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

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

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Abstract. Understanding the complex and unpredictable ways ecosystems are changing and predicting the state of ecosystems and the services they will provide in the future requires coordinated, long-term research. This paper is a product of a U.S. National Science Foundation funded Long Term Ecological Research (LTER) network synthesis effort that addressed anticipated changes in future populations and communities. Each LTER site described what their site would look like in 50 or 100 yr based on long-term patterns and responses to global change drivers in each ecosystem. Common themes emerged and predictions were grouped into state change, connectivity, resilience, time lags, and cascading effects. Here, we report on the "state change" theme, which includes examples from the Georgia Coastal (coastal marsh), Konza Prairie (mesic grassland), Luquillo (tropical forest), Sevilleta (arid grassland), and Virginia Coastal (coastal grassland) sites. Ecological thresholds (the point at which small changes in an environmental driver can produce an abrupt and persistent state change in an ecosystem quality, property, or phenomenon) were most commonly predicted. For example, in coastal ecosystems, sea-level rise and climate change could convert salt marsh to mangroves and coastal barrier dunes to shrub thicket. Reduced fire frequency has converted grassland to shrubland in mesic prairie, whereas overgrazing combined with drought drive shrub encroachment in arid grasslands. Lastly, tropical cloud forests are susceptible to climate-induced changes in cloud base altitude leading to shifts in species distributions. Overall, these examples reveal that state change is a likely outcome of global environmental change across a diverse range of ecosystems and highlight the need for long-term studies to sort out the causes and consequences of state change. The diversity of sites within the LTER network facilitates the emergence of overarching concepts about state changes as an important driver of ecosystem structure, function, services, and futures.

Key words: arid grassland; coastal grassland; coastal marsh; sea-level rise; shrub invasion; Special Feature: Forecasting Earth's Ecosystems with Long-Term Ecological Research; tallgrass prairie; tropical mountain cloud forest.

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INTRODUCTION

Ecosystems across the United States are changing in complex and unpredictable ways (Grimm et al. 2013). Challenges for predicting ecosystem responses have increased in recent years along with escalating climate change, air and water pollution, land-use change, and species redistribution (Steffen et al. 2005). Stakeholders from a variety of professions require knowledge about how ecosystems are changing to make effective decisions about resources and management. The following questions should be addressed to support stakeholder decisions/needs: (1) What populations and communities will dominate major ecosystems in 20, 50, or 100 yr? (2) Will communities interact with changing environmental conditions to assemble into novel ecosystems? (3) 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 research and monitoring networks, which began to develop in the 1960s (Golley 1996). 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 across a wide range of ecosystems. The LTER network began in 1980, with roots in earlier network efforts such as the International Biosphere Program (Callahan 1984). LTER sites were not chosen to represent major ecosystem types or natural biomes and do not collect synchronized sets of monitoring data. Rather, LTER sites were chosen in a competitive process based on the intellectual merit of ideas about how to study phenomena over long periods of time, using experiments, long-term monitoring, modeling, and comparative studies. LTER sites carry out integrative, cross-site research, and although monitoring is not synchronized, data collection is organized around the same five core research areas at each site: primary production, population studies, movement of organic matter, movement of inorganic matter, and disturbance patterns.

This paper addresses the concepts of *threshold*, the point at which a persistent change in an ecosystem quality, property, or phenomenon occurs, and *state change*, where small changes in an environmental driver transform the structure or function of the ecosystem (Holling 1973). These ideas have regained prominence over the last decade (Groffman et al. 2006, Biggs et al. 2018). Scientists and managers have had to reconsider factors historically thought to influence ecosystem stability, resilience, and state changes. This is due to the importance of non-equilibrium conditions, the need to integrate social, physical, and biological sciences in management, the overarching role of climate change as a driver, and improved detection of fundamental shifts in the structure and function of ecosystems (Gunderson 2000, Walker et al. 2006, Peters et al. 2007, Hicks et al. 2016, Jiang et al. 2018). Most recently, there has been a focus on how population, community, and evolutionary processes influence thresholds and state changes (Ratajczak et al. 2017*a*, Schiel et al. 2018, Dakos et al. 2019). There is a critical need to apply developing knowledge about state changes to provide evidence-based guidelines for ecosystem management (Suding and Hobbs 2009, Selkoe et al. 2015).

Recent efforts to make practical use of knowledge about state changes have focused on monitoring and predicting impending state changes (Scheffer et al. 2009, Brock and Carpenter 2010, Carpenter et al. 2011, Jiang et al. 2018), intervention strategies to prevent such changes (Biggs et al. 2009, Selkoe et al. 2015), and management of thresholds to direct ecosystems toward a favored state (Samhouri et al. 2010). These studies demonstrate that hallmarks of the LTER program, long-term data and experiments, are essential in diagnosing the causes of abrupt state changes in real-world systems (Ratajczak et al. 2018). There is also great interest in using ideas about thresholds and state changes to set goals and/or expectations for ecosystem services and functions in particular landscapes (Bestelmeyer 2006, Schiel et al. 2018). LTER studies also highlight the importance of population and community dynamics (the topic of this special issue) in state changes. Documenting and predicting state changes remain a grand challenge that is rarely addressed in monitoring and management programs at large scales (CCSP 2009, Jiang et al. 2018). There is a clear need for compilation and synthesis of empirical studies showing state changes across ecosystems to develop general principles that can inform management (Moore 2018). Key questions and issues that arise when applying threshold concepts to real ecosystems include identification of true state changes vs. nonlinear responses (Dodds et al. 2010), potential for state reversibility and the time scale of reversibility, and feedback mechanisms underlying hysteresis (Bestelmeyer et al. 2011, Biggs et al. 2018).

Use of the terms state change, threshold, tipping point, regime shift, and resilience varies in the literature (Van Nes et al. 2016). Our objective here is not to delve into the theoretical nature of ecosystem stability, or to propose new and standard terminology. Instead, our goal is to present clear examples of changes in ecosystem states within the LTER network to predict future states of these systems across the planet. Thresholds, tipping points, regime shifts, and resilience are implicated as processes and mechanisms that invoke state change, but are not directly addressed in this review. Consistent with our objective of developing a vision of future states, we present clear examples of ecosystem state changes that have occurred or will likely occur over the next 50–100 yr. These examples will be useful for theoretical efforts focused on standardizing terminology and advancing theory (Gaiser et al. 2020).

Here, we provide examples of state change analyses from five LTER sites: the Georgia Coastal (coastal), Konza Prairie (mesic grassland), Luquillo (tropical forest), Sevilleta (arid grassland), and Virginia Coastal (coastal) sites. The examples were selected by researchers at sites where evidence for state change is strong. They illustrate how long-term data collection can shed light on the causes and consequences of state change both within and across ecosystems. Examples range from analysis of climate change impacts upon tidal marshes, tropical cloud forests, and transitions among dryland ecosystems, to how the future of tallgrass prairie depends on managing disturbance regimes and restoration strategies, to long-term change in barrier island vegetation. We then discuss overarching concepts emerging from these examples.

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

1. Georgia Coastal Wetlands and a Changing Climate: Steven C. Pennings, Merryl Alber, Adrian Burd, Christopher Craft, Ellen Herbert, Christine Hladik, Daniela Di Iorio, Fan Li, John O'Donnell and John Schalles
2. The Future of Tallgrass Prairie Depends on Managing Disturbance Regimes and Restoration Strategies: Jesse B. Nippert, Sara G. Baer, Walter K. Dodds and John M. Blair
3. Climate Change and Tropical Mountain Cloud Forests in Puerto Rico: Grizelle González
4. Transitions among Dryland Ecosystems under Increasing Climate Variability: Jennifer A. Rudgers, Seth D. Newsome, Marcy E. Litvak, William T. Pockman and Scott L. Collins
5. Long-Term Change in Barrier Island Vegetation of the Virginia Coast Reserve: Julie C. Zinnert and Donald R. Young

Georgia Coastal Wetlands and a Changing Climate

Long-term data collected at the Georgia Coastal Ecosystems Long Term Ecological Research site (GCE) shed light on possible state changes within coastal wetlands from graminoid marshes into lower-stature and less-productive succulent marshes and/or to mangroves mediated by long-term changes in sea level, temperature, and land use. Tidal marshes provide important ecosystem services, from supporting coastal food webs to enhancing water quality to providing protection from wind and waves. The plants that dominate these habitats are ecosystem engineers that physically create wetlands by trapping sediments and depositing organic material, and foundation species that provide food and habitat for most of the other species in the ecosystem. Marshes on the Georgia coast are experiencing rising sea levels, warmer temperatures, and less space for upland migration, while predictions of future precipitation and river discharge are uncertain. Sea level is rising at an average rate of 0.32 cm/yr, but with tens of centimeters of variation among years (NOAA 2017). Temperatures in the southeast United States have been rising for the last five decades, with an increase of about 1°C in the southeast region since the 1970s (Carter et al. 2014). Precipitation has been variable over recent decades, and downscaled climate model predictions for the southeast show an increase, a decrease, or no change in precipitation depending on the model (Christensen et al. 2007, Karl et al. 2009). The human population of coastal Georgia is small but rapidly rising (Crossett et al. 2005, Evans et al. 2015), leading to both direct and indirect effects on coastal ecosystems.

There are four dominant habitat types in low-energy intertidal areas flooded with salt water (Fig. 1A): salt marshes dominated by graminoids, salt marshes dominated by succulents, un-vegetated salt pans, and mangroves (Gabler et al. 2017). The GCE site is dominated by graminoid salt marsh, with some succulent salt marshes and salt pans in areas where porewater evaporates and soils become hypersaline (Schalles et al. 2013). Mangroves are not currently present.

GCE scientists have monitored permanent plots and estimated plant productivity from Landsat 5 satellite images to determine how salt marsh plant productivity and community composition have changed over the last three decades. Years with high freshwater input from precipitation and river discharge have low soil porewater salinities and high plant growth (Więski and Pennings 2014, Li and Pennings 2016, O'Donnell and Schalles 2016). Years with high sea levels also have greater plant growth, probably due to increased flushing of salts out of intertidal soils. Unusually, hot summers, in contrast, lead to reduced plant production, either because porewater salinities increase or because plants exceed their thermal optimum.

Between 1984 and 2011, primary productivity of graminoid-dominated salt marshes in the GCE study area decreased by over 30% due to frequent droughts (Fig. 1B). It is not clear if these trends will continue, largely because of the uncertainty in predicting future precipitation. If frequent droughts continue, the most likely outcome is a state change in many areas from graminoid marshes into lower-stature and less-productive succulent marshes, as occurred in some Georgia marshes during the prolonged 1998–2002 drought (Fig. 1C). If the coastal climate warms enough that hard freezes no longer occur, mangroves are expected to spread from Florida up along the Georgia coast during this century (Osland et al. 2013), ultimately leading to a state change from graminoid salt marshes to mangroves (Fig. 1A).

Moving upstream in an estuary, the major intertidal habitats shift to brackish and fresh marsh. Rising seas are projected to push saline water further upstream into these habitats (Fig. 2A). Experimental studies show that increased salinities will suppress growth of the plants characteristic of low-salinity habitats (Fig. 2B), leading to communities typical of high salinities. Model scenarios across the Georgia Coast predict that sea-level rise is likely to cause wide-scale migration of tidal fresh, brackish, and salt marshes upstream at the expense of tidal fresh forest (Fig. 2C).

The platform of intertidal marshes must grow vertically to maintain elevation as sea-level rises; otherwise, marshes will submerge and convert to un-vegetated mudflat (Fig. 2A). Georgia estuaries are relatively high in suspended sediment and support high plant productivity, so the combination of sediment deposition and organic accumulation is likely to allow the majority of marshes to keep up with moderate rates of sea-level rise (Fig. 2C). Tidal fresh forests, however, have relatively low vertical accretion rates and are not keeping pace with the current rate of sea-level rise. Furthermore, salt water intrusion into tidal fresh forests and tidal fresh marshes will increase decomposition of their highly organic soils, due to increased sulfate reduction stimulated by the high sulfate content of seawater (Jun et al. 2013). This will slow vertical growth, making these habitats even more vulnerable to the push of saline water upstream (Craft 2012). At the same time, saline intrusion is likely to lead to an efflux of nutrients, especially N, from low-salinity wetland soils due to desorption of ammonium-N from cation exchange sites and increased decomposition, resulting in an input into the estuary.

Another important issue will be whether marshes have the room to migrate upslope as sea-level rises. Where marshes are allowed to migrate upland, models predict an increase in total marsh area in response to moderate rates of sea-level rise. However, many properties on the Georgia coast have armoring along the marsh edge that is designed to prevent tidal flooding and marsh migration (Alexander 2010). Shoreline hardening or armoring is a widespread management tool in populated coastal areas with potentially negative consequences for biodiversity and ecosystem services (Gittman et al. 2016, Dugan et al. 2018). Armoring reduces the "accommodation space"—room for the marsh to migrate inland—and is likely to become more prevalent as the human population increases and sea level continues to rise. The likely result will be a loss of high marsh habitats that will be the first to be squeezed between armoring and rising seas.

We expect coastal marshes in Georgia to persist over the coming century. However, we expect sea-level rise to cause losses in tidal fresh forests and both upstream and upslope expansion of salt- and flood-tolerant marsh vegetation types. The most likely changes will be a retreat up the estuary of species adapted to low salinities, upslope migration of marshes into what is now terrestrial habitat, and loss of high marsh habitats in areas with the densest human populations where the coastline is armored. State changes in the productivity and species composition of future marshes will also depend on freshwater input and temperature. If reduced precipitation continues, marshes will be less-productive in the future, and salt marshes may change state into dominance by succulents instead of grasses. This may have negative effects on the vigorous shellfish, finfish, and bird populations that rely on marshes and are important to humans. Alternatively, if precipitation increases over the coming century, marsh productivity will increase. Our ability to predict these longer-term changes is limited by uncertainties about future precipitation rates, freshwater inputs to the coast, and a lack of information on how difficult these state changes may be to reverse. There is a clear need for continued long-term monitoring of the drivers of these changes, a search for potential indicators of impending change, and analysis of the costs and benefits of changes to diverse stakeholders.

THE FUTURE OF TALLGRASS PRAIRIE DEPENDS ON MANAGING DISTURBANCE REGIMES AND RESTORATION STRATEGIES

Long-term monitoring and experiments at the Konza Prairie LTER site (KNZ) have shed light on a grassland state change to shrubland and forest. The KNZ LTER site was established in 1980 to study the ecology of the once vast (>1.5 million km^2) but now greatly reduced in extent (<25,000 km^2) North American tallgrass prairie. Located at the Konza Prairie Biological Station (KPBS) in the Flint Hills of northeast Kansas, KNZ contains an experimental platform of watershed-level fire and grazing treatments. Since its inception, KNZ has focused on fire, grazing, and climatic variability as three critical and interactive drivers that impact grassland dynamics. Current KNZ research builds upon a legacy of long-term studies to investigate primary productivity responses to climate change, including increased variability in rainfall frequency which corresponds with increased frequency of extreme events including droughts and flooding events (Knapp et al. 2015, Petrie et al. 2018). KNZ research also examines the potential for restoration to reinstate the diversity, ecosystem services, and sustainability of degraded grasslands, providing important insights for more effective management and conservation of this "globally endangered ecosystem" (Hoekstra et al. 2005).

Mesic grasslands, such as tallgrass prairie, vary in their sensitivity and resilience to changes in critical ecosystem drivers, which can lead to altered ecological states through time (Blair et al. 2013, Ratajczak et al. 2014). At the start of the KNZ program, plant composition was similar across KPBS, reflecting a history of relatively uniform grazing and fire management. Nearly 40 yr

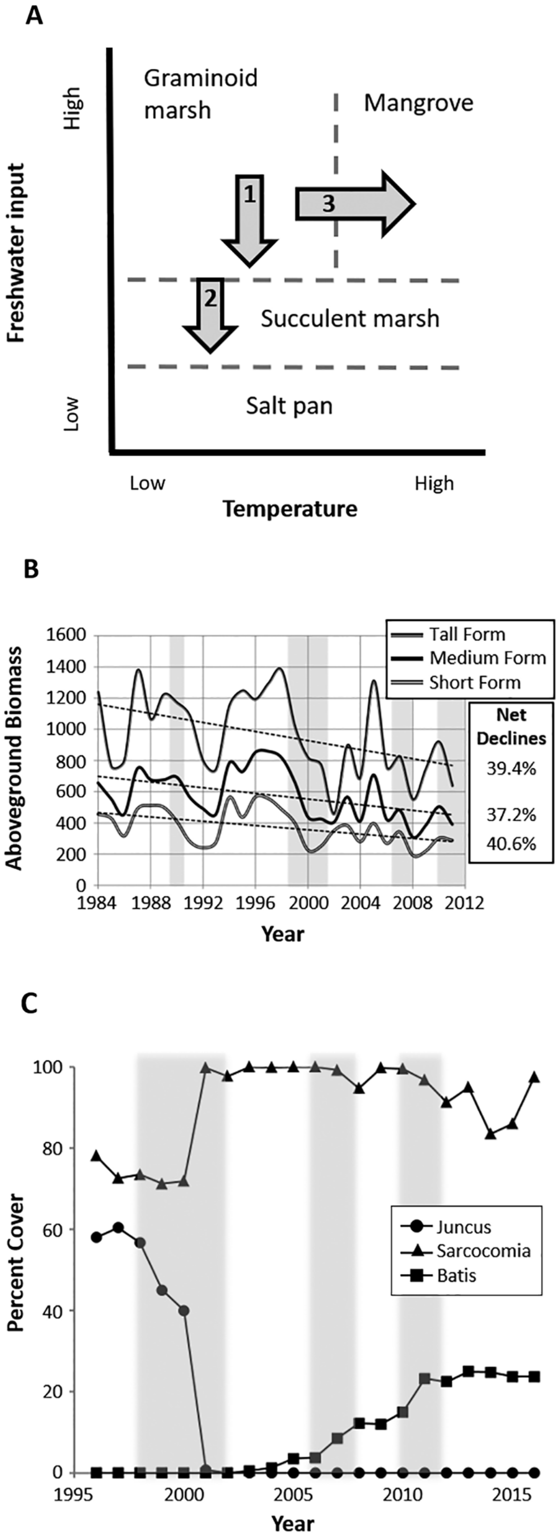

Fig. 1. Response of Georgia marshes to changes in freshwater input and temperature. (A) Conceptual model of how variation in freshwater input and temperature leads to four different habitat types in coastal wetlands (Gabler et al. 2017). (B) A long-term decline in precipitation has led to a long-term decline in standing biomass of graminoid marshes (tall, medium, and short forms of the grass *Spartina alterniflora*), corresponding with arrow 1 in panel A. Periods of extended drought are shaded. (C) A four-year drought in 1998–2002 led to a state change from co-dominance by graminoids (*Juncus*) and succulents (*Sarcocornia* and *Batis*) to dominance only by succulents in vulnerable marshes, corresponding with arrow 2 in panel A. Periods of extended drought are shaded. Continued increases in winter temperatures over future decades may lead to a state change from graminoids to mangroves (woody encroachment), corresponding with arrow 3 in panel A.

of experimental manipulations of fire, grazing, climate, and nutrients, coupled with ongoing environmental change, have led to a range of ecosystem states and ecological legacies. The dynamic sensitivity of the tallgrass prairie ecosystem to varied drivers provides a tractable model system for assessing ecosystem responses to disturbance (Baer and Blair 2008, Coolon et al. 2013), climate change (Brunsell et al. 2014, Hoover et al. 2014), and woody expansion (Ratajczak et al. 2011, Riley and Dodds 2012). Here, we detail the threat of contemporary woody encroachment to tallgrass prairie and describe the current state of the science for ecological restoration of this ecosystem.

The most recent and ongoing landscape change at KPBS is the conversion of upland grasslands to shrubland (woody encroachment). In the absence of fire recurring at annual to 3-yr intervals, woody plants increase in cover and frequency, displacing the herbaceous community and driving changes in species richness (Ratajczak et al. 2012) and productivity (Knapp et al. 2008). Woody encroachment at KPBS is not due to invasion of exotic species; rather, it results from increased abundance and cover of *Juniperus virginiana* (eastern red cedar) and native clonal shrubs including *Cornus drummondii* (roughleaf dogwood) and *Rhus glabra* (smooth sumac) in response to changes in a suite of local and global drivers (Briggs et al. 2005).

Long-term plant composition data sets from the experimental watersheds at KNZ provide evidence of thresholds between grass and shrub ecosystem states and abrupt state changes occurring on the landscape (Ratajczak et al. 2014, 2017*a*). Watersheds with fire return intervals greater than every 3 yr have experienced nonlinear increases in woody cover, with rates of change varying with topographic position and grazing history. These temporal increases in woody cover and abrupt shift to shrubland correspond with declines in C_4 grass cover (Ratajczak et al. 2014; Fig. 3). Increasing shrub cover reduces grass biomass, resulting in lower subsequent fire intensities and less shrub mortality following fires, creating positive feedback to further woody expansion.

Long-term KNZ data illustrating changes in shrub and grass cover provide critical information for the management and conservation of tallgrass prairie. For example, Ratajczak et al. (2014) identified thresholds of grass and shrub cover that precede shifts between ecosystem states. Similarly, landscape changes in spatial variance in grass cover increased prior to the transition to shrubland (Ratajczak et al. 2017*a*), which may provide an early warning indicator forecasting subsequent woody encroachment.

Changes in woody species cover have not been restricted to upland grassland areas at KNZ. Over the last 25 yr, woody riparian vegetation along grassland headwater streams has also expanded in watersheds burned less frequently than every 2 yr (Fig. 4; Veach et al. 2014). Similar to woody encroachment in other locations at KPBS, a positive feedback exists between fire and woody cover whereby riparian corridors are less susceptible to fire promoting further woody riparian maintenance and expansion.

Replacement of grassy riparian vegetation with trees fundamentally alters stream metabolism and aquatic community structure (Riley and Dodds 2012, Reisinger et al. 2013), primarily as a result of decreased light levels and increased reliance of stream communities on allochthonous leaf inputs as an energy source for aquatic food webs. Longitudinal patterns of in-stream primary (1°) and secondary (2°) productivity reveal substantial shifts in food webs with transitions from grass to woody riparian vegetation (Whiting et al. 2011). An experimental removal of woody riparian vegetation (50-m corridors) along two 100-m stream reaches stimulated filamentous green algae growth and activity and total gross primary production in the stream (Riley and Dodds 2012). Subsequently, abundance, biomass, and production of grazing stream invertebrates and total invertebrate production increased in removal reaches relative to forested controls. Riparian forest removal also increased denitrification in riparian soils by 50% (Reisinger et al. 2013) suggesting woody riparian expansion has influences beyond the stream food web that influence processes regulating water quality.

The widespread conversion of tallgrass prairie to row-crop agriculture and current transformation to shrubland and woodland following woody encroachment will require human intervention to increase the extent of this endangered ecosystem. Reconstructing prairie on formerly cultivated or densely forested lands, however, is challenged by a soil seed bank comprised mostly of agricultural weeds (Willand et al. 2013), degraded soil structure and altered composition of soil organisms (Bach et al. 2011), high levels of residual nutrients from agriculture (Baer et al. 2002), homogeneous conditions that favor a few dominant species (Baer et al. 2003), and interannual variability in climate that can hinder the germination and survivorship of seedlings (Manning and Baer 2018). Thus, restoring prairie requires overriding dispersal limitations through seed addition and knowledge of endogenous and exogenous factors that influence restoration outcomes, particularly when plant diversity is a goal (Klopf et al. 2014; Fig. 5).

Research from KNZ over the past ~40 yr has illustrated the key ecological role of frequent disturbance, such as fire and grazing, along with climatic variability, as essential for the maintenance and conservation of tallgrass prairie. Although conversion to agriculture resulted in the largest losses of prairie in the past, the greatest current and future threat to this ecosystem is the conversion of grassland to shrublands and woodlands. At present, 56% of tallgrass prairie in the greater Flint Hills ecoregion is susceptible to future woody encroachment based on fire frequencies greater than every 3 yr (Ratajczak et al. 2016).

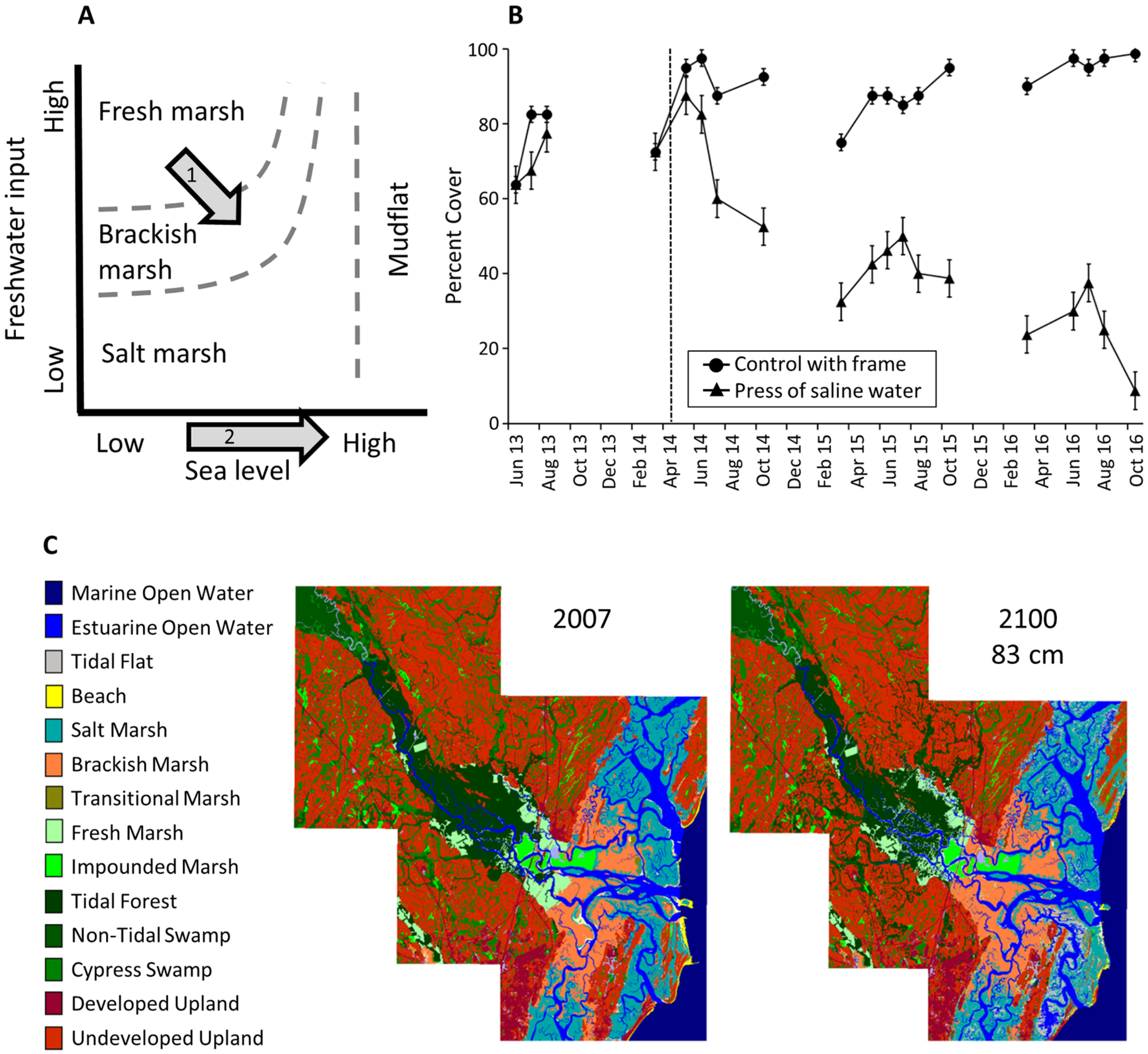

Fig. 2. Response of estuarine marshes on the Georgia coast to changes in freshwater input and sea level. (A) Conceptual model of how variation in freshwater input and sea level leads to four different habitat types in estuarine wetlands. (B) Experimental salinization of a tidal fresh marsh led to the decline in cover of the dominant plant species, *Zizaniopsis miliacea* (F. Li and S. C. Pennings, *unpublished manuscript*), corresponding to arrow 1 in panel A. Immigration of brackish marsh plant species occurred slowly in the experiment due to low propagule pressure, but experimental addition of brackish marsh plants confirmed that they would grow rapidly in salinized plots in the fresh marsh habitat (S. Pennings, *unpublished data*). (C) Model simulations for the Georgia coast suggest that predicted sea-level rise of 83 cm by the year 2100, corresponding to arrow 2 in panel A, will cause all vegetation types to migrate laterally up the estuary, and toward and onto the upland. The model predicts that tidal fresh forest (= tidal swamp) will decrease in area by 39 ha (23%), whereas tidal fresh marsh, brackish marsh, and mudflats will increase in area by 51 ha (190%), 7 ha (6%), and 23 ha (123%), respectively (E. Herbert and C. Hladik, *unpublished data*). Only part of the Georgia coast is shown, centered on the Altamaha River estuary.

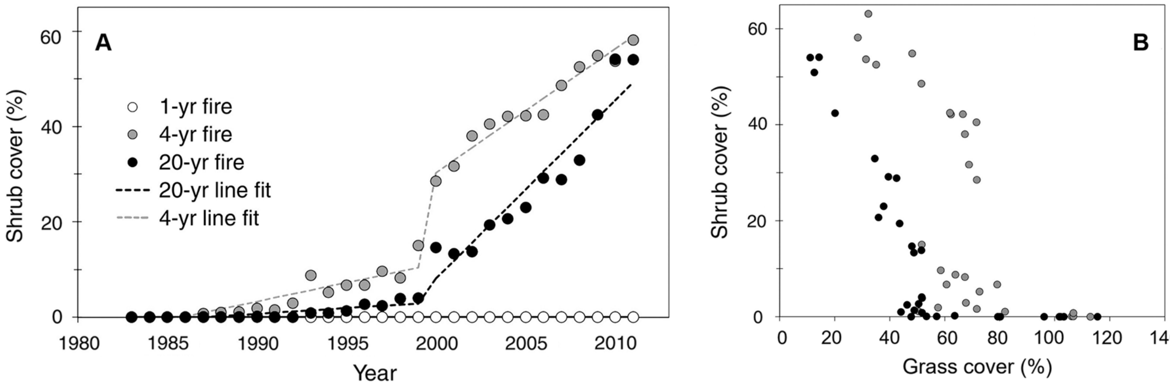

Fig. 3. Shrub cover exhibits nonlinear increases in 4- and 20-yr fire frequencies over time, but not in 1-yr fire frequency (A). Grass cover shows concomitant declines over the same period (B). KNZ data previously published in Ratajczak et al. (2014).

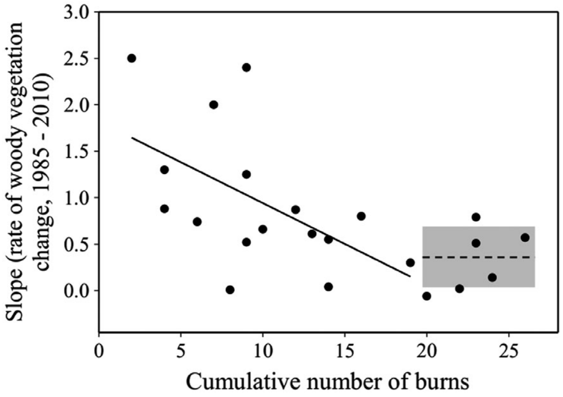

Fig. 4. Percent yearly increase in riparian woody vegetation expansion as a function of number of watershed burns between 1985 and 2010. KNZ data previously published in Veach et al. (2014).

Urbanization and management practices that maintain infrequent fire frequencies over the next 50–100 yr will exacerbate transition of this ecosystem to shrubland, perpetuating a new woody state. A shift in ecosystem state from herbaceous-dominated grassland to woody-dominated shrubland has pronounced impacts on ecosystem dynamics, including lower plant diversity (Ratajczak et al. 2012), altered carbon cycle (Barger et al. 2011), altered hydrological cycle (Vero et al. 2018), and reduced forage for ungulate grazers (Anadón et al. 2014). Based on the negative consequences of this state transition, we propose two strategies for conserving the tallgrass prairie. First, we must protect the remaining prairie using management strategies based on long-term data that provide a framework for identifying suitable fire frequencies and forecasting landscapes susceptible to state change (Ratajczak et al. 2017*b*). Second, we need to restore tallgrass prairie from woody states and agricultural conditions. KNZ data demonstrate that restoration from these alternate land cover states can be labor-intensive (Larson et al. 2019), will take many years to accomplish, and that restoration goals need to consider the effects of dispersal limitation, habitat heterogeneity, and interannual climate variability on restoring biodiversity (Baer et al. 2016, 2019). Long-term ecological research has been, and will continue to be, invaluable for identifying appropriate ecological disturbance regimes required for long-term conservation of tallgrass prairie.

Climate Change and Tropical Mountain Cloud Forests in Puerto Rico

Long-term research at the Luquillo LTER site (LUQ) investigates ecosystem drivers and state changes involving potential loss of tropical montane cloud forests. The conditions of cloud forests, with high rainfall rates and extensive immersion in cloud cover, strongly affect energy and nutrient cycling and provide unique habitat for endemic plant and animal communities driven by cloud water interception. Climate and land-use changes that affect cloud heights cause

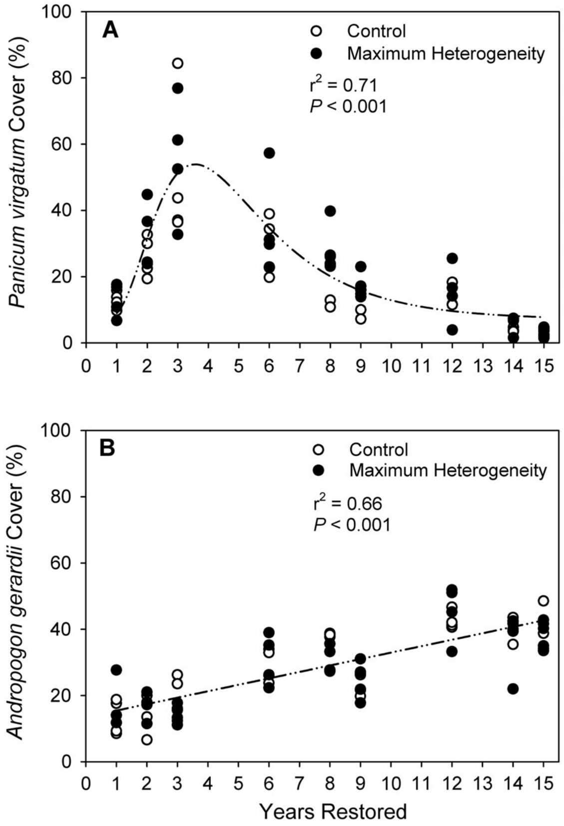

Fig. 5. Change is grass cover over time for two dominant species following restoration from agricultural lands.

dramatic change in plant communities, especially endemic epiphytes and orchids, birds, mammals, and nutrient cycling.

The LUQ LTER site was established in 1988 to study the long-term effects of natural and anthropogenic disturbances on tropical ecosystems in the Luquillo Mountains of Puerto Rico. While the cloud forests of the Luquillo Mountains are well adapted to cycles of hurricane disturbance, climate change model projections indicate a shift in seasonal precipitation patterns with more extreme rain events and droughts projected for the future. Downscaled models show increasing precipitation variability being marked by a general drying trend and more frequent and profound drought events (Hayhoe 2013, Henareh Khalyani et al. 2016; Fig. 6). Rainfall drives the distribution of ecological life zones in the U.S. Caribbean (Ewel and Whitmore 1973). Projected decreases in rainfall foreshadow relative increases in dry life zones and the shrinkage and disappearance of wetter life zones. Ecological implications of these shifts include effects on biodiversity, carbon cycling, forest composition and structure, and nutrient and water cycling (Henareh Khalyani et al. 2016, Helmer et al. 2019, Henareh Khalyani et al. 2019), as well as social–ecological implications including tourism, water quality/quantity, and other ecosystem services.

Mountains play a key role in collecting atmospheric moisture in tropical regions (Wohl et al. 2012). Around 500 tropical mountain cloud forests have been identified worldwide on mountains with frequent cloud cover, almost all within 350 km of a coast and topographically exposed to higher humidity air (Jarvis and Mulligan 2011). Up to 60% of the moisture input to tropical mountain cloud forests is derived from cloud water interception from low clouds (Bruijnzeel et al. 2011), and cloud water has been deemed critical for the health of these ecosystems, specifically for the abundant epiphytes which require consistent moisture input from the atmosphere (Gotsch et al. 2015). Cloud water interception adds moisture directly to the soil through the process of canopy interception and fog drip (Giambelluca et al. 2011) and indirectly alters the moisture budget through foliar uptake (Eller et al. 2013), lowering the saturation deficit of the atmosphere, and suppressing transpiration (Alvarado-Barrientos et al. 2014).

Low peak-elevation tropical mountain cloud forests are vulnerable in a changing climate, because slight increases in cloud base altitude could end cloud immersion for the entire forest (Foster 2001, Lawton et al. 2001, Ray et al. 2006). Rainfall and relative humidity in these forests are high so that some species, once established, may be able to survive if rainfall remains high (Martin et al. 2011), but the diversity and numbers of epiphytes and other species that depend on cloud immersion might decline over time (Fig. 7). During a past wet-season drought at Luquillo, trade-wind precipitation became very important in the absence of deep convection (Clark et al. 2017). If trade-wind cloud layers become thinner and shallow convection weakens, drought effects on the tropical mountain cloud forest could be even more significant (Van Beusekom et al. 2017). Van Beusekom et al. (2017) showed cloud levels in

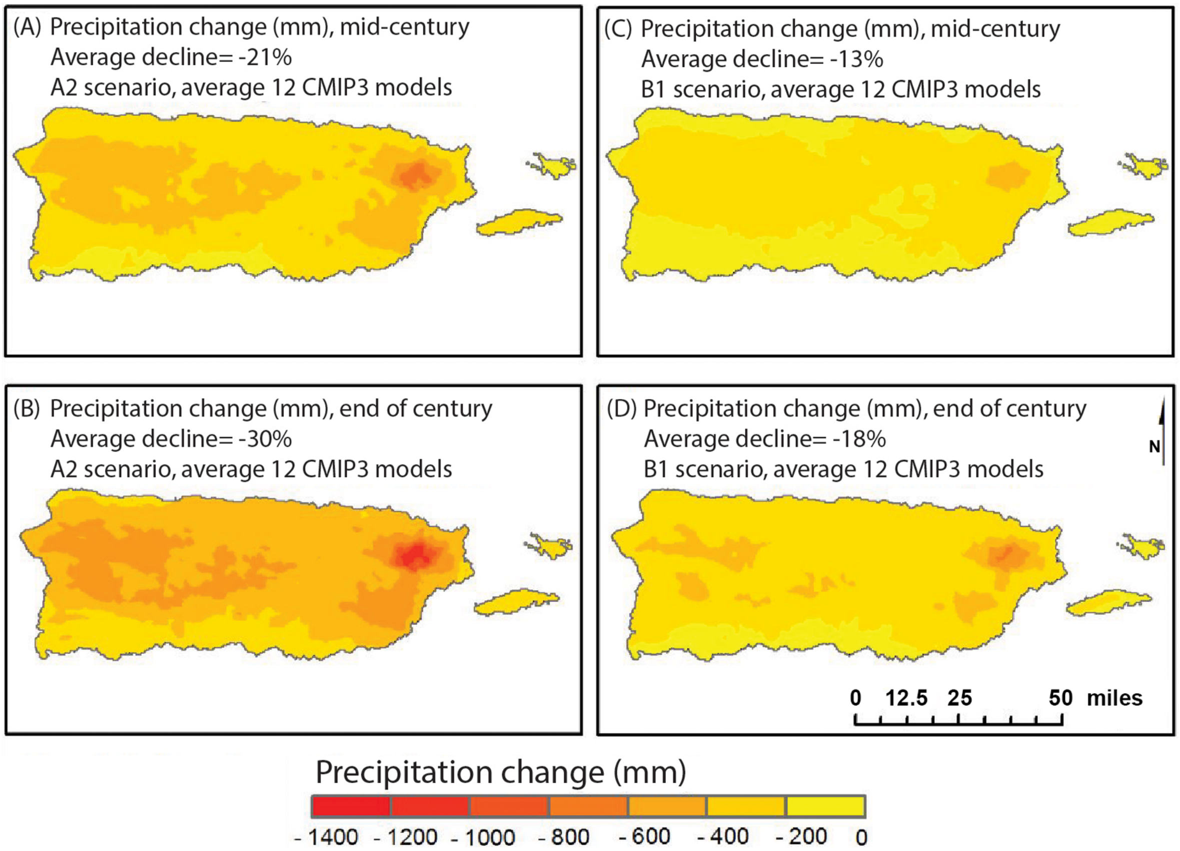

Fig. 6. Rainfall changes over Puerto Rico under high (A, B) and low (C, D) emissions scenarios projected from the average of 12 statistically downscaled CMIP3 models. (A) and (C) show the changes from the period of 1960–1990 to 2041–2070 while (B) and (D) show the same changes to 2071–2099. Figure modified from Henareh Khalyani et al. (2016).

the dry season are consistently as low, or lower, than in the wet seasons at a low-elevation tropical mountain cloud forest under the current climate regime at LUQ, indicating that the tropical mountain cloud forest ecosystem may be more vulnerable to wet-season drought periods than was previously assumed.

As is true of many tropical regions, northeastern Puerto Rico is an ecologically sensitive area with biological life that is highly elevation dependent on precipitation and temperature (Van Beusekom et al. 2015). Climate change has the potential to increase the risk of losing endemic species and habitats. Van Beusekom et al. (2015) showed that daily minimum temperatures are increasing by 0.02°C/yr while daily maximum temperatures are decreasing at a much larger rate (possibly due to changes in cloud cover induced by urbanization) along an elevation gradient in northeast Puerto Rico. Changes in temperature can have detrimental effects for many tropical montane tree species whose average altitudinal range is 500 m and for animals whose ranges are typically much narrower (Bruijnzeel et al. 2011). To keep pace with these changes, montane species are shifting their ranges upslope and due to narrow thermal tolerance ranges, may be soon forced beyond their upper elevational limits (Laurance et al. 2011). Montane forest features that may be affected by rising temperatures include cloud base height, cloud moisture, and pathogen virulence and diversity (Stork et al. 2009). Because of their smaller geographic spread as well as high energy and area requirements, highland-specialist bird and mammal species are thought to be more prone to extinction than are lower-zone specialist ectotherms and plants (Laurance et al. 2011). For example, in the Luquillo Mountains the elevational distribution of eight of 21 avian species changed significantly over a span of 17 yr (1998–2015; Campos-Cerqueira et al. 2017). In East Peak (top of LM), Lasso and Ackerman (2003) found a correlation between flowering of *Werauhia sintenisii* (bromeliad) and mean minimum temperatures three months prior to flowering. They document an observed 30-yr trend in increasing minimum temperatures and note a change toward a later flowering season compared to observations made 35 yr prior (Nevling 1971). Though the most important environmental constraint for vascular epiphytes is water availability, Olaya-Arenas et al. (2011) found the flowering of the orchid *Lepanthes rupestris* at LUQ to be temperature dependent. Given projected warming, they expect a dramatic reduction of reproductive individuals and population growth rates of *L. rupestris*, which will in turn affect seedling production, future recruitment, and reproductive capacity (Jennings et al. 2014). The Orchidaceae is the largest and most diverse family of vascular epiphytes (Fay and Chase 2009) and is a key group in conservation because of its diversity, cultural appeal, and vulnerability from over-collection and habitat loss (Pillon and Chase 2006, Swarts and Dixon 2009).

Nutrient cycling in tropical mountain cloud forests, important to the composition and physiognomy of montane forests, is strongly tied to regimes of rainfall and cloud cover (Dalling et al. 2016). Global and regional drivers, including conversion of lowland forest to other land uses, may have the combined effects on the location and height of the cloud base (Still et al. 1999, Foster 2001, Nair et al. 2010, van der Molen et al. 2010, Dalling et al. 2016).

Cloud water tends to be elevated in both inorganic and dissolved organic nitrogen relative to rain water, so that changes in cloud cover and duration will likely affect nitrogen cycling (Vong et al. 1997, Weathers et al. 2000). Long-term nitrogen deposition and climate effects may act synergistically to facilitate the replacement of montane species, which are characterized by conservative nutrient use efficiency, slow-growth rates, and low litter quality, with faster-growing lower-elevation species that display the opposite traits (Dalling et al. 2016). Changes in nitrogen cycling may favor arbuscular over ecto-mycorrhizal species, which has been shown to result in net loss of soil carbon (Averill et al. 2014).

In the Caribbean region, reductions in air quality from long-range transport of dust and other contaminants (Pringle and Scatena 1999)—leading to acid rain and dry deposition (Stallard 2001)—are increasingly becoming an issue (McClintock et al. 2019). From 1985 to 1998, levels of nitric acid, sulfuric acid, and ammonia deposition increased significantly in the Luquillo Mountains, with most pollutants coming from long-range transport from the northern hemisphere (Stallard 2001, Gioda et al. 2013). Nitrogen deposition increased in the Luquillo Mountains at a rate of 0.08 kg $\text{nitrogen} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ from 1986 to 2004. Assuming current trends continue, Ortíz-Zayas et al. (2006) project nitrous oxide (N_2O) emissions to increase in Puerto Rico at an average rate of 7.8% per yr, with fuel combustion as the primary source of these emissions. In a study on the effects of increased nitrogen deposition on soil microbial communities, Cusack (2013) and Cusack et al. (2011, 2012) found shifts in community structure with increased fertilization, including an increase in fungal abundance at higher elevation sites and an increase in bacterial abundance at lower-elevation sites in the Luquillo Mountains. These changes affect soil carbon storage potential and nutrient cycling.

Other potential drivers of state change in tropical forests include fires and hurricanes. Although cloud-affected forests are unlikely to burn, past or present fire regimes may at least affect the edges of, or set limits to, the distribution of tropical mountain cloud forests (Martin et al. 2007, Jain et al. 2008, Monmany et al. 2017, Van Beusekom et al. 2018*a*, Huang et al. 2019). Of more immediate relevance, rising temperatures will generally increase regional sea surface temperatures, which tends to increase the maximum intensity of hurricanes in the Caribbean region (Kossin et al. 2017, Gould et al. 2018). Hurricanes cause substantial vegetation disturbance (Van Beusekom et al. 2018*b*) and are the primary driver of forest transformation in the hurricane belt of the tropics (Boose et al. 1994). In the Luquillo

Fig. 7. Tropical montane cloud forests in the Luquillo Mountains in Puerto Rico receive >4 m of precipitation annually and are characterized by the frequent clouds immersion, reduced tree stature, and anaerobic soils. Photo credit: Maria M. Rivera.

Mountains, we expect that increased frequency of severe storms will increase the dominance of shade-intolerant, pioneer plant species, which will increase soil carbon storage relative to aboveground carbon storage over the long term (Shiels et al. 2015).

Tropical mountain cloud forests are highly unique ecosystems that exist due to specialized conditions, especially cloud water interception. Long-term research at LUQ shows that climate and land-use change can cause marked changes in these conditions that can lead to state changes involving conversion to other forest types. These conversions would result in loss of endemic plant and animal communities. Continued long-term monitoring will be necessary to determine which drivers are most likely to be indicators of change or predictors of thresholds, and what can be done to monitor/manage them.

Transitions Among Dryland Ecosystems Under Increasing Climate Variability

Research at the Sevilleta Long Term Ecological Research (SEV) site is addressing the causes and consequences of two ongoing dryland state changes under climate change: woodland to savanna and grassland to shrubland. Drylands are climate-driven ecosystems strongly dependent on water availability, which is a function of both precipitation and temperature (Sala et al. 2012). Climate models for the southwestern United States predict increasing aridity over the next 100 yr, which is likely to be driven more by increasing temperature than by decreasing rainfall (Cook et al. 2015). For example, recent forecasts suggest that drylands may experience 40% greater warming than humid ecosystems (Huang et al. 2017). Long-term data from SEV, located in and around the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, suggest these climate dynamics are already occurring (Fig. 8; Petrie et al. 2014*a*, Rudgers et al. 2018, Maurer et al. 2020) and that the combination of increases in aridity and variability in precipitation will be strong drivers of state change. Central New Mexico spans multiple ecotones that are common and representative of the southwestern United States (Anderson-Teixeira et al. 2011). Two ecotones, in particular, have been the focus of considerable research: (1) the slow transition from grassland to shrubland, which has occurred regionally for ~150 yr; and (2) the transition from piñon–juniper woodland to juniper savanna, a more recent but relatively rapid phenomenon associated with piñon pine mortality triggered by episodic regional drought.

Many dryland ecosystems worldwide are undergoing state transitions from C_4 grassland to C_3 shrubland or woodland (Eldridge et al. 2011, Bestelmeyer et al. 2015). In the southwestern United States, shrub encroachment is attributed to multiple factors, including overgrazing, changing precipitation regimes, increasing atmospheric carbon dioxide concentrations, and altered fire regimes (Van Auken 2000); yet, the relative importance of these drivers has likely shifted over time. Historically, livestock grazing reduced grass cover and increased shrub cover in the southwestern United States (Schlesinger et al. 1990). Although grazing pressure has been greatly reduced today (Bestelmeyer et al. 2013), shrub encroachment continues in many regions and may now be driven more by increasing aridity (Valencia et al. 2015) and atmospheric carbon dioxide (Bond and Midgley 2012) than by grazing pressure. Indeed, a model including fire, grazing, and climate drivers predicted that shrub encroachment will continue in our region even in the absence of grazing (Caracciolo et al. 2016), because increasing aridity reduces competition by grasses, ultimately favoring dominance by drought-tolerant shrubs.

At the SNWR, encroachment by the dominant shrub, creosotebush (*Larrea tridentata*), depends on the species composition of dominant grasses. Specifically, replacement of one grass (blue grama, *Bouteloua gracilis*) by another (black grama, *Bouteloua eriopoda*) facilitates shrub invasion because creosotebush does not invade blue grama patches (Peters et al. 2006). The reasons for the resistance of the blue grama patches are complex, and are a topic of active investigation. Grassland composition in the SNWR had strong directional change from 1989 to 2008, driven largely by increased cover of black grama (Collins and Xia 2015). Thus, the stage may be set for further shrub encroachment, with important consequences for both carbon sequestration (Anderson-Teixeira et al. 2011, Petrie et al. 2014*b*) and microclimate (D'Odorico et al. 2010, He et al. 2010). We predict this change will come in pulses because the transition from blue to black grama can be reset by fire (Collins et al. 2020) and recruitment by creosotebush is episodic (Moreno-de las Heras et al. 2016). Our records show that creosotebush seedlings established in wet years (1997, 2004, 2013), and while the shrub boundary at SNWR has not advanced northward since 2001, infilling has occurred.

Sequential wet years may be one factor that initiates episodic recruitment of creosotebush. The Pacific Decadal Oscillation (PDO) influences long-term precipitation cycles in the region (Gutzler et al. 2002, Milne et al. 2003, Petrie et al. 2014*a*). In 1998, the PDO switched to the cool phase, resulting in prolonged regional drought, tree die-off (Breshears et al. 2005), and years of low grassland productivity (Muldavin et al. 2008). Around 2015, the PDO returned to the warm phase (Meehl et al. 2016), portending greater annual precipitation over the next two decades. The warm phase may accelerate shrub encroachment if wetter monsoons promote shrub recruitment, or may decrease encroachment by increasing the abundance and competitiveness of black grama grass. However, greater precipitation under the warm phase may be counteracted by climate warming, causing higher aridity that may favor shrubs over grasses. Future work at SEV will investigate recruitment dynamics under different climate change scenarios to help resolve this uncertainty.

Severe drought triggered rapid tree mortality across the southwestern United States in 2001–2002 (Breshears et al. 2005), and piñon–juniper woodlands suffered similar mortality following a drought in 2011–2013. Drought-induced mortality is much greater for piñon pine (*Pinus edulis*) than for co-dominant juniper (*Juniperus monosperma*), due to key differences in their drought tolerance traits (Plaut et al. 2013), amplified by bark beetle attack on piñon pine (Gaylord et al. 2013). However, loss of piñon pine could indirectly impact juniper, particularly during drought. A large-scale girdling experiment to simulate piñon mortality (~1600 trees) showed that juniper did not rebound from competitive release as anticipated, but instead declined (Morillas et al. 2017). Piñon pine may play a key role in maintaining water availability for juniper by reducing near-ground solar radiation and soil evaporation rates (Royer et al. 2010, 2011) and by connecting deep and shallow soil water sources

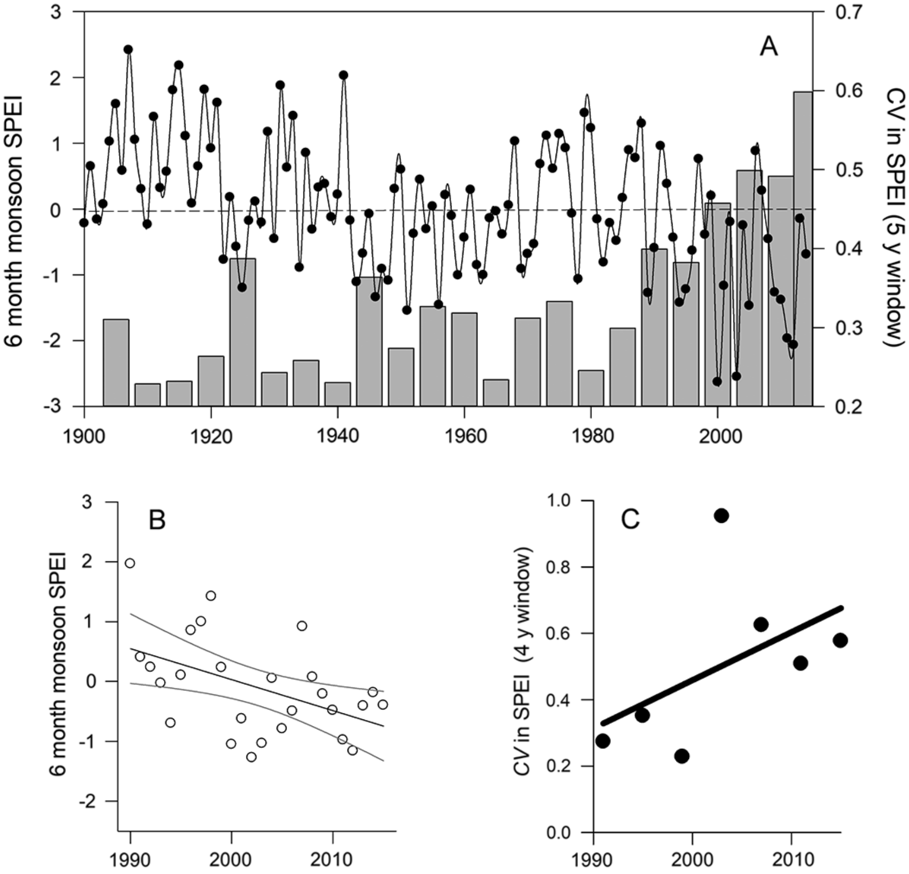

Fig. 8. Temporal trends in a new drought index (Standardized Precipitation Evaporation Index, SPEI). Negative *SPEI* values indicate dry and hot conditions. (A) Long-term data from Socorro, New Mexico: Points show the 6-month integrated SPEI over the preceding monsoon season, recorded since 1900. Bars show the coefficient of variation (CV) in the SPEI for non-overlapping five-year time windows. The mean SPEI has significantly declined over time ($P < 0.0001$), while the variability in SPEI, as captured by the CV, has significantly increased ($P = 0.0003$). (B) The 6-month integrated SPEI and (C) the CV of this index over non-overlapping four-year windows, both calculated from meteorological station data at the Sevilleta National Wildlife Refuge, New Mexico, collected by SEV-LTER since 1989. (Reproduced from Rudgers et al. 2018.)

through hydraulic distribution (Morillas et al. 2017). A state transition to juniper savanna, or potentially to dominance by understory grasses, such as blue grama or side oats grama (*Bouteloua curtipendula*), may be in progress across the region, with potentially large consequences for both climate sensitivity and carbon sequestration.

The consumer community at the SNWR is dominated by small mammals and insect herbivores, and our long-term data and consumer exclusion experiments show that consumer abundance largely tracks primary production (Báez et al. 2006, Lightfoot 2011, Noble et al. 2019). Nutritious, herbaceous C_3 plants constitute an important component of production for consumers (Yeakel et al. 2020). Small mammals track summer monsoon C_3 production in grasslands, whereas in shrublands they respond most to spring C_3 biomass (J. A. Rudgers and S. Newsome, *unpublished data*). For example, grasshoppers were ~2–7 times more responsive to C_3 production than to total primary production, and their response function (Rudgers et al. 2018) suggests that higher variance in C_3 resources will be costly for this consumer group. C_3 plant biomass has recently declined in all SNWR biomes, and declines will likely continue if precipitation that is more variable threatens C_3 plants under a warmer climate (Collins et al. 2017, Mulhouse et al. 2017). Climate-induced shifts in vegetation composition will affect the foraging decisions that determine consumer survival, body condition, and reproduction (Yeakel et al. 2020). However, the physiological mechanisms that underlie consumer dynamics over these changing resource landscapes are not yet resolved. We are working to link variation in seasonal resource abundance and quality to small mammal, grasshopper, and bee population abundances to improve forecasts of changing consumer dynamics at the transitions between major dryland biomes (M. R. Kazenel et al., *unpublished manuscript*). Altered consumer abundances that accompany state changes may feedback to alter primary production, biodiversity, and ecosystem services, such as pollination or top-down control.

At SEV, long-term data and experiments predict a changing landscape of ecosystem transitions during the next 50–100 yr, driven by the combined effects of climate warming, increasing variability in precipitation regimes, and episodes of extreme drought. Continued long-term research will link responses across trophic levels and gain deeper resolution of plant recruitment dynamics to improve forecasts on the future of dryland ecosystems.

Long-Term Change in Barrier Island Vegetation of the Virginia Coast Reserve

At the Virginia Coast (VCR) LTER site, long-term data have characterized a transition from grassland to shrubland in the terrestrial portion of barrier islands (i.e., upland). Dry grasslands once comprised a large portion of the barrier island upland prior to shrub expansion. This change has marked effects on microclimate, physical stability of the island ecosystems, and response to sea-level rise.

Coastal barrier systems comprise 15% of coastlines globally and occur on all continents except Antarctica (Pilkey and Fraser 2003, Kennish and Paerl 2010, van Heteren 2014). Along the Atlantic coast of North America, barrier islands are the frontline ecosystem to 78% of coastline. Although the majority of the Atlantic coast is heavily populated, barrier islands along the Virginia coast are undeveloped and VCR represents a unique opportunity to study islands in their natural state (Hayden et al. 1991). Barrier islands tend to migrate landward to maintain position relative to sea level. Many geophysical factors controlling rates of island migration have been identified; however, in light of the ecological and economic dimensions of sea-level rise, there is a need for a better understanding of coastal biogeomorphic processes (Zhang and Leatherman 2011, Lazarus et al. 2015).

Ecosystem processes on barrier islands may be placed within the context of three interacting free surfaces: sand, saltwater, and freshwater (Hayden et al. 1995), which determine the abiotic constraints in the system (e.g., land elevation, freshwater table, and sea level). Sandy soils typical of North American Atlantic and Gulf coast barrier islands have minimal water holding capacity, which determines vegetation distribution dynamics based on physiological constraints of species. The extent of this effect can be mediated by the depth to the water table, which changes freshwater availability. The shallow seaward slope of coastal barrier systems makes these landscapes particularly sensitive to sea-level rise, leading to flooding and salinity stress. Understanding these connections has been a major research focus at VCR (Hayden et al. 1995, Young et al. 2007, Young et al. 2011).

Changes in the abundance of woody vegetation, especially the expansion of native shrubs in historically herbaceous communities, as seen at other LTER sites (Young et al. 1995, Goslee et al. 2003, Wessman et al. 2004, Sturm et al. 2005, Nippert et al. 2013), are also occurring at VCR. Although ecosystem state change between grassland and shrubland has occurred at an unprecedented rate worldwide (Rundel et al. 2014), barrier island state change is unique as vegetative communities are closely coupled to both atmospheric and oceanic drivers. Over the last 30 yr, Virginia barrier islands have experienced significant changes in plant species dominance, with over 40% of land cover changing from grassland to shrub thicket on most islands along with a ~10 cm rise in sea-level and substantial (~29%) reduction in upland area (Fig. 9; Young et al. 2007, Zinnert et al. 2016). The dominant woody species on Virginia barrier islands, *Morella cerifera* (formerly *Myrica cerifera*), is an evergreen, nitrogen-fixing shrub that quickly establishes and forms 5–7 m tall monospecific thickets in <15 yr. Leaf area index (12 ± 3) and annual net primary productivity (ANPP, 1138 ± 90 g/m^2) are high (Fig. 10), resulting in a three- to fivefold increase in ANPP as grassland is converted to shrubland (Knapp et al. 2008). High litterfall and low nitrogen resorption input a substantial amount of this nutrient into an otherwise nitrogen-limited system (169 $kg\ N \cdot ha^{-1} \cdot yr^{-1}$, Brantley and Young 2008). The role of nitrogen in woody expansion has not been explored for this ecosystem engineer, but enhanced nitrogen may increase grass density at the edge of shrubs in dry grassland to facilitate survival of shrub seedlings (Moulton 2017; L. K. Wood and J. C. Zinnert, *unpublished data*).

Climate warming and a reduction in low temperature events (less than −16°C) have driven the rapid expansion of *M. cerifera* (Huang et al. 2018). Once shrubs establish in grassland, individual shrubs, and thickets contribute immediate and significant alterations to microclimate, with warmer winter and cooler summer temperatures (Thompson et al. 2017, Huang et al. 2018). A small increase (~1–2°C) in temperature is enough to induce a nonlinear shift from grassland to *M. cerifera* dominated landscape (Huang et al. 2018). The moderated microclimate under shrubs in summer keeps temperatures near the optimum for photosynthesis (30°C), resulting in higher growth and evapotranspiration (ET; Young 1992, Shao et al. 1995, Aguilar et al. 2012, Shiflett et al. 2013, Thompson et al. 2017). Frequency and intensity of summer droughts are expected to increase in response to predicted shifts in global climate patterns (Karl et al. 2009) while microtopography will exacerbate these effects. In barrier islands, the dependence of plant communities upon the freshwater lens, which varies both spatially and temporally, is likely to be a key driver of grassland/shrubland transition (Hayden et al. 1995, Shao et al. 1995). Shrubs appear to modify depth to the water table through control on ET (L. K. Wood and J. C. Zinnert, *unpublished data*). We are currently testing the effect of shrub expansion on water table depth through natural and manipulative field experiments.

Vegetation is an important functional component of coastal systems, which affects geomorphological change by trapping sediment and promoting organic matter deposition, both of which are critical processes for shaping coastal landscapes (Rastetter 1991). Trapping of sediment also creates new substrate for further colonization by plants or it can alter elevation resulting in ecological-topographic feedbacks at the local scale (Stallins 2005, Zinnert et al. 2017). The ability of woody vegetation to colonize and expand across the landscape affects the resilience of barrier islands (Zinnert et al. 2017). In short timeframes, woody vegetation is a green solution in coastal management for protecting coastal areas and stabilization of sediments (U.S. Army Corps of Engineers 2013) creating resistance to storms and overwash. However, over longer timeframes (i.e., decades), we have evidence that shrubs limit sediment movement across the barrier island (Claudino-Sales et al. 2008; Figs. 9, 11). Increased woody vegetation shapes sediment dynamics associated with island migration by slowing down or blocking overwash as barrier islands erode and/or migrate, thus impeding island migration and reducing chances of islands adapting to sea-level rise (Zinnert et al. 2019).

Most studies of barrier islands and coastal areas tend to focus only at the dune scale, thus ignoring a considerable amount of landscape (i.e., the island interior) that plays a functional role in determining resilience (Lentz et al. 2016, Zinnert et al. 2016). Plant communities beyond the dune system interact with abiotic components of the landscape (Chapin et al. 1997, Corenblit et al. 2011) and determine island level responsiveness to variations in sea-level rise (Zinnert et al. 2019). There is relatively limited understanding of the effects of climate change on coastal ecological communities, especially barrier islands; this is surprising considering the importance of the ecosystem services they provide (i.e., storm surge protection, creation of economically important lagoons, and wetlands, etc.). Based on our long-term measurements, observations, and current understanding of barrier island dynamics, we expect vegetation communities to shift across the landscape over the next 50–100 yr as islands migrate with sea-level rise. Areas receiving sufficient sediment supply will continue to convert to shrubland, whereas locations with little sediment will erode or migrate depending on the current community composition. Areas that

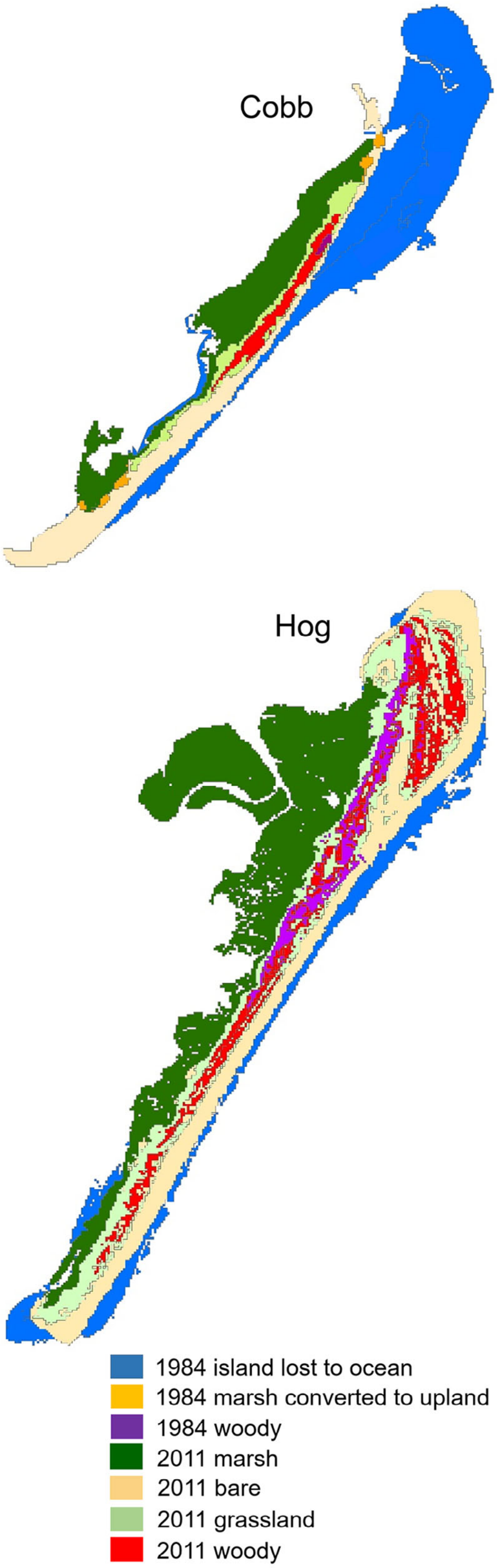

Fig. 9. Two Virginia barrier islands showing increase in woody cover and decrease in island upland between 1984 and 2011. There is little to no conversion of marsh to upland as seen on islands with little to no woody cover. Data were classified from Landsat Imagery as detailed in Zinnert et al. (2016).

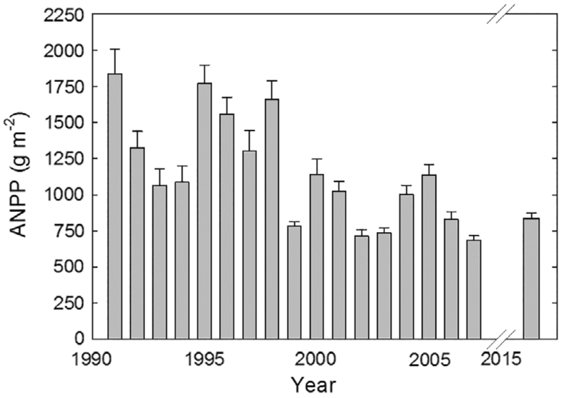

Fig. 10. Changes in annual net primary productivity (ANPP) for *Morella cerifera* from 1991 to 2016. Shrubs were ~8 yr old in 1991. No measurements were recorded between 2008 and 2015.

convert to shrubland are lower in biodiversity and at higher risk of not adapting to sea-level rise, thus affecting the mainland communities by reducing protection from storms as barrier islands erode (Zinnert et al. 2019). Position of islands on the landscape determines sediment flux, and as they move through time, sediment dynamics change. New land can form that is suitable for expansion of shrubs in locations that were previously highly disturbed. Continued long-term research in this highly dynamic system is enabling us to include ecological processes into physical models for predicting barrier island response to storms and sea-level rise.

SUMMARY AND CONCLUSIONS

State change is a dominant theme across a diverse range of ecosystems that vary in rainfall, temperature, access to freshwater and species composition (Table 1). Long-term research is required to document these state changes, put

Fig. 11. Photo depicting the extent of woody vegetation on Cobb Island taken 31 August 2011, close to the image acquisition of Cobb in Fig. 1. Evidence of shrub death near the shoreline is visible with little sediment transferred inland. Photo credit: John Porter.

them in historical context, and understand mechanisms leading to the state changes. What do these examples from the LTER network tell us about the mechanisms of state change and how ecosystems across the nation are likely to look in 50–100 yr? The strong message is that change is nonlinear, often dramatic, and likely to result in altered ecosystem function and services. The drivers of these changes are complex and dependent on contingences such as inherent site resources (e.g., soil and sediment) and species interactions (e.g., plant competition).

Not surprisingly, coastal ecosystems are highly susceptible to state changes. The analysis of Georgia coastal tidal marshes and forests suggests that if sea level and climate trends continue, there could be a state change to succulent marsh and/or mangroves. Uncertainty about future precipitation rates and freshwater inputs to the coast limits our ability to predict longer-term changes. Barrier systems along the Virginia coast are also sensitive to sea-level rise, yet change here has involved a surprising shift from grassland to shrub thicket due to winter climate warming. This state change has consequences for the future of barrier islands, such as erosion of islands, reducing storm protection, and altering landscape dynamics as sediment is redistributed in the system. Continued long-term research at the land–sea interface is critical for informing coastal management where rising sea level and alterations in freshwater access present challenges for communities.

Shrubs appear to be "on the march" across ecosystems. In addition to possible state changes from grass to woody vegetation at the GCE and VCR coastal sites, woody encroachment is also likely at inland grasslands. The tallgrass prairie at KNZ is undergoing conversion from grassland to shrubland and riparian forest (woody encroachment) by native clonal shrubs due to long-term reductions of fire frequencies and intensities and potentially increased carbon dioxide favoring C3 vegetation. At the SEV aridland site, models suggest an increase in shrub encroachment even in the absence of grazing, which has been a strong catalyst of encroachment in the past. Thus, the mechanisms driving encroachment change over time. Long-term research is essential to understand the drivers and consequences of these state changes, to predict how these systems will change in the future, and to guide restoration efforts and land management decisions in these ecosystems.

Lastly, tropical cloud forests appear to be particularly susceptible to climate-induced state

Table 1. Summary of type of, evidence for, and mechanisms driving state changes at five LTER sites.

System	State change	Evidence	Mechanism
Georgia coastal marshes	From graminoid marshes into lower-stature and less-productive succulent marshes and/or to mangroves	Long-term monitoring of permanent plots and satellite images shows that between 1984 and 2011, primary productivity of graminoid-dominated salt marshes decreased by over 30%	Long-term changes in sea level, temperature, precipitation, and land use that affect freshwater delivery, porewater salinities, and plant growth. If warming eliminates hard winter freezes, mangroves will colonize coastal marshes in Georgia
Konza tallgrass prairie	Grassland to shrubland and forest.	Long-term plant composition data sets show nonlinear increases in woody cover and declines in C4 grass cover with rates of change varying with fire frequency, topographic position, and grazing history	Reduction in fire frequency allows shrub establishment. Increasing shrub cover reduces grass biomass, resulting in lower fire intensities and less shrub mortality, creating positive feedback to further woody expansion
Luquillo tropical montane cloud forest	Montane cloud forest with potential transitioning to drier forest types	Warming minimum temperatures tied to altered flowering season of endemic montane forest species. The elevational distribution of avian species has changed significantly between 1998 and 2015	Increases in cloud base height, driven by changes in both climate and land use, may reduce cloud immersion which is a dominant water source for the forest. Changes in temperature and humidity affect tropical montane biota that have natural narrow altitudinal ranges
Sevilleta dryland ecosystems	Two ongoing state changes: woodland to savanna and grassland to shrubland	Observations of strong directional change in grassland composition 1989–2008, establishment of creosotebush seedlings from 1997 to 2014, long-term data, and consumer exclusion experiments showing links between consumer abundance and primary production	Overgrazing, changing precipitation regimes, increasing atmospheric carbon dioxide concentrations, and altered fire regimes
Virginia coastal barrier islands	Transition from grassland to shrubland	Over the last 30 yr, over 40% of land cover changed from grassland to shrub thicket	Climate warming and a reduction in low-temperature events. Shrub establishment alters microclimate to further favor shrubs over grass

change. Climate change may increase cloud base height and reduce cloud immersion for entire low peak-elevation cloud forests resulting in a community composition shift to driver forest types. Disturbance is expected to increase in these systems, dramatically altering species composition at several trophic levels, biodiversity, and nutrient cycling. Long-term research is critical to understanding how species will respond to climate change and increased storm intensity.

Ultimately, our ability to predict, prevent, manage, and respond to ecosystem state change depends on monitoring ecosystem response to change in drivers and corresponding environmental conditions to reveal thresholds. State change may be reversible if drivers can be managed (reversed) to achieve conditions that support previous, less degraded, or more desired states, provided that feedbacks have not developed to increase the resilience of altered states (Ravi et al. 2009, Ratajczak et al. 2017*b*). Nonlinear threshold responses coupled with reinforcing feedbacks may exhibit hysteresis, which (if possible at all) will require more intervention and time to reverse. If changes result from drivers that cannot be controlled (e.g., climate variability), then long-term research is needed to understand and prepare for the consequences of ecological state change. Knowledge of how ecological drivers interact will be paramount for managing ecosystems for their persistence, achieving specific conservation goals, or provisioning ecosystem services. If the state changes are produced by global as opposed to local drivers, trying to reverse them may be impossible at the local scale. Determining the importance of global vs. local drivers again requires detailed site knowledge and long-term studies.

Through long-term research, we have identified drivers and trajectories of change across a range of ecosystems, which is apparent in these examples. Rising temperatures, precipitation changes, fire, and storm frequency affect systems in different ways. A strength of the LTER network is that it allows sites to tailor research questions to the unique drivers of change. It is interesting to note that LTER sites were not established with state change research in mind, yet many sites, including the five discussed here, have identified state changes as a dominant theme for their future. This suggests that state changes are not rare events that only occur in models or unusual systems, but are likely to be common in a wide variety of ecosystems (here salt marsh, barrier island, terrestrial grassland, and forest). Therefore, managers and decision-makers need to think about state changes as possible outcomes in planning for the future. Research from each site can thus play an important role in shaping public policy and management decisions. Together, the network of sites provides insights into patterns, mechanisms, and consequences underlying ecosystem response to complex environmental change.

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