadal Oscillation, North Pacific Gyre Oscillation) time scales. In general, variance spectra for ocean phenomena are considered "red" (Steele 1985, Di Lorenzo and Ohman 2013), that is, by analogy with red light there is more variability at lower frequencies. Hence, the longer the time period of observation, the more inherent variability is uncovered in natural ocean ecosystems. Variations in abundance and biomass of many members of the pelagic food web reflect these low-frequency climate variations, including zooplankton (Lavaniegos and Ohman 2007), fishes (Hsieh et al. 2009), seabirds (Abraham and Sydeman 2004), and others. Against this background of intense, natural, low-frequency ocean variation it can be especially challenging to resolve underlying progressive secular changes in marine ecosystems. Differentiating change from the background variability requires both long time-series observations and an understanding of mechanistic connections.

The CCE LTER site is fortunate to be co-located with the preexisting California Cooperative Oceanic Fisheries Investigations program, an important multidisciplinary ocean observing program that has censused the planktonic fauna of the region, together with the physical and chemical environment, for 70 yr. This extensive ocean record is among the few available in the world ocean that permits long-term changes in the planktonic fauna to be differentiated from interannual and decadal variability. The importance of such a record is exemplified by considering interannual variations in springtime

abundance of total euphausiids (krill) in the CCE LTER region in 20-yr intervals (Fig. 3). Considering the past 65 yr in these time intervals, there is a faint suggestion of a negative trend in abundance for both of the first two time intervals (Fig. 3a, b), although neither of these trends is statistically significant ($P > 0.20$). The third and most recent time interval (Fig. 3c) similarly shows no significant trend. Although there is considerable interannual variability (note the logarithmic scales of krill abundance), some of which is related to depressions in abundance of the dominant euphausiids during El Niño events (Brinton and Townsend 2003), each of the three 20-yr intervals yields the same conclusion: There has been no significant temporal trend. One might conclude that there is long-term stability of the assemblage, punctuated by interannual perturbations. One might also conclude that any of the three time periods provides results that are sufficiently consistent with the other two and that there is little point in sustaining the measurement program beyond a 20-yr time frame. However, considered in its totality over a 65-yr span, a very different result emerges from the euphausiid time series (Fig. 4a).

A long-term secular *increase* in euphausiid abundance ($P < 0.0001$) becomes discernable only when the entire record is examined. This increase is masked by the year-to-year and decade-to-decade variations. The increase is robust to some changes in protocol over the time series (Brinton and Townsend 1981, Ohman and Smith 1995) and reflects a change in abundance of one of the dominant types of mesozooplankton in this ocean region. Euphausiids are important mediators of carbon export in this system (Stukel et al. 2013) and are significant prey items for a variety of marine fishes, seabirds, and marine mammals. Individual euphausiid species in this region often show variations in abundance that closely reflect specific interannual (Brinton and Townsend 2003) and inter-decadal time scales of forcing (Di Lorenzo and Ohman 2013) rather than this temporal trend, because of species-specific biogeographic distributions and life history traits (Brinton 1976, Di Lorenzo and Ohman 2013). However, summed across all euphausiid species, there is a progressive increase that cannot be discerned without sustained measurement programs spanning multiple decades.

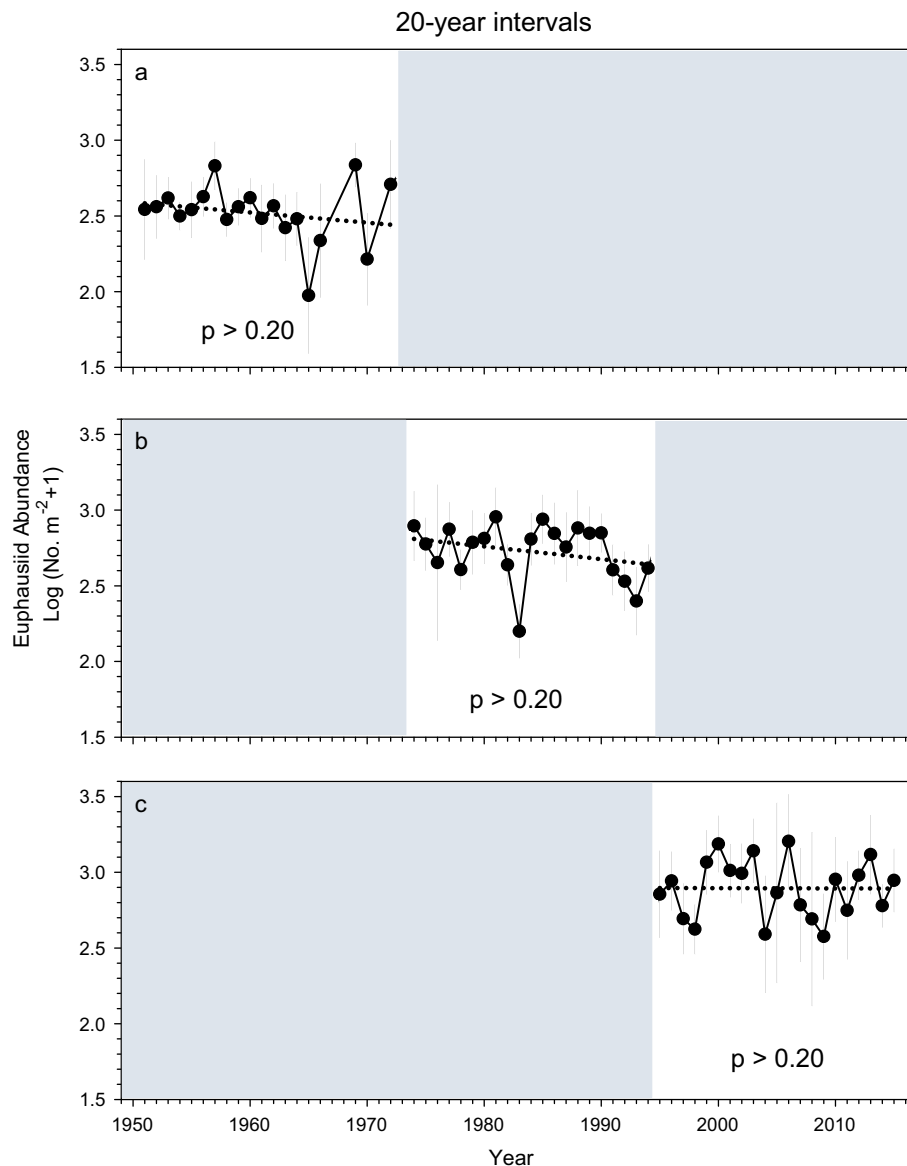


Fig. 3. Temporal variability in abundance of total euphausiids (krill) in the California Current Ecosystem LTER site, considered in three time intervals, each ~20-yr duration: (a) 1951–1972; (b) 1973–1993; and (c) 1994–2016. Linear regressions are not significant ($P > 0.20$) for any of the three time intervals.

Although increased euphausiid abundance (Fig. 4a) is correlated with long-term increases in sea surface temperature (Fig. 4b), the connection between these variables is indirect rather than a direct physiological effect of temperature. Ocean warming has led to increased density stratification in the North Pacific (Kim and Miller 2007). An accumulation of higher concentrations of dissolved nitrate occurs in deep waters as organic

matter is slowly remineralized during the longer residence time of deep waters that occurs in more stratified conditions (Ryckaczewski and Dunne 2010). These higher nutrient concentrations in the subsurface source waters that are eventually upwelled into the euphotic zone (Ryckaczewski and Dunne 2010, Bograd et al. 2015) explain a long-term increase in phytoplankton biomass (Aksnes and Ohman 2009). Such increases in

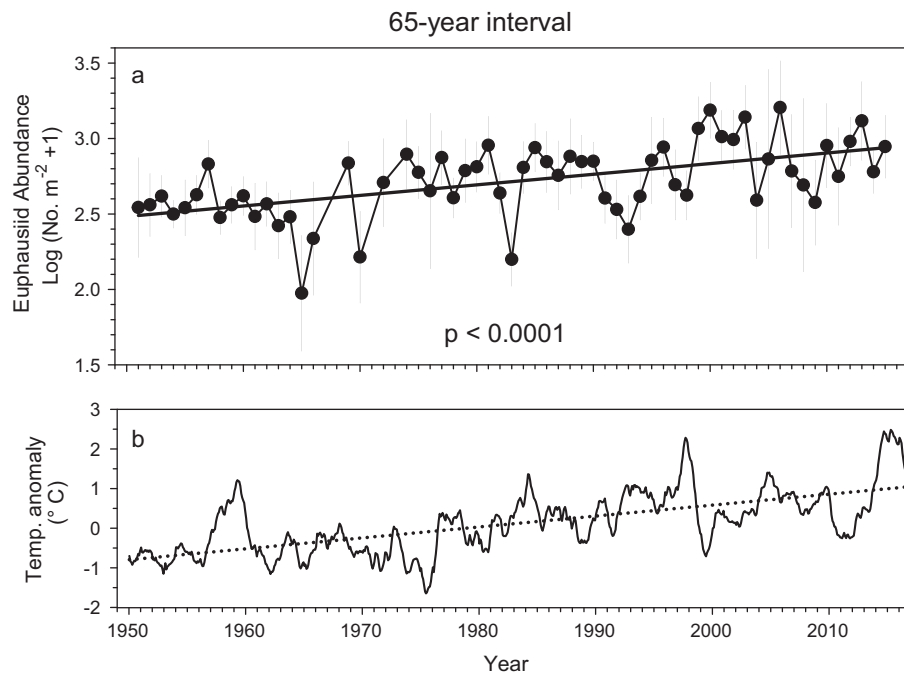


Fig. 4. (a) Temporal variability in abundance of total euphausiids (krill) in the California Current Ecosystem LTER site, considered over the entire 65-yr record. The linear regression is highly significant ($P < 0.0001$). (b) Temporal variability in ocean temperature anomalies at the Scripps pier, La Jolla, California. The linear regression is highly significant ($P < 0.0001$). Data courtesy of Shore Stations Program (<https://shorestations.ucsd.edu/data-sio/>).

phytoplankton prey for euphausiids lead to improved euphausiid growth and survivorship.

This result—the importance of sustained long-term measurements to discern temporal trends against a natural background of high ecosystem variability—recalls John Magnuson's (1990) metaphor of the “invisible present.” He underscored the importance of ecological processes that act slowly, or with time lags, in altering natural ecosystem dynamics. Undetected by the normal time scale of ecological research and the immediate experience of individual humans, such slowly acting, progressive changes might ultimately restructure natural ecosystems. Moreover, in the southern California Current System, progressive, long-term changes interact with natural interannual and multi-decadal variations in ways that are not fully understood. Interactions of processes on multiple time scales might lead to rapid crossing of ecological thresholds and abrupt changes in ecosystem state (cf. Scheffer et al. 2009, Bestelmeyer et al. 2011). Developing a

framework for forecasting future ecosystem states depends upon sustained time-series measurements closely integrated with mechanistic process studies.

COWEETA LTER: WHAT CAN LONG-TERM DATA CAN REVEAL ABOUT HOW SOUTHERN APPALACHIAN FORESTS WILL RESPOND TO INVASIVE SPECIES, LAND MANAGEMENT, AND CLIMATE CHANGE?

At the Coweeta (CWT) LTER site, a series of lagged responses to vegetation change associated with invasive species has caused surprising ecosystem state changes. Unexpected responses to climate variation also appear to be driven by lagged events. The surprising nature of these changes makes it very difficult to predict future ecosystem states.

Concurrent with climate change, fundamental changes in forest species composition and structure have occurred in the southern Appalachian

Mountains over the last century. An 80-yr forest monitoring record at the Coweeta Hydrologic Laboratory (location of the CWT LTER) has documented losses of foundation tree species (Elliott and Swank 2008) and the subsequent spread of a native evergreen understory shrub (Elliott and Vose 2012, Ford et al. 2012). The losses are driven by invasive species, and the resulting forest succession is influenced by ongoing responses to human activities (extractive logging, agriculture, fire exclusion, and species introductions) and increasing hydroclimatic extremes. Increasing air temperatures and seasonal and annual precipitation variability—with drier dry years, wetter wet years (Fig. 5; Laseter et al. 2012), and fewer rain days during summer and higher rainfall event amounts during the autumn (Burt et al. 2018)—have been documented in the long-term climate record at Coweeta. The potential growing season is lengthening, with warmer temperatures during both spring and late growing season months (Oishi et al. 2018). Observed spring leaf-out is occurring earlier than in previous decades, but leaf senescence is also arriving earlier, not later, because of late growing season droughts (Hwang et al. 2011, 2014). Consistent with our climatological and phenological observations, general circulation models project that the region will experience warmer temperatures and more frequent and severe drought (IPCC 2014).

Such consistent changes in climate should alter the competitive relationships among forest tree species by shifting interactions between biotic and abiotic processes within ecosystems. Such interactions include plant species responses to temperature, drought, and competition for light and moisture. Of particular interest are observations of forest composition change that do not match those predicted by coupled climate-envelope vegetation models (Iverson et al. 2004). The recent observed and predicted climate trends since 1980 would suggest a shift toward an oak-hickory (more conservative water use with ring-porous xylem anatomy) forest (McEwan et al. 2011, Vose et al. 2016), in agreement with climate-envelope vegetation models (Iverson et al. 2004). However, these projections are not yet supported by trends in our long-term vegetation data. Instead, mesophytic species (less conservative water use with diffuse-porous xylem anatomy) such as red maple (*Acer rubrum* L.) and tulip poplar (*Liriodendron*

tulipifera L.) have proliferated (Elliott and Vose 2011, McEwan et al. 2011, Caldwell et al. 2016; Fig. 6), that is, mesophication (sensu Nowacki and Abrams 2008).

While oaks are dominant in the region, their regeneration over the last century is lower than that of red maple and other mesophytic species (McEwan et al. 2011). Fire exclusion could partially explain recent declines in oak regeneration (Abrams 2005). In the Coweeta Basin, tree recruitment has also likely been suppressed by the expansion of rhododendron (*Rhododendron maximum* L.), which is in turn a consequence of American chestnut (*Castanea dentata* (Marsh.) Bork.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) loss. Our long-term forest demography data suggest that a chain of disturbances—starting with widespread logging in the 19th century, the loss of American chestnut by the mid-20th century, and finally the hemlock woolly adelgid (*Adelges tsugae* Annand) invasion in the late 20th century—led to a cascade of overstory, midstory, and soil responses that permitted an expansion of rhododendron (Fig. 6). Our research shows that the dense rhododendron subcanopy strongly attenuates light (Clinton 2003), suppresses herbaceous plant and tree seedling growth and density (Clinton et al. 1994, Beckage et al. 2000, Hille Ris Lambers and Clark 2003), is associated with reduced overstory tree productivity and height (Bolstad et al. 2018), and reduces nitrogen availability in the soil mineral and organic horizons (Wurzburger and Hendrick 2007, 2009). Therefore, the response of future forests to hydroclimatic extremes might depend on these tree–shrub interactions that manifest through disturbance legacies and indirect effects.

Reasons for the lack of alignment between long-term vegetation records and climate–vegetation models are unclear. One possibility is lagged effects: Perhaps we have not observed the system long enough for climate shifts that might cause differential mortality in the regeneration layer to be promulgated to the overstory tree composition. Interactions with topography may also be buffering the downslope communities from the otherwise negative effects of hydrologic or atmospheric drought. Downslope communities display much more sensitivity to hydroclimate variation than upslope communities (Elliott et al. 2015); however, in years that are only

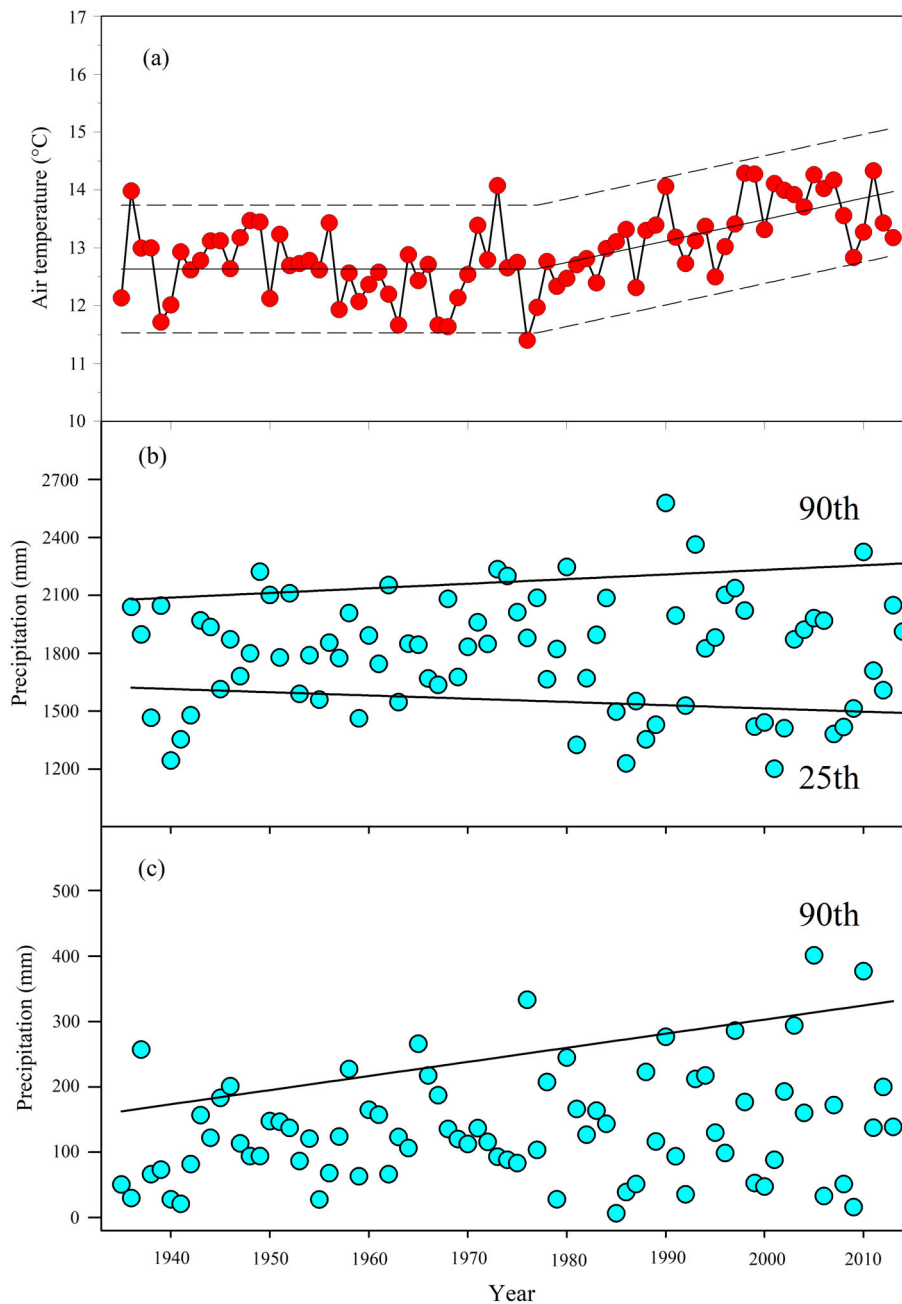


Fig. 5. Annual air temperature, annual precipitation, and September precipitation at Coweeta Hydrologic Laboratory since 1934. (a) Annual air temperature: Minimum, average, and maximum temperatures have increased over time. Calculated from 1975, 1977, or 1987, temperatures have been increasing at the same rate of 0.4°C per decade. (b) Annual precipitation: No trend in the average precipitation is evident, but precipitation is becoming more variable, with wet years becoming wetter and dry years becoming drier. Summer months are becoming drier while fall months are becoming wetter. (c) September precipitation: Only the most extreme part (>85%) of the distribution increased over time due to an increase in high intensity, shorter duration storm events, such as tropical storms, as opposed to an increase in the number of storms per month (Laseter et al. 2012).

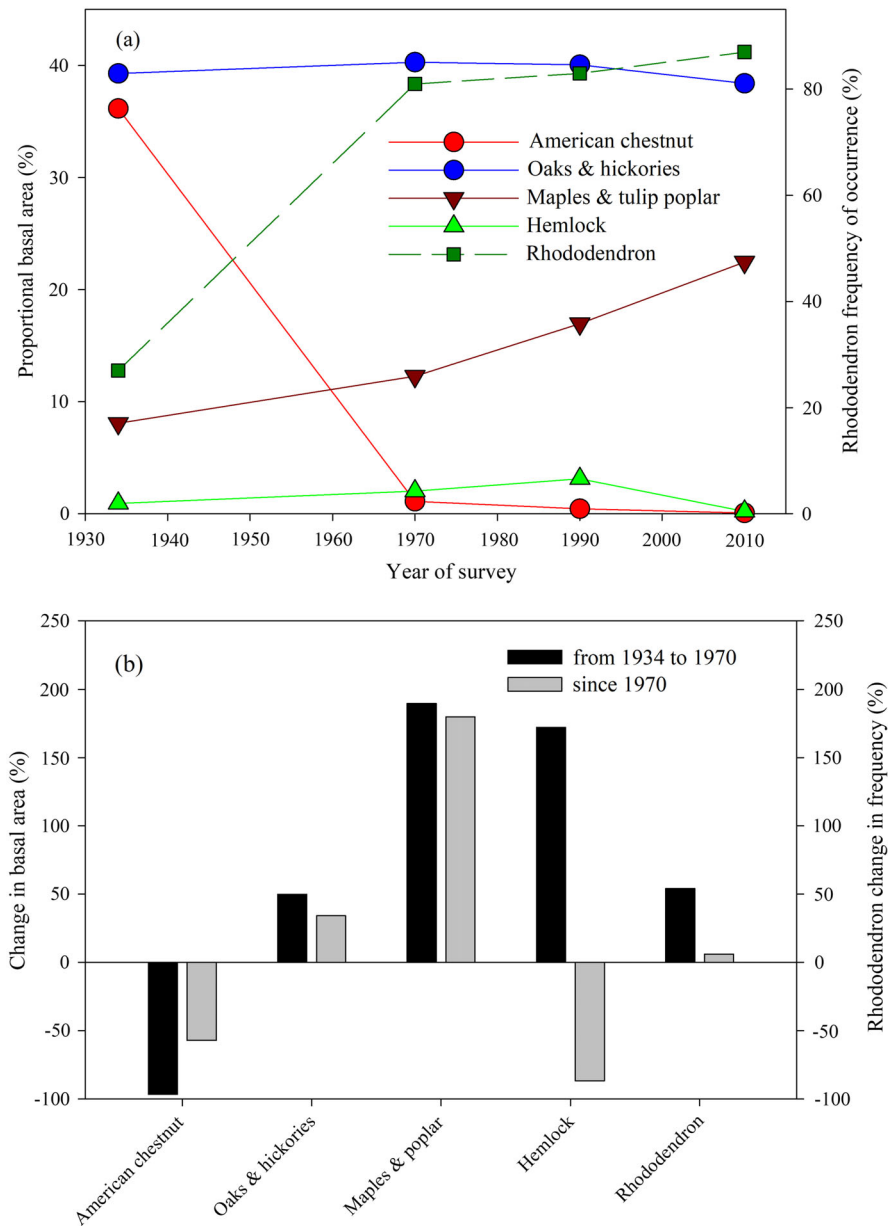


Fig. 6. Compositional changes for the dominant species grouped by functional type. (a) Proportional basal area for American chestnut, all oaks and hickories (OH, conservative water use, ring-porous), all maples plus tulip poplar (MP, less conservative water use, diffuse-porous), and eastern hemlock on left y -axis; and frequency of occurrence for *Rhododendron maximum* on right y -axis (Elliott and Vose 2012). Only presence-absence data were available for rhododendron for the survey in 1934. (b) Dominant species changes in basal area from 1934 to 1970, following the chestnut blight pandemic (Elliott and Swank 2008), and from 1970 to 2010.

moderately dry, they maintain similar water use as in wet years, due in part to soil moisture subsidies from upslope areas (Hawthorne and Miniati 2018). Downslope communities also experience

cold-air drainage flows along topographic paths during drought conditions that minimize nighttime respiratory carbon losses (Novick et al. 2016).

Even though we have not yet seen mortality of mesophytic tree species and recruitment into the canopy of more drought-tolerant oaks and hickories, we have documented long-term differences in growth between these functional groups (Fig. 7). Across all topographic positions, tree growth for both functional groups (i.e., mesophytic vs. oak-hickory) was more sensitive to the distribution of rainfall (i.e., number of small storms and dry-spell length) in the current and previous growing seasons than to the total amount of rainfall (Elliott et al. 2015). However, the percent increase in basal area growth from a drought to a wet year depended on the xylem characteristics of the functional group (Fig. 7). Under extreme wet conditions compared to the extreme drought conditions, such as the 1985–1988 drought, the mesophytic group had 78% higher radial growth, whereas growth for the oak-hickory group was only 16% higher. Under drought, on upslope sites, the mesophytic group

grew significantly less (23% less) than the oak-hickory group (Fig. 7). These results suggest that small storms can provide sufficient relief from moisture stress and potentially increase carbon assimilation; of particular concern is that the long-term climate record shows that the number of small storms is decreasing. While our data show that mesophytic trees can take advantage of wet periods more than oak-hickory trees can, during dry periods the mesophytic trees will be at a disadvantage. A “big” surprise from our long-term data is that variation in the temporal distributions of rainfall in years with similar rainfall totals can alter aboveground biomass growth by as much as 25–29%.

While the oak-hickory group might replace the mesophytic group in the long run across all topographic positions because of more frequent and longer droughts predicted under climate change, this process might take decades, as have other ecological shifts at Coweeta (Hwang et al. 2014,

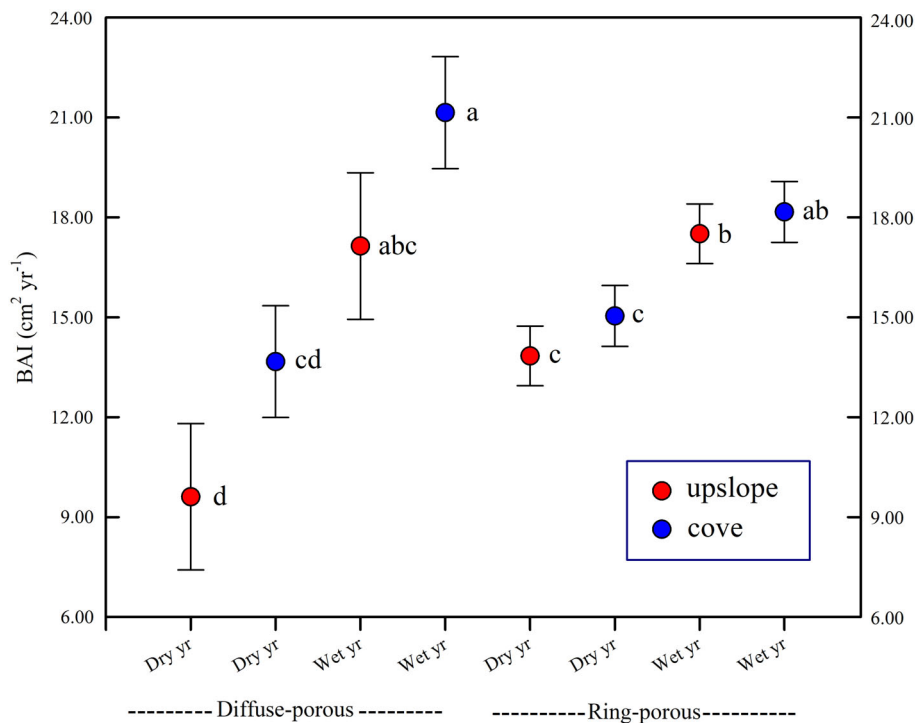


Fig. 7. Basal area increment (BAI, cm^2/yr ; mean \pm standard error) for dry years (1986, 2000) and wet years (1973, 1995) of diffuse-porous (*Acer rubrum*, *Liriodendron tulipifera*) and ring-porous (*Quercus alba*, *Q. montana*, *Q. rubra*) functional groups growing on cove or upslope topographic moisture conditions. Letters (a, b, c) denote significant differences. (From Elliott et al. 2015.)

Jackson et al. 2018). We would expect, however, that the transition to increased abundance of oaks and hickories would be realized soonest on the drier, upslope topographic positions in the southern Appalachian Mountains. By tracking species compositional changes and climate, we will be able to document these longer-term, species–climate interactions.

VULNERABILITY TO EXTREME CLIMATE EVENTS: EFFECTS OF A 100-YR COLD EVENT ON FISH COMMUNITIES AND FISHERIES IN THE FLORIDA COASTAL EVERGLADES LTER

At the Florida Coastal Everglades (FCE) site, long-term data were used to evaluate lagged effects of a cold spell on coastal fish communities and the valuable recreational fisheries they support. There were surprising effects across multiple trophic levels, raising questions about our ability to predict the future state of these ecosystems in the face of anticipated increases in climate variability in this region.

Forecasts of anthropogenic climate change predict not only shifts in average conditions, but also an intensification and increased frequency of extreme climate events (IPCC 2012, Diffenbaugh et al. 2017), including extreme cold spells (Gao et al. 2015). These extreme cold spells could have profound effects in shaping the distribution of species, with implications for ecosystem structure, function, and services, particularly at the latitudinal extremes of species distributions (Boucek et al. 2016, Osland et al. 2017a, b). One example of extreme cold events affecting species range dynamics is in the subtropics, such as the extreme 2010 cold event that affected the southeastern United States, South Florida, and the FCE.

In January 2010, a record negative state of the Arctic Oscillation allowed for cold air from the jet stream to be deflected further south than normal, bringing unusually frigid temperatures to the Everglades region. South Florida experienced extremely low temperatures, including a record low at Key West of 6°C, the second lowest temperature since 1873. Conditions were particularly extreme in the estuaries of FCE, where water temperatures rapidly dropped to levels known to be lethal within 3–4 d for many native and nonnative tropical species (<10°C) and remained

at sublethal levels for about two weeks (see next section for effect on mangrove forests). Based on the severity of extreme cold events reaching south Florida over the past 85 yr, the 2010 cold spell was likely a 100-yr event (Boucek and Rehage 2014; Fig. 8).

Despite their importance, there are relatively few studies of extreme climate events compared to those examining gradual climate change (Jentsch et al. 2007). This discrepancy underlines the importance of long-term data collection to capture episodic extreme events and, importantly, to establish baseline conditions that can be used to evaluate the magnitude and severity of ecological responses and lags. Further, long-term data sets on higher-order trophic levels are often lacking, making it difficult to examine the response of key consumers and ecosystem service providers to extreme climate events. We used three long-term data sets to track the effects of the 2010 cold spell on coastal fish communities

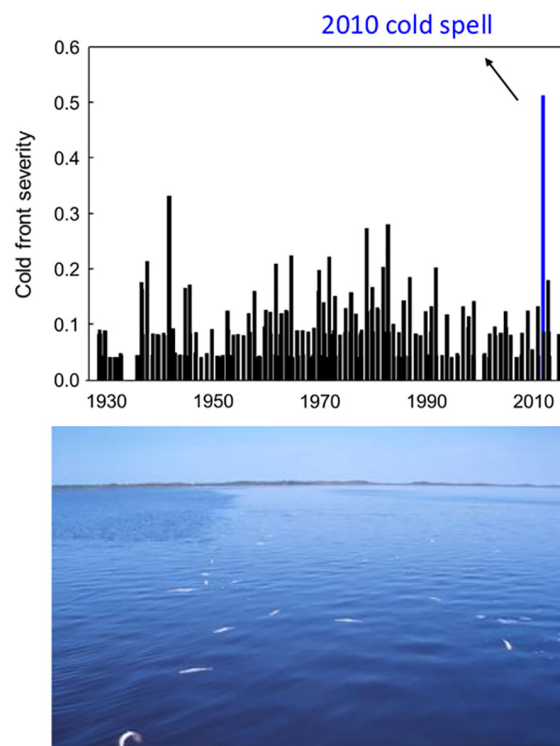


Fig. 8. Severity of the January 2010 cold spell relative to 319 previous cold fronts recorded in the Everglades region since 1927. (Modified from Boucek and Rehage 2014.)

and the valuable recreational fisheries they support in areas around the Florida Coastal Everglades. These included the following: (1) electrofishing aimed at tracking fish community dynamics (Boucek and Rehage 2014, Rehage et al. 2016, Stevens et al. 2016), (2) recreational fish records to examine recreational species responses (Santos et al. 2016), and (3) acoustic telemetry aimed at tracking fish distribution and space use (Boucek et al. 2017). The combination of these three data sets provides a robust understanding of the multifaceted response of coastal fish assemblages to extreme temperature events.

Using a functional trait approach, we showed that the 2010 extreme cold front caused major shifts in community structure (Boucek and Rehage 2014). Interspecific differences in cold tolerance drove predictable changes in the functional traits represented in the fish community, with the 2010 event negatively affecting half of the fish community, severely reducing the abundance of tropical euryhaline and nonnative species, and reorganizing dominance in favor of temperate freshwater species. For instance, tropical Common Snook showed a 62% decline in catch per unit effort (CPUE) in the three years post-event

(Fig. 9). Notably, nonnative fishes were virtually eliminated from the system (93% decline, Fig. 9, likely reflecting slow recolonization due to the long distance to warmer canal refuge populations) and did not recover for several years (Rehage et al. 2016). This slow recovery suggests the potential for management-intervention windows associated with extreme events. In contrast, temperate taxa such as Florida largemouth bass showed no declines (Fig. 9).

Several species in the coastal fish community of FCE support an economically valuable recreational fishery. Using long-term catch records, we documented a significant shift in the recreational catch structure, indicating the high sensitivity of these fish populations and fisheries to extreme temperature events (Santos et al. 2016). While some fish species experienced an expected decline (due to thermal sensitivity; Bonefish, Common Snook, Goliath Grouper), others showed an increase in catch, potentially resulting from a release from competition or predation (i.e., Red drum, and Gray Snapper). By comparing pre- and post-cold spell population dynamics, Stevens et al. (2016) showed that both the resistance and resilience of recreational fish were low for FCE

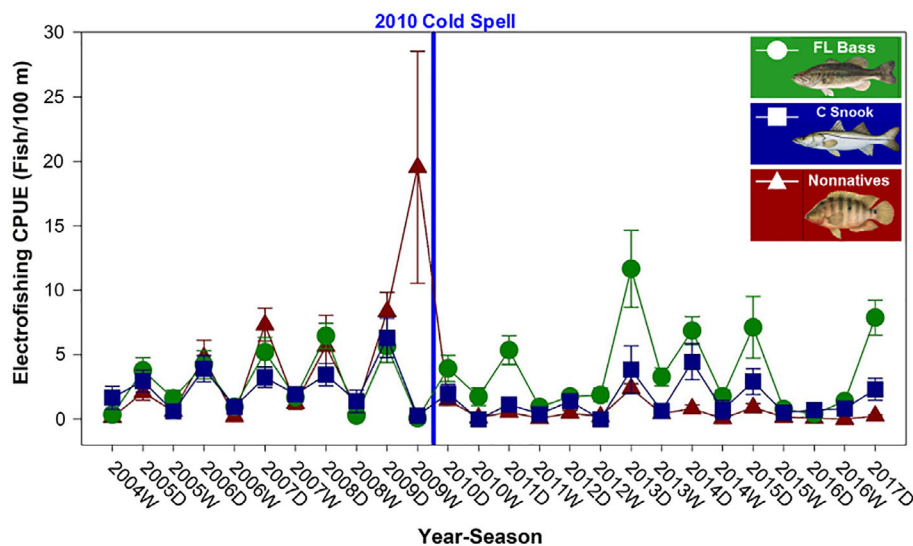


Fig. 9. Mean electrofishing catch per unit effort (CPUE) for Florida Largemouth Bass (FL Bass), Common Snook (C Snook), and all nonnative fish taxa combined (nonnatives) across wet (W) and dry (D) season samples for the period 2004–2017. Blue vertical lines show the timing of the 2010 cold event and associated declines in the tropical components of the fish community (C Snook and nonnatives) and no decline for the temperate FL Bass (Rehage 2019).

relative to northern estuarine areas along the western Florida coast (Charlotte Harbor and Tampa Bay). Common Snook experienced the highest level of population decline (94%) and the slowest recovery rates in the coastal Everglades (4 vs. 1–2 yr in northern estuaries). The reasons for this variation are unknown, but we hypothesize they are related to differences in estuary geomorphology and habitat availability (e.g., extent of deeper and warmer microhabitats), differences in the movement strategies of segments of the population, and possibly population-level variation in thermal tolerances.

Last, we focused on how the effects of the cold event might be mediated by animal movement and behavior (Boucek et al. 2017). Increasingly, new tracking techniques are highlighting the importance of animal movement in influencing ecosystem processes (Doughty et al. 2016). An acoustic array deployed in the coastal mangroves has allowed us to examine a variety of consumer dynamics at a long-term temporal scale (>5 yr), which is quite rare in animal movement studies (Matich et al. 2017). By closely tracking small-scale temperature variation and snook distribution for several years, we showed the capacity for specific habitat patches within the landscape to modulate stress from extreme climate events and for variation in snook distribution to influence their vulnerability to cold spells. Snook habitat use varied across years of different hydrological conditions, resulting in temporally dynamic vulnerability to these extreme events.

In sum, extreme events such as the 2010 cold event can greatly inform our understanding of biological response across multiple levels of organization (see section on mangrove effects below), because they allow us to observe the rare tails in both driver and response (Smith 2011, van de Pol et al. 2017). These rare glimpses at biological responses can be instrumental in expanding the understanding of key ecological and evolutionary processes operating in our study systems, and of the drivers and constraints affecting recovery, time lags, and overall system trajectories. This is particularly important in the tropics, where changes in climate variability are likely to have especially important impacts (Diffenbaugh et al. 2017).

A key consideration for the relevance of these effects is what can we expect for extreme climate

events in the future? Climate simulations show that extreme events are attributable to human influences and that these events are expected to increase in probability and severity, with a non-linear dependence on warming trends. Fischer and Knutti (2015) showed that with a 2°C warming (present-day warming is 0.85°C), extreme precipitation events that occurred every 30 yr in pre-industrial conditions will occur every 10–20 yr, while the probability of hot extremes doubles between 1.5°C and 2°C global warming. Diffenbaugh et al. (2017) showed that historical global warming has increased the severity and probability of hottest days and months as well as the probability of the driest and wettest events. For extreme cold events in particular, recent evidence points to colder winters and an increased occurrence of extreme cold events along the eastern United States, eastern Asia, and the UK. These are expected as a function of warming in the Arctic and its effects on the position of the jet stream (Overland et al. 2016). These changes lead to arctic sea-ice loss and weakening and shifting of the polar vortex away from North America, allowing for cold arctic air to move to lower latitudes (Zhang et al. 2016). Overall, these trends point to an increased probability of crossing ecologically relevant thresholds that could result in an important reorganization of ecological systems, emphasizing the need to continue long-term data collection, along with mechanistic efforts that improve our understanding of the impact of extreme climate events on ecological and evolutionary processes.

MANGROVE WETLANDS: MARKING THE IMPACT OF CLIMATE CHANGE IN THE FLORIDA COASTAL EVERGLADES LTER

Long-term data from the FCE LTER site are currently used to evaluate mangrove wetlands resilience and resistance at the regional scale. These analyses encompass responses to cold spells, hurricanes, and sea level rise. They also include assessment of lagged effects when intense land-use change may inhibit the ability of mangrove wetlands to colonize new inland areas in response to warmer climate and saltwater intrusion associated with higher sea level.

The Florida Coastal Everglades contain the largest mangrove area in the continental United

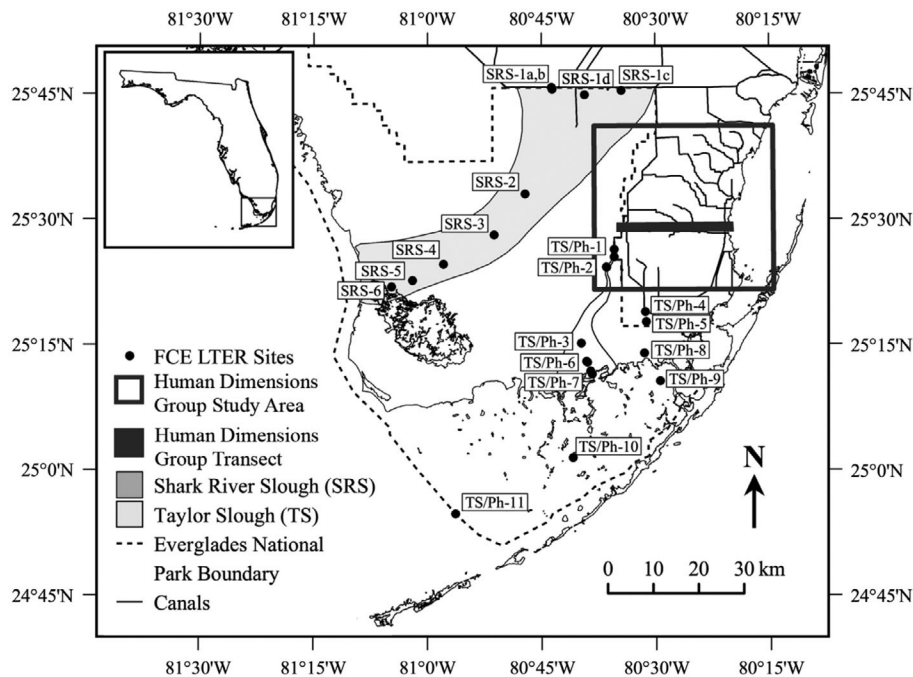


Fig. 10. Map of South Florida showing the 17 FCE LTER sites. SRS-1 through -6 are along the Shark River Slough transect; TS/Ph-1, -2, -3, -6, and -7 are in Taylor Slough; TS/Ph-4, -5, and -8 in the C-111 basin/ENP panhandle; and TS/Ph-9, -10, and -11 are in Florida Bay.

States, located within the boundaries of the Everglades National Park in South Florida (Simard et al. 2006, Gaiser et al. 2015; Fig. 10). This coastal region of the FCE is close to the boundary between temperate and subtropical regions where rapid shifts in habitats and foundation species (Dayton 1972, Ellison et al. 2005) and coverage are occurring at an accelerated pace (Osland et al. 2017a, b). This area is also highly impacted by both tropical storms and sea level rise associated with climate variability and change. We know that tropical storms are seasonal high pulsing disturbances with both negative and positive effects on the structural and functional properties of mangrove forests. However, it is not clear how mangroves will respond to the combined impacts of natural and landscape level human disturbances in the next decades. Here, we assess how the use of long-term records at different spatial-temporal scales has contributed to the understanding of mangrove resilience across the Everglades Mangrove Ecotone Region and how this ecosystem property needs to be considered in the economic valuation

and assessment of the sustainability of mangrove ecosystem services to society.

Our long-term studies of mangrove wetlands at FCE have produced information relevant to evaluating interactions among resources (e.g., nutrients), regulators (e.g., salinity, hydrogen sulfide), and hydroperiod (i.e., duration and frequency of inundation and water depth) that control functional mangrove attributes (e.g., net primary productivity, carbon storage, and sequestration) (Krauss et al. 2006, Castañeda-Moya et al. 2011, Castañeda-Moya et al. 2013, Rivera-Monroy et al. 2013). These studies are also relevant to assessments of the pulsing effect of climate drivers on mangrove biomass and productivity (Chen and Twilley 1999, Childers 2006). For instance, although the average temperature in South Florida is within the range of 10–30°C during the dry months (November–March), cold spells are recurrent in the region and could have a major impact on the survival rate and spatial distribution of organisms (Boucek and Rehage 2014, Boucek et al. 2016), including mangroves (Barr et al. 2012, Troxler et al. 2015,

Danielson et al. 2017). The 2010 cold spell was a statistically extreme disturbance (1927–2012) where the lowest registered minimum temperatures were -3.3°C (see section above for further details). Our long-term (2001–2014) data analysis of forest productivity (net primary productivity litterfall, NPP_L) revealed uneven canopy defoliation patterns in our sites caused by low temperatures, with the greatest effect in the site with the tallest mangrove canopy and higher soil total phosphorus density ($>15\text{ m}$, SRS-6; Ewe et al. 2006, Danielson et al. 2017). However, forest recovery was rapid; within a month of the initial disturbance, forests returned to average productivity values (NPP_L range: $0.4\text{--}1.0\text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$; Fig. 11).

Because the FCE and the Everglades Mangrove Ecotone Region are impacted by natural disturbances at different temporal and spatial scales, we were able to evaluate the combined mangrove forest response to both the 2010 extreme cold spell and Hurricane Wilma in 2005 (Danielson et al. 2017; Fig. 12). Despite the high pulsing recurrence of hurricanes in South Florida, little quantitative information exists concerning their impacts on mangrove forest structure, succession, species composition, mangrove-dependent fauna, or rates of ecosystem recovery (Zhang et al. 2008, Smith et al. 2009). Although the frequency of storms in the region is not projected to increase with global warming, it is expected that “potential destructiveness” will increase along with global temperatures (Emanuel 2005). In

2005, we were able to quantify mangrove forest recovery time after Hurricane Wilma, a category 3 storm at the time of landing in on the southwestern coast of the Everglades Mangrove Ecotone Region (Castañeda-Moya et al. 2010). Just as with the cold spell, the impact of Hurricane Wilma was uneven and dependent on the wind direction and the storm point of entrance at the mouth of the Shark River estuary (Figs. 10, 12). However, the recovery time was longer, ranging from four to five years (Fig. 12a–c; Danielson et al. 2017). This disturbance underscored the importance of ecophysiological differences among the mangrove forest foundation species (Fig. 13a) where the NPP_L of *Laguncularia racemosa* (Fig. 13c), a multi-stemmed shade-intolerant species with capacity for resprouting, stabilized faster in phosphorus-rich environments than other species lacking this adaptation (e.g., *Rhizophora mangle*; Fig. 13b; Danielson et al. 2017). Since resprouting confers persistence under disturbance, understanding this physiological trait is critical for assessing long-term vegetation dynamics such as the patterns of carbon accumulation in both aboveground and belowground organs as disturbance regimes shift under climate change (Bond and Midgley 2001, Bond et al. 2003, Bradley and Pregitzer 2007).

In contrast to the sudden impact of strong winds (hurricanes, Fig. 13d) and low temperatures (cold snap, Fig. 11), sea level rise represents a persistent impact on mangrove forest structure and productivity. Indeed, one of the current

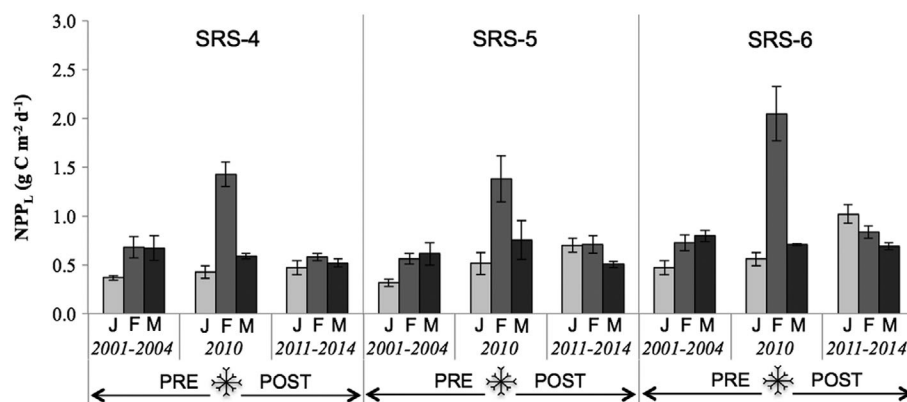


Fig. 11. Daily net primary productivity litterfall (NPP_L) rates ($\text{g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$; mean \pm standard error) before and after the cold snap event (marked by a snowflake symbol). Pre (January–March 2001–2004, January 2010), Post-Immediate (February 2010), and Post (January–March 2011–2014, March 2010). (From Danielson et al. 2017.)

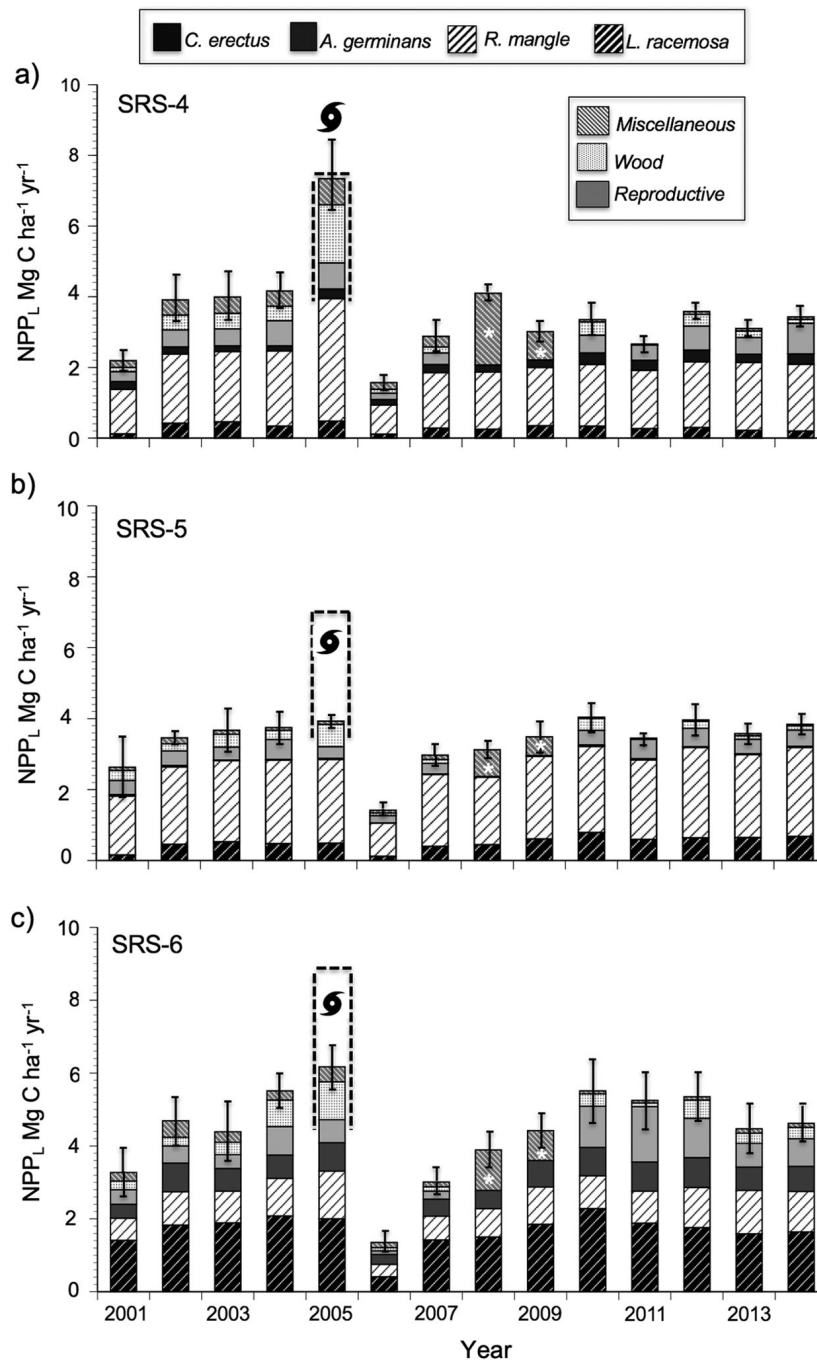


Fig. 12. Annual net primary productivity litter (NPP_L; Mg C·ha⁻¹·yr⁻¹) with Wilma defoliation estimates estimated for SRS-5 (b) and SRS-6 (c) based on litterfall directly measured in SRS-4 (a). Miscellaneous components with asterisks denote years when wood and reproductive components were included in the miscellaneous component. Dotted rectangle indicates defoliation estimates based on data from SRS-4 (a) (see Danielson et al. 2017 for details). The hurricane symbol above the 2005 bar indicates Hurricane Wilma impact.

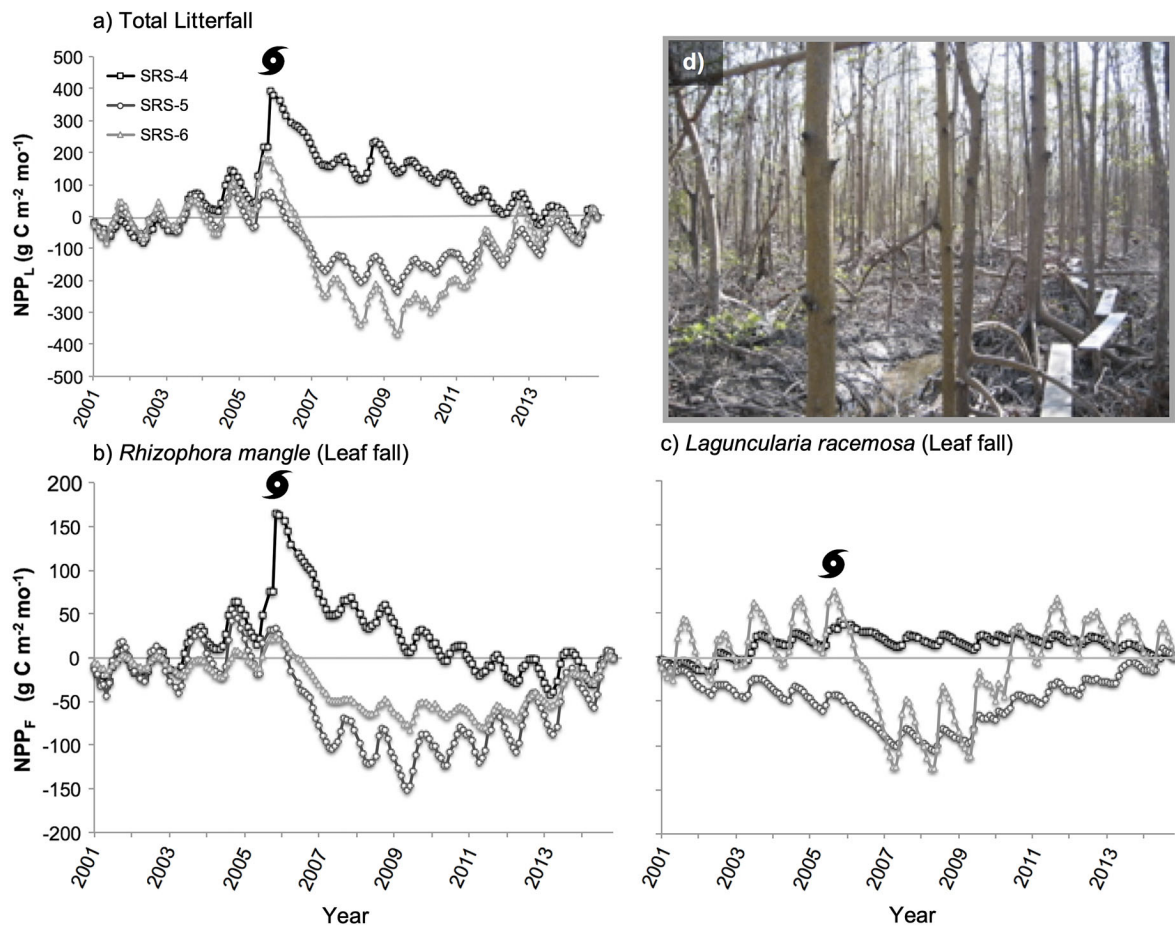


Fig. 13. Cumulative sum (cusum) graphs for (a) total litterfall (net primary productivity litter, NPP_L : g C·m⁻²·month⁻¹), (b) *Rhizophora mangle* leaves only (NPP_F : g C·m⁻²·month⁻¹), and (c) *Laguncularia racemosa* leaves only (NPP_F : g C·m⁻²·month⁻¹). A segment with a positive slope in a cusum graph indicates a period when values in the original series were above average, and vice versa, while a horizontal segment represents at-average values. The inset photograph (d) shows canopy defoliation in SRS-6 from Hurricane Wilma. (Photo credit: Victor H. Rivera-Monroy, December 2005.) (From Danielson et al. 2017.)

challenges to coastal Florida's socioeconomic sustainability in the context of climate change is increasing sea level (Nungesser et al. 2015, Dessu et al. 2018). It is expected that sea level will increase from 0.8 to 2.0 m in this century with major effects on the biodiversity and productivity of coastal ecosystems that provide critical ecosystem services (e.g., fisheries, tourism) to society close to an urban center (i.e., Miami metropolitan area, population 6 million). In contrast to the potential negative impacts of sea level rise to human-dominated systems (e.g., urban and agriculture areas), our palynological studies

show that mangrove wetlands are readily adapted to increasing sea level and they are excellent indicators of major shifts in coastal vegetation composition and dominance during the mid-Holocene (~6000 cal yr. BP; Yao et al. 2015). Contemporary observations indicate that this transgression is still taking place in the Everglades where *R. mangle*-dominated scrub mangroves have replaced sawgrass-dominated wetlands since the 1940s (Ross et al. 2000). It is projected that if sea level rise reaches 2.33 mm/yr in the 21st century in south Florida, mangrove establishment could reach central Florida (Yao

and Liu 2017). This regional “success story” of a net gain in mangrove wetlands and associated ecosystem services contrasts with global mangrove coverage, which has been dramatically reduced (~50%) by human activities during the last four decades (Giri et al. 2011, Rivera-Monroy et al. 2017). While Everglades mangroves have been able to expand because of their location inside the protected boundaries of Everglades National Park (Fig. 10), there are significant potential negative impacts associated with landscape level changes in hydrology and water quality associated with urban and agricultural development taking place thousands of kilometers upstream from the Everglades Mangrove Ecotone Region (Rivera-Monroy et al. 2019). Changes in mangrove extent have economic impacts since these ecosystems can store significant amounts of “Blue Carbon” (carbon captured by the world’s ocean and coastal ecosystems, including sea grasses, mangroves, and salt marshes) in soil and vegetation (Jerath et al. 2016), with a nominal economic value of \$13,859–\$23,728 ha⁻¹ (Rivera-Monroy et al. 2011, Jerath et al. 2016).

Our long-term studies have underscored the key ecological function and economic value of mangrove wetlands in the Everglades Mangrove Ecotone Region, a dynamic ecosystem regulated by complex interactions among natural (climate variability and change, sea level rise) and human impacts (hydrological restoration). Although ecosystem shifts are expected, there are major uncertainties related to the rate, magnitude, and ecosystem trajectory of such changes (i.e., tipping points, resilience, time lags) and their net long-term impact on the sustainability of natural resources underpinning human well-being.

SUMMARY AND CONCLUSIONS

Time lags remain one of the greatest challenges to developing a framework for forecasting future ecosystem state. Although the focus of our synthesis effort was to provide insight into the future state of ecosystems, analysis of time lags inherently looks at events in the past that have had effects on the current state. Still, the case studies presented here illustrate how sustained time-series measurements closely integrated with mechanistic process studies can help to address

this challenge in specific ways. Modeling results from the Arctic, where climate is changing more rapidly than anywhere on earth, suggest that ecosystem characteristics that integrate over longer periods of time might be better indicators of a response to climate change than rapidly responding characteristics. In the California Current Ecosystem, increases in nutrient concentrations associated with ocean warming have led to changes in zooplankton populations that have only become clear after 65 yr of monitoring. In Appalachian forests, the loss of foundation tree species is leading to profound changes in ecosystem structure, function, and services, but the legacy effects have taken 80 yr to become obvious. The structure and function of wetland vegetation and fish populations along the southeast U.S. coast are affected by infrequent extreme cold spells and recurrent hurricanes interacting with increasing sea level rise that will play out over decades.

Although most of our examples describe events in the past that have had effects on the current state, they also point the way forward for incorporating time lag effects into predictions of future ecosystem state. For example, the arctic example shows how long-term data and a simulation model can be combined to test concepts about different features of ecosystems respond to changes in climate at different time scales and how this affects our ability to predict both short- and long-term drivers of change.

Moreover, none of our examples are a “simple” time lag where there is an action and at some later time there is a consequence. Rather, as is appropriate for long-term ecological research, these examples are about interactions playing out over time. Still, while the patterns presented in the case studies are more about complex temporal dynamics than time lags per se, they all highlight the importance of recognizing that current (and future) conditions may well depend on events that occurred long in the past.

These case studies raise questions about emerging challenges and opportunities as the LTER network matures and begins to move from long-term to very-long-term ecological research. Further insights into time lags are likely to evolve over the next couple of decades and highlight how the diversity of biomes represented within the LTER network facilitates a broader

understanding of important drivers of ecosystem structure, function, services, and futures.

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