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

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Abstract. Ecosystems across the United States are changing in complex and surprising ways. Ongoing demand for critical ecosystem services requires an understanding of the populations and communities in these ecosystems in the future. This paper represents a synthesis effort of the U.S. National Science Foundation-funded Long-Term Ecological Research (LTER) network addressing the core research area of "populations and communities." The objective of this effort was to show the importance of long-term data collection and experiments for addressing the hardest questions in scientific ecology that have significant

implications for environmental policy and management. Each LTER site developed at least one compelling case study about what their site could look like in 50–100 yr as human and environmental drivers influencing specific ecosystems change. As the case studies were prepared, five themes emerged, and the studies were grouped into papers in this LTER Futures Special Feature addressing state change, connectivity, resilience, time lags, and cascading effects. This paper addresses the "connectivity" theme and has examples from the Phoenix (urban), Niwot Ridge (alpine tundra), McMurdo Dry Valleys (polar desert), Plum Island (coastal), Santa Barbara Coastal (coastal), and Jornada (arid grassland and shrubland) sites. Connectivity has multiple dimensions, ranging from multi-scalar interactions in space to complex interactions over time that govern the transport of materials and the distribution and movement of organisms. The case studies presented here range widely, showing how land-use legacies interact with climate to alter the structure and function of arid ecosystems and flows of resources and organisms in Antarctic polar desert, alpine, urban, and coastal marine ecosystems. Long-term ecological research demonstrates that connectivity can, in some circumstances, sustain valuable ecosystem functions, such as the persistence of foundation species and their associated biodiversity or, it can be an agent of state change, as when it increases wind and water erosion. Increased connectivity due to warming can also lead to species range expansions or contractions and the introduction of undesirable species. Continued long-term studies are essential for addressing the complexities of connectivity. The diversity of ecosystems within the LTER network is a strong platform for these studies.

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INTRODUCTION

Ecosystems around the world are changing in complex and often surprising ways (Grimm et al. 2013). Analysis of these changes requires coordinated networks of geographically distributed sites for long-term ecological research (Golley 1996, Peters et al. 2014a). The challenge of studying ecosystem change has intensified in recent years along with accelerating climate change, air and water pollution, land-use change, agricultural intensification, and species movement (Steffen et al. 2005). A major challenge for ecologists is to understand how ecosystems change in order to predict the consequences of these changes for diverse elements of society. Because ecosystems comprise interactions across populations, communities, and the environment, forecasting how changing environmental conditions will drive ecosystem transformations and their associated functions and services will demand coordinated analytical and comparative approaches.

The capacity for environmental science to provide societally relevant information on ecosystem change is greatly facilitated by the existence of research and monitoring networks (Peters et al. 2008). The Long-Term Ecological Research (LTER) network funded by the U.S. National Science Foundation (NSF) is a group of long-term, site-based research programs aimed at understanding ecological processes over the long term in a wide range of different ecosystem types. The LTER network began in 1980, with roots in earlier network efforts such as the International Biosphere Program (Callahan 1984). LTER sites were selected through a competitive process based on investigator-driven ideas about how to study ecological phenomena over long time periods using experiments, long-term monitoring, modeling, and comparative studies. Since the program began, data collection at each site is organized around five core research areas: primary production, population dynamics, movement of organic matter, movement of inorganic

matter, and disturbance. LTER sites also carry out integrative, comparative research at multiple sites within the LTER network to examine commonalities and trends at scales broader than a single site.

Synthesis to facilitate the flow of information from site-based and network-level LTER studies to diverse sectors of society is accomplished via several mechanisms, including thematic working groups at network meetings. During one such working group focused on the core research area of populations and communities, it became apparent that each LTER site had at least one compelling case study about what their site could look like in 50–100 yr as a result of changing human and environmental conditions. Here, we compiled these case studies as a broadly applicable and relevant assessment of how ecosystems across the network are changing and to show the importance of long-term data collection and experiments for addressing the hardest questions in basic science ecology that have significant implications for environmental policy and management. The emergence of consistent themes among sites catalyzed the identification of five different papers focused on the following topics: state change, connectivity, resilience, time lags, and cascading effects.

This paper addresses the topic of connectivity and includes case studies from the Phoenix (urban), McMurdo (Antarctic polar desert), Niwot Ridge (alpine), Plum Island (coastal, estuarine), Santa Barbara (coastal), and Jornada (drylands) sites. Spatial and temporal connectivity is a key factor influencing the structure, function, and dynamics of ecosystems (Huston 1999, Peters et al. 2008). Connectivity can involve multi-scalar interactions in space (Holling 1992, Peters et al. 2004, Peters et al. 2007) as well as complex interactions with time (Carpenter and Turner 2000, Foster and Aber 2004) that influence transport of materials (Reiners and Driese 2003). Similarly, the significant movement of organisms that determines ecosystem structure can occur over multiple spatial and temporal scales (With et al. 1997, Crowl et al. 2008). The case studies presented here illustrate the expanding scope of connectivity research within the LTER network and range from showing how land-use legacies interact with climate to alter the structure and function of arid ecosystems to analysis of how climatic variation drives flows of resources and

organisms in Antarctic polar desert, alpine ecosystems, urban, and coastal marine ecosystems. The case studies highlight that continued long-term studies are essential for addressing the complexities of connectivity and that the diversity of ecosystems within the LTER network is a strong platform for these studies.

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

1. What Could the Central Arizona–Phoenix Region Look Like in the Future? David M. Iwaniec, Elizabeth M. Cook, and Melissa J. Davidson
2. Connections Will Moderate a Polar Desert Ecosystem's Future: McMurdo Dry Valleys, Antarctica: Michael Gooseff, Byron Adams, Jeb Barrett, and Diane McKnight
3. Connections Are Key to Explain Ecological Responsiveness to a Changing Climate: high Mountain Landscape of Niwot Ridge: Katharine Suding, Chris Ray, Daniel Preston, Pieter Johnson, Marko J. Spasojevic, and Timothy Seastedt
4. Home on the Expanded Range in the Plum Island Ecosystems: How Do Climate Migrants Influence Their New Ecosystems? David Samuel Johnson
5. What Long-Term Data Tell Us About Short-Lived Species in the Santa Barbara Coastal Ecosystem: Daniel C. Reed, Max C. N. Castorani, Robert J. Miller, and Andrew Rassweiler
6. The Future of Landscapes in the American Southwest: Jornada Basin: Debra P. C. Peters, Laura F. Huenneke, Robert L. Schooley, Osvaldo E. Sala, Enrique R. Vivoni, Gregory S. Okin, Niall P. Hanan, Brandon T. Bestelmeyer

WHAT COULD THE CENTRAL ARIZONA–PHOENIX REGION LOOK LIKE IN THE FUTURE?

Central Arizona–Phoenix (CAP) LTER is one of two urban ecosystem LTER sites. Urban ecosystems provide unique opportunities to evaluate multiple dimensions of connectivity, from biophysical drivers such as climate to social drivers such as economics and human preferences. Situated in the Sonoran Desert, the study region

consists of 23 municipalities including the city of Phoenix, the fifth most populous municipality in the nation. Since 1997, CAP LTER has been conducting interdisciplinary research to understand urban ecosystems, including the connections between natural and built components of this social–ecological system. In addition to being one of the fastest growing municipalities in the nation, the future of the Phoenix urban ecosystem faces a number of pressing challenges.

One of the most pressing challenges for this area is climate change. Regional temperatures are expected to climb over the next century. Summer temperatures are projected to rise an average 1.9°C by 2050 and up to 5°C from 2070 to 2099 (Overpeck et al. 2013). Even without accounting for likely increases in urbanization, the region could face an additional 30 d per year with temperatures above 35°C, plus an additional 30 d per year with a maximum temperature over 46°C (Kunkel et al. 2013). Higher temperatures lead to exponentially higher deaths and heat-related illnesses, increased power use and carbon dioxide emissions from air conditioning, increased wildfire risks at urban–wildland interfaces, and reduced snowpack at elevation. While temperatures rise, drought projections for the region also rise. Annual precipitation in central Arizona is projected to decrease 10–20% by the end of the 21st century with increasing likelihood of extended droughts (Kunkel et al. 2013, Overpeck et al. 2013). At the same time, extreme precipitation events (high rainfall per hour) are likely to increase and cause flash flooding. Heat stress, increasing temperatures, and rising evapotranspiration will exacerbate reduced water supplies.

Cities increasingly face interdependent future challenges that are difficult to predict and plan for, especially in the long term. As with all hot, arid cities, heat and water are especially important challenges that interact with social factors, infrastructure, land, water, and energy. Decision-makers struggle with approaches to understand, explore, and plan for the future. Moreover, predictive models of complex urban social–ecological systems do not exist and are challenged by keeping up with rapid human innovation. Rather than relying on business-as-usual or predictive future models, at CAP, we are investigating the future of the region by integrating a long-term historical understanding of the system with a participatory approach to co-develop diverse long-term future scenarios (Iwaniec et al. 2020a, b). The scenarios integrate CAP long-term data on heat and climate dynamics, human population, socioeconomic, and institutional dynamics, land-use/land cover patterns, and human provisioning and management of water. The development of these scenarios allows for the exploration of changing connectivity among the future urban social and ecological systems, as well as potential implications, trade-offs, and uncertainties of future trajectories of social–ecological change.

Research on urban social–ecological systems generates essential knowledge on the development of cities. However, the formulation of innovative ideas and solutions for the future of cities requires connected and integrative approaches that address not only spatial and temporal connectivity but also connections among diverse research and city planning needs. We brought together a diverse group of social and environmental leaders from across the region to explore the unique challenges and opportunities we face in our urban desert environment. The process enabled the collaboration of decision-makers, researchers, and practitioners as full partners in developing future scenarios. Together, we developed scenarios that explore challenges and solutions to issues such as future population growth, urban development, diminishing resources, increasing heat, extreme events, and improving the community's well-being. Through a series of workshops, the participants developed alternative future scenarios and pathways from the present to 2060 for the Phoenix urban ecosystem through activities such as creating actor-oriented narratives and participatory systems mapping. The scenarios were then evaluated by participants with quantitative and qualitative model outputs that, for example, address future changes in connectivity of land use/land cover (Fig. 1), water use and availability, regional and human-scale heat and flood vulnerability, and other sustainability and resilience assessments (Georgescu et al. 2011, Zhang et al. 2013, Middel et al. 2014, Georgescu 2015, Sampson et al. 2020, Iwaniec et al. 2020b).

Among the scenarios, our partners co-identified three that explore how the region can adapt by 2060 to extreme drought, heat, and flooding:
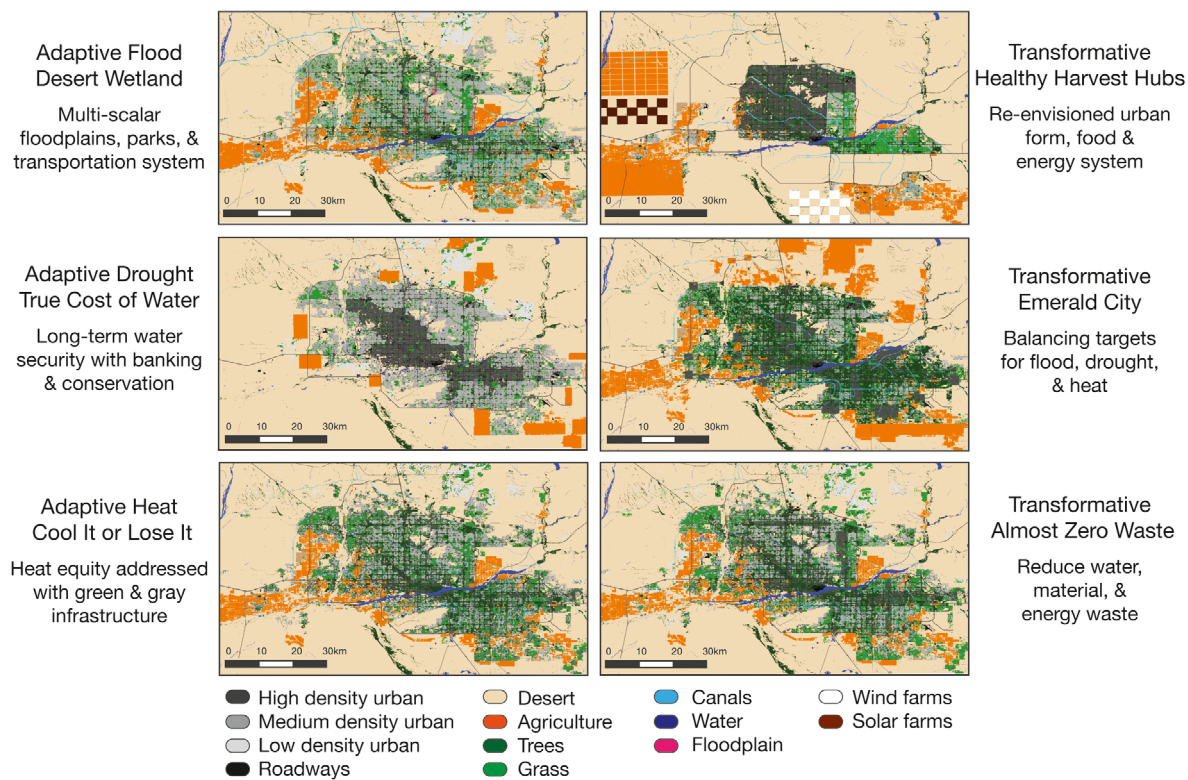
Fig. 1. Central Arizona–Phoenix 2060 regional land use/land cover representing major urban form changes explored in the six co-developed scenarios.

1. The *True Cost of Water* scenario addressed adaptation to extreme drought with strategies focused on long-term water security and aggressive water conservation, centralized water capture and reuse, and an emphasis on banking water underground. This scenario explored potential implications involving large decreases in urban vegetation and peri-urban agriculture in the face of future droughts.
2. The *Cool It or Lose It* scenario addressed heat equity with green and gray infrastructure connected throughout the urban region for increased walkability. These strategies prioritized human-scale adaptations in infrastructure and livable microclimates rather than regional effects of urban heat island.
3. The *Desert Wetland* scenario addressed future urban flooding by incorporating a multi-scalar (neighborhoods, cities, region) network of connected floodplains and parks. During extreme precipitation events,

the highway system becomes an additional floodway to increase hydrologic connectivity and convey water out of the city to water recapture and storage areas, as well as agricultural zones.

The collaborating practitioners and researchers also co-developed three transformative scenarios that suggest radically different, yet desirable futures for the CAP region:

1. The *Healthy Harvest Hubs* scenario explored implications of a highly centralized and connected urban form. This scenario envisioned concentrated hubs of agriculture and renewable energy systems connected via high-speed transit and green corridors to dense urban hubs throughout the region.
2. The *Emerald City* scenario balanced trade-offs among strategies to address future drought, flood, and heat. For example, similar to the *True Cost of Water* scenario, this

scenario featured aggressive water conservation strategies for drought, yet much of the water infrastructure in the *Emerald City* was decentralized and supported on-site green infrastructure to mitigate rising urban temperatures.

3. The *Almost Zero Waste* scenario featured strategies to reduce water, material, and energy waste. To meet these goals, this scenario shifted away from large-scale, peri-urban agriculture to small-scale urban agriculture, decentralized solar energy infrastructure, tightly coupled rain and stormwater capture infrastructure, and novel green economy innovations to support reused materials diverted from the waste stream.

The development of these six scenarios allowed the transdisciplinary group of participants to explore alternative future actions, policies, and strategies with different forms of connected infrastructure, green space, and governance to improve urban sustainability and resilience (https://sustainability.asu.edu/future-scenarios/). This form of futures research allows us to address different challenges, connect diverse stakeholders and sectors to co-develop innovative solutions, and contribute to future planning and decision-making across connected scales.

CONNECTIONS WILL MODERATE A POLAR DESERT ECOSYSTEM'S FUTURE—MCMURDO DRY VALLEYS, ANTARCTICA

The McMurdo Dry Valleys (MDVs) of Antarctica are an ecosystem that is driven strongly by connectivity between glaciers, streams, and lakes through streamflow from melting glaciers, which is controlled by climate. The valleys are a polar desert consisting of glaciers, streams, ice-covered closed basin lakes, and exposed arid soils with no vascular vegetation present. It is the largest ice-free region of Antarctica. The climate is cold (mean annual air temperature of −18°C, Doran et al. 2002*a*) and dry (<10 mm of snow water equivalent annually, Fountain et al. 2010). There are no "higher" plant or vertebrate animal taxa in this system; hence, the biology is driven by microbes and a very limited number of microscopic invertebrate species. The ecosystem is poised at the phase change of water with multiple freeze–thaw cycles occurring over daily timescales during the brief austral summer (Fountain et al. 1999). Therefore, this ecosystem and its resident biota are sensitive to small changes in climate (Fountain et al. 2016, Knox et al. 2017, Wlostowski et al. 2018).

Average summer air temperatures decreased significantly between 1987 and 2002 (Doran et al. 2002*b*). This led to several physical changes to the ecosystem, such as declines in glacial meltwater generation, thickening ice covers on lakes, declining lake levels (lakes are endorheic, so levels are a balance of added glacial melt and loss due to evaporation of liquid water in the summer and sublimation of ice cover year round), and reduced photosynthetically active radiation flux to the lake water columns underneath the 4 m thick ice cover. Further, the connections of glaciers to streams, streams to lakes, and soils to glaciers, streams, and lakes were diminished during this period. These changes also had an impact on communities and ecological processes as populations of soil nematodes and lake primary productivity, and the biomass of stream microbial mats decreased (Doran et al. 2002*a*, Kohler et al. 2015*b*). However, in 2002 a period of warm, sunny weather induced record glacial meltwater generation causing record streamflow and lake-level rise. This single season "flood" event was followed by a decade of stabilized modal summer air temperatures and high solar flux (Gooseff et al. 2017). Consequently, lake ice thinned, lake levels rose, and glacial meltwater generation was greater than observed during the cooling period, enhancing physical (i.e., streamflow and winter aeolian) connectivity of the landscape. The ecosystem responded with increasing lake primary productivity, a stabilization of soil invertebrate populations, and increasing stream algal mat biomass (Fig. 2). These decadal trends in the McMurdo Dry Valley ecosystem are a direct result of corresponding climate patterns and events.

Models of future climate in this region of Antarctica predict a warming trend over the next several decades (Chapman and Walsh 2007, Walsh 2009). Given the close proximity to McMurdo Sound, which loses its sea ice at least partially every austral summer, there is uncertainty about how the climate of the MDVs will
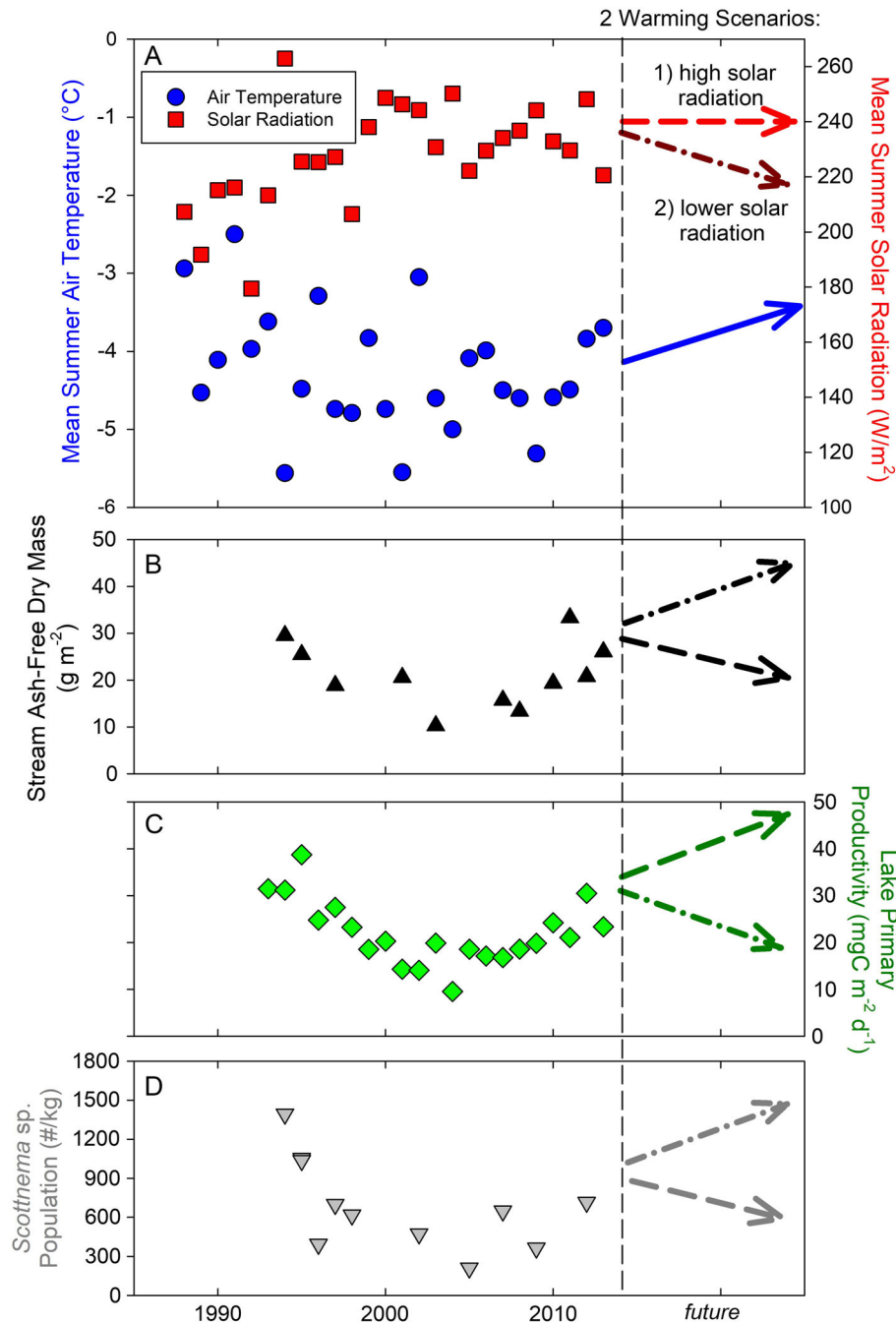
Fig. 2. Past observations and future projections in the McMurdo Dry Valleys of (A) mean summer air temperature and solar radiation, and ecosystem properties: (B) stream algal mat biomass reported as ash-free dry mass for streams in the Lake Fryxell basin, (C) primary productivity of West Lobe of Lake Bonney, and (D) soil invertebrate *Scottnema* sp. populations.

respond. Solar radiation is the greatest surface energy flux during the austral summer. However, warming of air temperatures may cause increased cloud formation from open ocean waters, shading the solar flux to this ecosystem. With little change to solar radiation, a warmer climate would cause increased melt of snow and ice. The increased melt would increase

streamflows, lake levels, and soil moisture across the landscape. The biological responses to these changes would likely include decreased stream algal mat biomass due to high streamflow scour (Kohler et al. 2015*a*, *b*), increased surficial freshwater habitat in our highly stratified lakes which may support increased primary productivity in lake water columns, and changes in invertebrate species abundance and community composition (Fig. 2; Gooseff et al. 2017, Andriuzzi et al. 2018). Alternatively, because solar radiation is the largest contribution to the surface energy balance, decreased solar radiation (due to increased cloudiness) would result in decreased snow and ice melt (air temperature rise is not likely to compensate for decreased solar radiation) and therefore decreased streamflow, soil moisture, and lowering of lake levels (Fig. 2). The biological response to these changes would likely be decreases in soil invertebrate populations (Doran et al. 2002*a*), decreased algal mat biomass if streamflow seasons shorten and increased algal mat biomass if flows are low but streamflow seasons remain unchanged, and lower primary productivity in lake water columns, which are strongly light-limited. Whereas the increased surface energy input to the landscape would be expected to enhance physical connectivity within this ecosystem, the opposite would be expected for lower surface energy input. These two contrasting potential future ecosystem states illustrate the important interactions between summer air temperature and controls on the hydrologic cycle driven by radiation.

Another unanticipated response to the "flood" event in 2002 was the appearance of a wetland in an area that had been dry during the previous decade. Fortuitously, long-term soil experiments had been established in this area. The detailed data on the distribution of soil biota prior to the re-activation of the wetland had shown a greater diversity of soil fauna with species typically found in near stream environments more abundant than in dry soil environments (Nielsen et al. 2012). Subsequent mapping of the soil biota along transects in the wetland area showed that the spatial patterns in the soil biota composition matched with the boundaries of the saturated area during the flood event (Nielsen et al. 2012). During the three higher flow summers following the initial 2002 flood event, the wetland was also re-activated. During the 2008/09 event, we studied the flowpaths and water retention in the wetland by adding a conservative tracer to the inflow spring (Wlostowski et al. 2019). The pulse of tracer rapidly attenuated downstream and was undetectable in the main wetland area, indicating a large multi-year reservoir of water that had thawed during the warm summer. This hydrologic condition contrasts with the drainage of the hyporheic zone adjacent to streams at the end of the summer and explains the uniform chemistry of the interstitial water throughout the wetland. In contrast to the diverse soil fauna in the wetland, the perennial microbial mats in the channels of the wetland have a less diverse diatom flora dominated by taxa that are present but much less abundant in the stream microbial mats. As a whole, these studies suggest that the re-activation of distinctive wetland ecosystems during warm sunny summers contributes to landscape connectivity of the MDVs.

Whereas the short warming event of January 2002 induced substantial changes across the MDVs landscape, should those warm, sunny conditions become the norm, we would expect a significant physical reorganization of this landscape, which would cause changes to habitats, biogeochemical cycling rates, and likely food webs. However, for any changes to manifest from one austral summer to the next, the changes have to persist through the cold, dark winters of Antarctica, which remain an important barrier to adaptation.

CONNECTIONS ARE KEY TO EXPLAIN ECOLOGICAL RESPONSIVENESS TO A CHANGING CLIMATE—HIGH MOUNTAIN LANDSCAPE OF NIWOT RIDGE

Research at the Niwot Ridge high-mountain LTER site (NWT) shows how connectivity of resources and organisms between ecosystems and the atmosphere, between different components of the landscape, and across seasons creates variation in ecosystem sensitivity to climate. Indeed, responsiveness to climate drivers has been shown to vary widely among ecosystems in many locations (Williams et al. 2008, Ackerly et al. 2015). A major theme of the research at NWT is to explain this variability and forecast where and when changes in climate drivers will

result in ecosystem change. Why are some systems and some locations apparently insensitive to seemingly large shifts in climate, while others shift dramatically in response to comparatively small changes to the environment?

Mountain ecosystems are traditionally characterized as both extreme and highly variable (Fig. 3, Billings and Mooney 1968). Almost 60 yr ago, Bliss (1956) concluded that the alpine tundra environment was one of the most severe on earth, with stronger winds, higher maximum radiation, higher surface temperatures, and greater desiccation risk than even the arctic tundra. High topographic relief and variation in substrate age and depth associated with glacial and periglacial activity yield high spatial heterogeneity (Leopold et al. 2008, Litaor et al. 2008, Malanson et al. 2012). In addition, precipitation can vary by threefold between a wet and dry year, and monthly temperatures can vary by as much as 10°C between a warm and cold year.

In a recent Intergovernmental Program on Climate Change report, winter snow cover was noted as one of the fastest-changing climate features (Vaughan et al. 2013). Consistent with global patterns, long-term records at our study site indicate increased positive degree-days and earlier snowmelt times (Kittel et al. 2016, Preston et al. 2016), with rising spring temperatures, earlier snowmelt, and drier summers. Niwot Ridge has also experienced increased "dust on snow" events over the last decade, which reduces albedo and further accelerates melting (Painter et al. 2007, Neff et al. 2008). An earlier snowmelt results in a longer growing season, higher growing degree-days, and often a larger soil moisture deficit (Schoeb et al. 2009, Wipf 2010). Across Colorado, snowmelt timing has progressed by approximately three weeks since the 1970s (Clow 2010), including an increase in lake ice-off dates by a week (Preston et al. 2016); similar progression in snowmelt timing is occurring regionally (Stewart 2009, Pederson et al. 2011).

Given this high variability in environmental drivers combined with high sensitivity of the alpine biota to these drivers, we expect the responsiveness of mountain ecosystems to vary widely. Nonetheless, earlier snowmelt, warmer springs and summers, and more frost-without-snow events are likely to be characteristic of an

Fig. 3. Mountain ecosystems, such as Niwot ridge and the Green Lakes Valley, shown here, are traditionally characterized as both extreme and variable, with complex terrain creating high spatial variability. This variability can both influence the exposure to climate in a particular area in the landscape as well as the sensitivity to those changes. Photo credit: W. Bowman.

ongoing and important change across high-elevation mountain regions. In looking to the future, we expect that many of the changes at Niwot will depend on how longer summers (or more precisely, a longer snow-free period) will affect different elements of the system.

We expect large declines in populations of pika (*Ochotona princeps*, an important herbivorous small mammal in this system), with the possibility of local extinction at our study sites on Niwot Ridge within a decade. Chronic stress in pikas that inhabit warming sub-surface microclimates indicates the detrimental loss of sub-surface ice (Wilkening et al. 2013, Wilkening et al. 2015) and much lower survival in chronically stressed pikas (Wilkening and Ray 2016). We found that the composition of available forage and of forage cached for overwinter survival in the haypiles of American pikas shifted over time (Bhattacharyya and Ray 2016), resulting in a reduction of forage quality. Pikas born early in longer summers may be forced to disperse during peak, stressful temperatures (Wilkening et al. 2015). At the other extreme, cold events in the absence of insulating snowpack increase mortality (Ray et al. 2012, Yandow et al. 2015). Climatic factors governing local habitat quality and sub-population connectivity are projected to drive the decline of pikas in at Rocky Mountain National Park near Niwot (Schawlm et al. 2016, Fig. 4).

With increased growing season length, tundra vegetation will likely expand uphill into currently barren soils (Suding et al. 2015), for which microbial communities may facilitate plant colonization in some areas (King et al. 2012, de Mesquita et al. 2016). At the very highest elevations, vascular plant abundance is limited due to the short growing season (<20 d in some areas). Here, we expect that a longer growing season will enable plants to expand into these barren areas, which have already been detected over the last three decades. We further predict that future plant communities will be structured by the diverse and active microbial communities that thrive in these unvegetated sites (King et al. 2010), as strong symbiotic relationships will allow plants to tolerate the severe nutrient limitation inherent to these high elevations (Knelman et al. 2014, Schmidt et al. 2015). Within the established tundra, we expect similar responses in
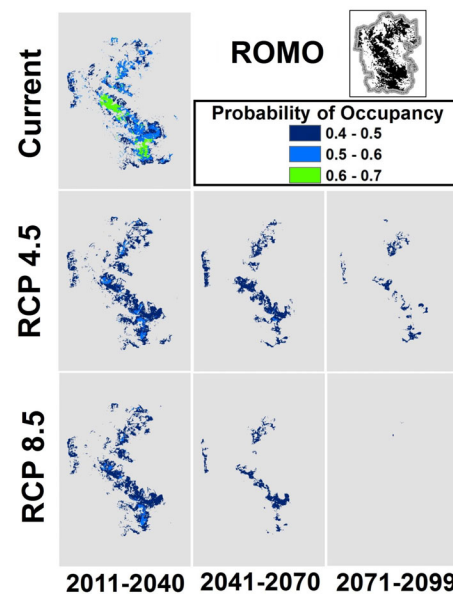
Fig. 4. Example of a pika population predicted to experience a steady decline throughout this century in an area near Niwot Ridge, Rocky Mountain National Park (ROMO). Shown are the total potential habitats and predicted occupant probability using an ensemble climate model with two carbon forcings; RCP 8.5, a "business as usual," "high emissions," "worst-case" scenario, and RCP 4.5, a stabilization scenario, where warming is stabilized by reductions in greenhouse gas emissions. (After Schwalm et al. 2016.)

snowbed areas, where a longer growing season would enable more plants to persist (Fig. 5).

As opposed to tundra expansion, treeline areas are not anticipated to move upward in response to longer growing seasons because of moisture stress. Forest expansion has been much slower and has mostly consisted of infilling lower elevation areas. Earlier snowmelt and warmer summers have been linked to decreased primary productivity in subalpine forests (Hu et al. 2010) and accelerated tree mortality (Smith et al. 2015, Conlisk et al. 2017). Warmer temperatures and enhanced evapotranspiration further increase the soil moisture deficit (Moyes et al. 2013, Knowles et al. 2014), suggesting that water limitation may be a primary constraint on treeline expansion. These same constraints on treeline do not appear to hold for woody shrub expansion into the tundra. Over the last several decades, shrubs
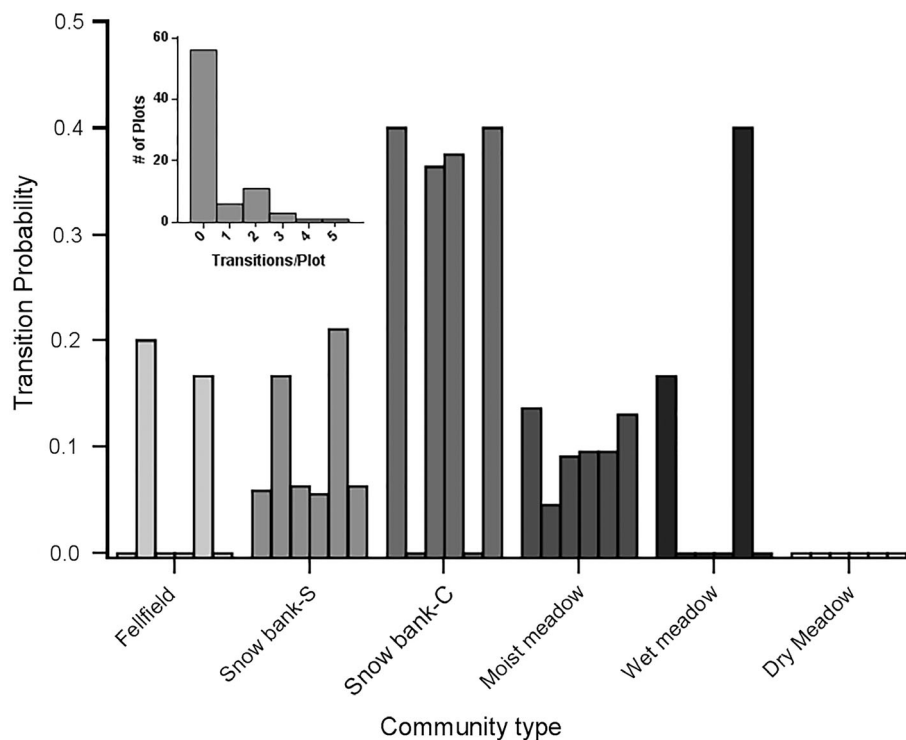
Fig. 5. Transition probabilities from one community type to another observed between long-term census intervals at Niwot Ridge. For a given community type, each bar represents a time interval, ordered earliest to latest: 1989–1990, 1990–1995, 1995–1997, 1997–2006, 2006–2008, 2008–2010. Transitions are described by initial community type designation and are calculated as the number of transitions relative to the number of total plots of that designation. *Inset:* Histogram describing the number of times a plot transitioned to another type, with 0 indicating that the plot never transitioned over the course of the surveys. (After Spasojevic et al. 2013.)

(largely *Salix* species) have expanded rapidly into the tundra (Formica et al. 2014); an ongoing *Salix* seedling transplant experiment indicates increased nitrogen deposition and higher summer temperatures jointly facilitate willow (*Salix*) growth (Formica et al. 2014), consistent with the general finding that shrubs are invading the herbaceous tundra (Elmendorf et al. 2012).

Correspondingly, we expect that the ecology of alpine lakes will change substantially in the future, due both to changes in climate as well as the upward movement of terrestrial subsidies related to tundra and forest change (Fig. 6). Earlier ice-off and warming are associated with reductions in summer streamflow, increased surface water temperatures, stronger thermal stratification of the water column, higher nitrate and dissolved organic carbon concentrations, and increased delivery of rock weathering products

(Miller and McKnight 2012, Preston et al. 2016) (Fig. 6). Increases in lake water residence time (Flanagan et al. 2009) associated with lower flushing rates help to drive greater system stability and productivity, including higher chlorophyll a levels (Hood et al. 2005, Preston et al. 2016) and higher potential for zooplankton (e.g., by large-bodied *Daphnia* spp.) grazing on phytoplankton and more complex food web dynamics.

Dissolved organic matter inputs from the surrounding terrestrial environment help to attenuate the harmful effects of ultraviolet radiation on phytoplankton and zooplankton communities, while simultaneously providing an added source of carbon to fuel food web dynamics (Hood et al. 2005, Dodds and Cole 2007, Sadro et al. 2011). We expect to see the most rapid changes in the highest elevation lakes, as expansion of tundra vegetation into previously unvegetated areas
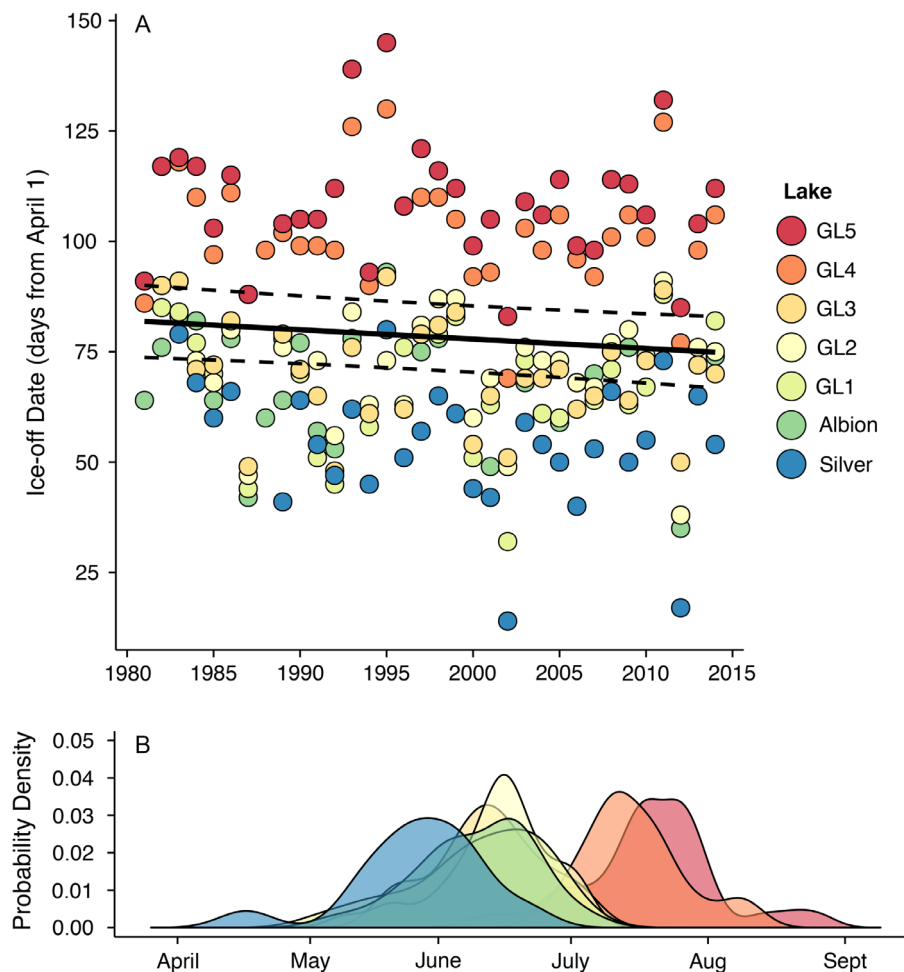
Fig. 6. Ice-off dates from 1981 to 2014 for seven lakes that have been monitored within the Niwot Ridge LTER site in Colorado, USA. The black linear regression line with 95% confidence band corresponds to a shift in ice-off timing of 7 d earlier over 33 yr. The legend at right lists the lakes from lowest (Silver, 3126 m) to highest elevation (GL5, 3620 m) (A). The probability distribution of ice-off timing for each of the seven lakes over the course of the season is shown in the lower panel. The colors correspond to lake identities in the upper panel (B). (From Preston et al. 2016.)

increases terrestrial subsidies of dissolved organic matter into lakes and enhances aquatic primary production (Miller and McKnight 2012). Such effects will likely be less pronounced in lakes below treeline for which terrestrial inputs are already significant.

While the relevance of these predictions will almost certainly vary among high-elevation sites, the responses already observed at NWT likely illustrate a larger, widespread pattern typical of many heterogeneous landscapes: Responses to climate change can be negative, positive, or largely undetectable, depending on the life history and traits of the organisms involved, the scale of ecological organization, and the spatial variability associated with landscape position. Connectivity of resources and organisms between ecosystems and the atmosphere, between different components of the landscape, and across seasons underlies much of the variation in these responses. Predictions based on how climate exposure might change via energy and resource limitation may allow predictions across these heterogeneous systems.

HOME ON THE EXPANDED RANGE IN THE PLUM ISLAND ECOSYSTEMS: HOW DO CLIMATE MIGRANTS INFLUENCE THEIR NEW ECOSYSTEMS?

Climate change is altering the connectivity between ecosystems as species ranges expand or shift to higher latitudes and altitudes worldwide (Sorte et al. 2010, Johnson 2014, Johnson 2015, Pecl et al. 2017). Populations of species that colonize new ranges as a result of climate change are climate migrants. LTER sites, with their long-term monitoring of populations and biodiversity, are perfectly poised to pinpoint the arrival of climate migrants. For instance, when the ocean heat wave of 2012 struck the Gulf of Maine in the northwest Atlantic, summer surface water temperatures were 1.3°C higher than the average of the previous decades (Johnson 2014, 2015). That same year, researchers at the Plum Island Ecosystem (PIE) coastal LTER in northeast Massachusetts discovered that the blue crab, *Callinectes sapidus*, had expanded its range beyond its historical northern limit of Cape Cod, Massachusetts (Williams 1974) into PIE and as far north as Canada (Johnson 2015, Fig. 7). In 2014, we discovered that the fiddler crab, *Minuca* (=*Uca*) *pugnax*, had expanded its range into PIE and beyond (Williams 1984, Johnson 2014, Fig. 7). In addition to the blue and fiddler crabs, at least two other crabs—the talon crab, *Euchirograpsus americanus*, and the ghost crab, *Ocypode quadrata*—have recently expanded their range in the Gulf of Maine (McDermott and Kraeuter 2015, Wilson and Pohle 2016), likely because of recent ocean warming.

While we have documented thousands of climate migrants (Perry et al. 2005, Sorte et al. 2010, Pinsky et al. 2013, Johnson 2014, 2015), we know little of their impacts on the structure and functioning of recipient ecosystems (Strayer 2012, Pecl et al. 2017). Here, we focus on climate migrants that are ecosystem engineers (sensu Jones et al. 1994), which can modify, create or maintain habitats, and use fiddler crabs as a case study. To develop an intellectual framework, we borrow from the extensive invasive ecology literature. Like invasive species, climate migrants are new to the habitats that they colonize (i.e., non-native), though by different means (i.e., climate vs. direct human intervention). For nonnative species that modify their environment

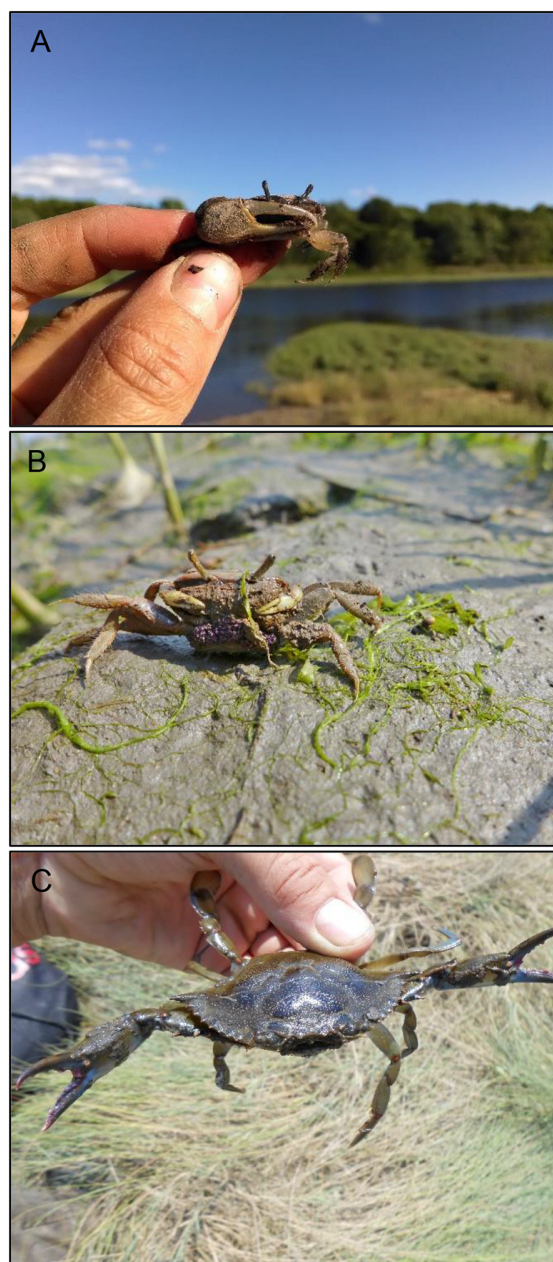Fig. 7. (A) Male fiddler crab, *Minuca pugnax*, (B) egg-bearing female *M. pugnax*, and (C) blue crab, *Callinectes sapidus* collected in the Plum Island Ecosystem Long-Term Ecological Research site. Photo credits: D. S. Johnson.

(engineering species), they may first have direct impacts on ecosystem functioning that then have indirect effects on communities and populations (Fig. 8, Strayer 2012). Furthermore, ecological
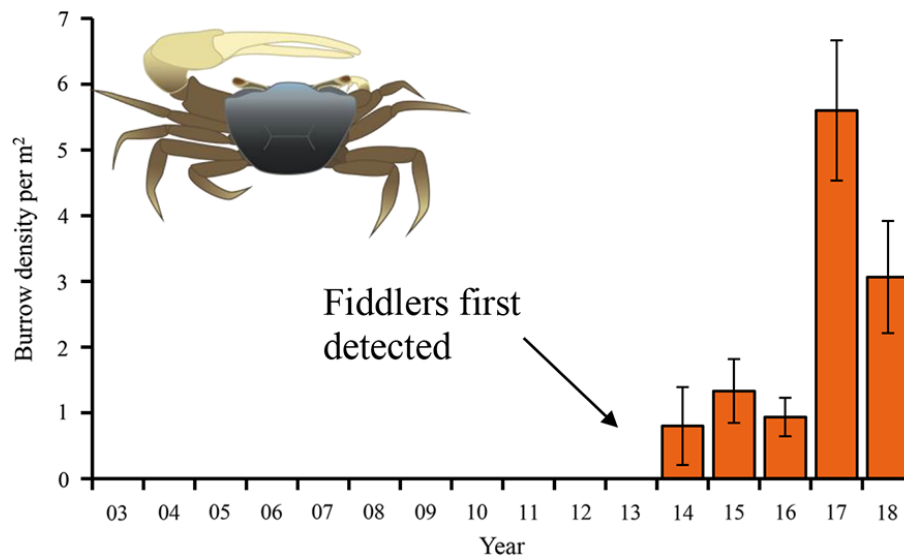
Fig. 8. Fiddler crab burrow density (mean $\pm$ 1 SE; n = 60–120 per year) in the Plum Island Ecosystem (PIE) LTER, a site where crabs recently expanded their range. For reference, the density in their historical range is ~60–120 burrows/m^2. The PIE LTER started sampling for saltmarsh invertebrates in 2003. Fiddler crab drawn by Lauren Huey.

theory predicts that the per-capita effects of non-native species can be disproportionately large when they modify resources, habitats, and keystone or foundation species (Parker et al. 1999). Finally, since the effect of nonnative species on ecosystem function can be expressed as the product of its range, per-capita effects, and population size (Parker et al. 1999), we can predict that climate-migrant effects will be amplified over time as their populations grow.

The fiddler crab lives in salt marshes, which are intertidal grasslands, along the east coast of the United States (Johnson 2014). As a burrower, fiddler crabs can directly affect marsh functioning by altering habitat, nutrient availability, and primary production (Gribsholt et al. 2003, Holdredge et al. 2010, Thomas and Blum 2010, Smith and Tyrrell 2012). Thus, fiddler crabs in PIE salt marshes serve as an excellent case study to address a number of hypotheses and questions related to climate-migrant impacts on ecosystem functioning including: (1) Do fiddler crabs in PIE (their expanded range) have larger per-capita effects than in their historical ranges (i.e., the vanguard hypothesis, Phillips et al. 2010)? The vanguard hypothesis states that individuals in vanguard populations (those at the leading edge of a range expansion) will have larger per-capita

effects than those individuals in core populations (those in the historical ranges). (2) What are the landscape-level impacts of fiddler crabs on saltmarsh functioning in their expanded vs. their historical ranges? Currently, the impacts of fiddler crabs in PIE are likely localized (m^2 scale) because their populations are small (<7 m^2 in PIE salt marshes vs. up to 100 m^2 in historical salt marshes, Fig. 9) and their distributions are patchy. Thus, the average effect of fiddler crabs on PIE marshes currently is likely low. However, their impact is expected to increase as their populations grow. (3) How do climate migrants interact with other global-change drivers to affect ecosystem functioning? For instance, as ecosystems at the interface of the land and the sea, accelerated sea-level rise threatens the persistence of salt marshes (Kirwan et al. 2010). Ecological theory tells us that fiddler crabs can enhance aboveground plant growth (Bertness 1985) and ecogeomorphic theory tells us that higher plant production increases a marshes ability to keep up with sea-level rise via increased sediment trapping (Fagherazzi et al. 2013, Kirwan and Megonigal 2013). Combining the two concepts suggests that fiddler crabs may help salt marshes maintain elevation with sea-level rise. However, ecology also tells us that fiddler crabs can
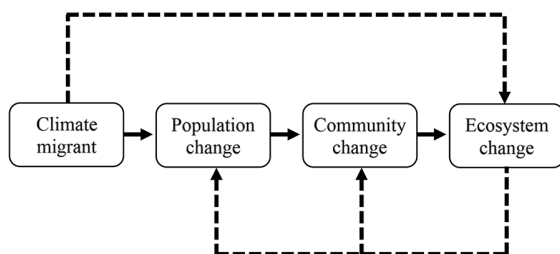
Fig. 9. Alternative pathways by which climate migrants may affect ecosystems. Solid lines = indirect pathway mediated by populations and communities. Dashed line = direct pathways via ecological engineering. (Modified from Strayer 2012.)

stimulate belowground decomposition (Gribsholt et al. 2003), which, according to ecogeomorphic theory, can lead to decreased accretion and thus the ability of a salt marsh to keep up with a rising sea (Fagherazzi et al. 2013, Kirwan and Megonigal 2013). Ultimately, the net effect of the interaction between fiddler crabs and sea-level rise is unknown. These questions and others can only be addressed by networks such as LTERs that allow for long-term observations, mathematical models, pre- and post-event data, mechanistic experiments, and cross-site (historical vs. expanded range) studies.

The flow of organisms between ecosystems is an aspect of connectivity that will have dominant effects on ecosystem populations and communities in a changing climate. The LTER network is well-poised to tackle these questions. For instance, two LTER sites on the U.S. east coast—Virginia Coastal Reserve (VCR) and the Georgia Coastal Ecosystem (GCE)—fall within the historical range of fiddler crabs. Cross-site comparisons between GCE, VCR, and PIE would allow for clarifying the relative impact of fiddler crabs in their expanded range (i.e., PIE). Long-term monitoring will allow us to track when new species arrive, and their dynamics over time. In a time of global change, LTERs are exactly the tools we need to understand and address these changes.

What Long-Term Data Tell us about Short-Lived Species in the Santa Barbara Coastal Ecosystem

Long-term data on the dynamics of giant kelp forests off the California coast collected by the Santa Barbara Coastal (SBC) LTER site illustrate the importance of several types of connectivity in this ecosystem ranging from connections between winter storms and growing season productivity, nutrient subsidies from bottom waters, and dispersal from adjacent ecosystems. These aspects of connectivity are fundamental controllers of the productivity and resilience of this ecosystem type.

The foundations of many ecosystems are formed by long-lived species with life spans ranging from decades to centuries (Dayton 1972, Ellison et al. 2010, Angelini et al. 2011, Osland et al. 2013). Populations of such species tend to react very slowly to rapidly fluctuating environmental conditions, thus necessitating observations over very long periods to detect responses to environmental change (Ellison et al. 2005). In some systems, however, foundation species live only a few years, fluctuating greatly in space and time in response to environmental variation (Miller et al. 2018, Bevilacqua et al. 2019). Despite the more rapid changes, a long-term perspective is still necessary in these systems to distinguish the effects of transient environmental variation from secular shifts in the environment, such as those associated with climate change (Dayton et al. 1992, Reed et al. 2016a). At the same time, short-lived foundation species offer better models for examining ecological responses to environmental change because data collected over multiple generations are more easily obtained (Reed et al. 2016b). Research at the Santa Barbara Coastal LTER (SBC) exemplifies the value of long-term data for understanding short-lived species as it focuses on coastal ecosystems dominated by the giant kelp *Macrocystis pyrifera*, a large, short-lived seaweed that provides the foundation for highly productive and diverse marine forests in coastal temperate seas worldwide.

Fifteen years of monthly observations show net primary production (NPP) by giant kelp alone can average 4 g $C \cdot m^{-2} \cdot d^{-1}$ or ~4.8 kg dry mass$\cdot m^{-2} \cdot yr^{-1}$ (Rassweiler et al. 2018) making giant kelp forests among the most productive ecosystems on Earth (Reed and Brzezinski 2009). However, unlike with most long-lived foundation species, this high productivity results from rapid growth (~3.5%/d) of a relatively small standing biomass (~0.4 kg dry mass/m^2) that
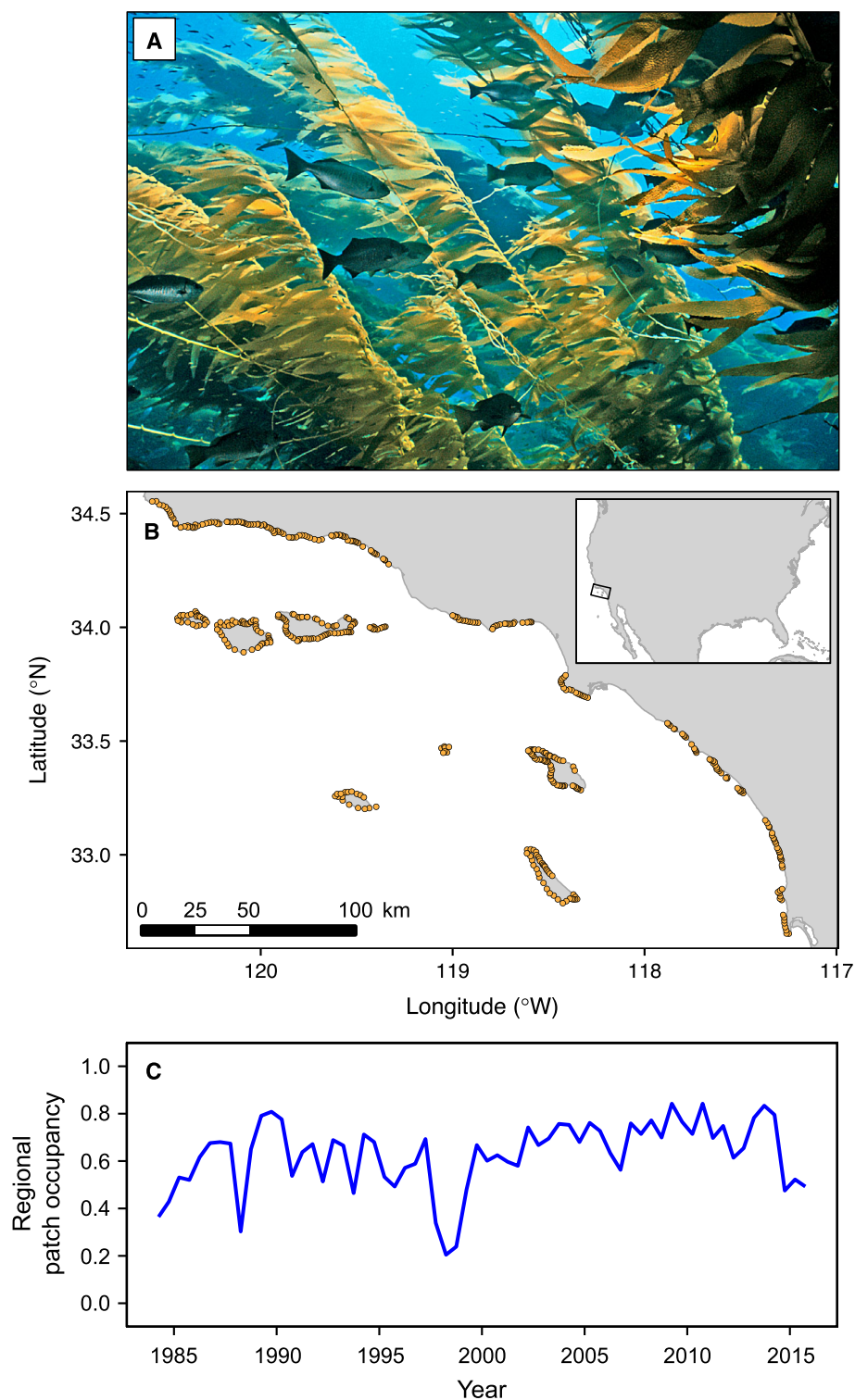
Fig. 10. (A) At the Santa Barbara Coastal LTER, the short-lived foundation species giant kelp, *Macrocystis pyrifera*, structures reef biodiversity by changing the physical environment and providing habitat and food to a

(Fig. 10. *Continued*)

diversity of fishes and invertebrates. Photo credit: Ron McPeak. (B) Distribution of giant kelp patches in southern California, USA, which are connected in a metapopulation network via the dispersal of planktonic spores. (C) A 34-yr giant kelp canopy time series from Landsat satellite imagery reveals high resilience at the regional scale (as evidenced by rapid increases in the proportion of patches occupied by giant kelp following disturbance) due in part to demographic connectivity among patches.

turns over about 12 times per year. Surprisingly, our long-term observations reveal that interannual variation in NPP is driven not by growth rates per se, but by variation in standing biomass at the beginning of the growth year, which is largely influenced by physical disturbance from waves produced by winter storms (Reed et al. 2008). Our results led us to hypothesize that storm-wave disturbances removing giant kelp prior to the start of the growing season overwhelm bottom-up and top-down processes to act as the principal determinant of NPP in giant kelp forests off California. We tested this hypothesis using regional comparisons of time-series data and found that giant kelp NPP was twice as high in the relatively calm Santa Barbara Channel than in more disturbed forests to the north despite substantially lower nutrients (bottom-up) and higher grazing (top-down) in the Santa Barbara Channel (Reed et al. 2011). Climate models predict changes in the frequency and severity of wave disturbance in coming decades (Wang et al. 2015), and our work suggests that such changes will alter the production of giant kelp forests. Control of NPP by disturbance is likely not unique to kelp forests, but it may be easier to detect because of the short longevity of giant kelp relative to the long duration and high frequency of our observations.

The SBC long-term data have also provided a greater understanding of regional kelp forest dynamics. Historically, giant kelp populations could only be studied at local scales due to the spatial constraints of scuba diving surveys. Researchers at SBC have overcome this limitation by taking advantage of giant kelp's ability to grow up through the water column and produce an extensive floating canopy at the sea surface that is visible from space. By bringing together traditional diver surveys with Landsat satellite imagery, we have created a long-term (>34 yr), high-frequency (6–10 × per year), high-resolution (30 m) time series of giant kelp canopy biomass across its >2000 km range in California and Baja California, Mexico (Bell et al. 2017). Analyses using this novel data set have revealed the relative roles of climate and environmental forcing on the dynamics and population synchrony of giant kelp (Cavanaugh et al. 2010, 2011, 2013) and its geographic variability (Bell et al. 2015, Cavanaugh et al. 2019). Furthermore, by combining satellite time-series data of kelp biomass in the region with oceanographic models, we uncovered remarkable resilience of giant kelp populations that reflects their demographic connectivity and ability to function as a metapopulation (Reed et al. 2006, Castorani et al. 2015). Contrary to the common assumption that local processes regulate kelp populations, our results show that dispersal from neighboring populations is needed to sustain forests and promote their recolonization after local extinction caused by disturbance (Castorani et al. 2015, 2017). If climate change alters wave disturbance regimes, then the spatial arrangement of kelp populations will be key to their demographic connectivity, local population persistence, and their ability to function as a resilient metapopulation (Fig. 10).

Because giant kelp is a foundation species, its demographic connectivity and the resulting persistence and stability of its populations have cascading effects on biodiversity, community structure, and ecological functions of the kelp forest ecosystem (Miller et al. 2015, 2018). The analysis of long-term data has allowed SBC researchers to quantify how storm disturbance mediates the direct and indirect effects of giant kelp on food web structure and complexity. Periodic storms tend to increase the complexity of kelp forest food webs, but if large storms occur year after year, the community may become less diverse and complex as species go locally extinct (Byrnes et al. 2011). The loss of complexity occurs primarily due to decreases in the diversity and complexity of higher trophic levels. Using a 9-yr

disturbance experiment, we found that the inter-annual frequency of disturbance outweighs year-to-year variation in disturbance severity, enhancing the relative dominance of understory primary producers and reducing biomass of important reef fishes and invertebrate consumers (Castorani et al. 2018). These findings provide insight into how kelp forests of the future may look if the frequency of severe storms increases as predicted. More generally, findings from this long-term experiment provide a framework for predicting how the loss of foundation species can restructure community guilds based on their dependence on key physical and trophic resources.

Recent declines in kelp forests in both hemispheres have been attributed to ocean warming (Krumhansl et al. 2016) and the Intergovernmental Panel on Climate Change predicted with high confidence that an increased frequency of marine heat waves and sea temperature extremes will result in further declines (Wong et al. 2014). A recent large-scale warming event in the North Pacific Ocean of unprecedented magnitude and duration (Di Lorenzo and Mantua 2016) allowed us to test this prediction for giant kelp forests off southern California and evaluate their value as a sentinel for detecting early signs of climate-related impacts. Surprisingly, we found that giant kelp and the majority of species that associate with it did not exhibit dramatic declines within the Santa Barbara region in response to this extreme warming event (Reed et al. 2016). Instead, we found that large seasonal and inter-annual fluctuations in giant kelp characterized all of southern California, and negative kelp biomass anomalies during the extreme warming of 2014–2015 were within the range observed during cooler years of the 32-yr time series (Fig. 11). However, in some areas farther south where warming was more intense, giant kelp populations crashed and showed little recovery two years after the heat wave ended (Cavanaugh et al. 2019). The lack of the expected large response to an extreme event, as in our study of kelp forests in the Santa Barbara region (Reed et al. 2016), reveals our limited ability to predict responses to longer-term changes. Such limits on our forecasting ability underscore the key role of long-term data in detecting the effects of climate change on ecosystems as they occur. Given the high cost of collecting long-term community data, it may seem wise to focus research efforts on sentinel species that are predicted to be most vulnerable and serve as a foundation for whole communities. However, our findings suggest that relying too heavily on untested sentinel species to detect ecosystem level effects may lead to a sense of complacency and missed opportunities to detect and avert greater ecological damage. Our findings also highlight the importance of several types of connectivity in these ecosystems: seasonal connections between winter storms and growing season productivity, nutrient subsidies from bottom waters, and dispersal from adjacent ecosystems. Long-term research is vital to understanding how short-lived foundation species and the ecosystems they support react to environmental change, including future climate change.

The Future of Landscapes in the American Southwest: Jornada Basin

Connectivity by wind and water that leads to high rates of losses of soil nutrients, reductions in air and water quality, losses of forage quality and quantity, and changes in other ecosystem services has long been a focus of research at the Jornada Basin (JRN) LTER program in southern New Mexico. Desert grassland landscapes in the American Southwest have experienced dramatic changes in ecosystem dynamics over the past 150 yr, similar to other arid and semiarid ecosystems globally. Periodic, multi-year droughts combined with overgrazing by livestock and a reduction in fire frequency have transformed ecosystems dominated by annual or perennial grass species to ecosystems dominated by xerophytic, grazing-tolerant woody species (Buffington and Herbel 1965, Havstad et al. 2006). The high rates of connectivity-driven nutrient losses driven by wind and water erosion have led to desertification of these ecosystems (Reynolds and Stafford Smith, 2002, Havstad et al. 2007, Yahdjian et al. 2015). Because of positive feedbacks between woody species and soil erosion driven by wind or water, these shrub-dominated ecosystems are notoriously difficult to return to grass dominance under current climatic conditions (Herrick et al. 2006). Thus, current landscapes consist of a mosaic of grasslands interspersed with large areas dominated by different species
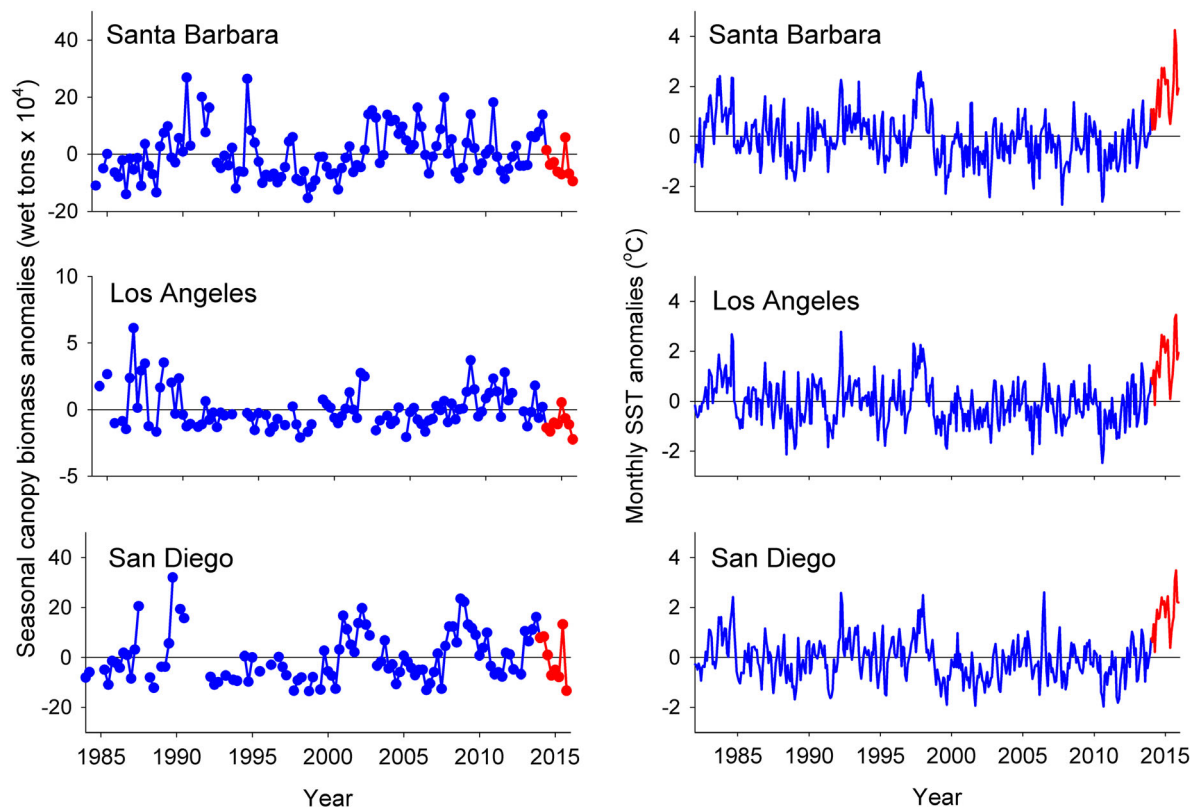
Fig. 11. Seasonal anomalies of giant kelp biomass in southern California estimated from Landsat satellite imagery for 1984–2015 and monthly sea surface temperature anomalies. Data for 2014–2015 warming event are shown in red. (From Reed et al. 2016*a*.)

of woody plants that are differentiated by landform, elevation, and soil properties (Peters et al. 2015). Future landscape dynamics will depend on a number of factors, including uncertainty in the magnitude and direction of changes in climate and land use interacting with spatial heterogeneity in landscape structure and function, as well as historical events and landscape processes (i.e., historic legacies; Monger et al. 2015). The Jornada Basin LTER Program is a 100,000 ha study site in the northern Chihuahuan Desert of southern New Mexico (32.5N, 106.45W), managed by the United States Department of Agriculture (USDA) Agricultural Research Service (ARS). At this site, we study how various biotic and abiotic components within ecosystem states respond to climate and land-use drivers, the connectivity among ecosystems within heterogeneous landscapes, and the integrated response of the landscape as a whole.

Here, we interpret results from long-term data and studies from the Jornada Basin LTER site in light of the two most likely changes in climate: an increase in temperature with either a directional decrease or increase in precipitation (Burke et al. 2006, IPCC 2007, Seager et al. 2007). Regional and global climate models often predict increasing aridity for the Southwest United States (Seager et al. 2007, Cook et al. 2015); however, annual rainfall amounts have generally increased over the past 50 yr (Karl and Wright 1998). Fortunately, the Jornada Basin LTER Program has experienced variation in rainfall amounting to a "natural experiment." We experienced seven years of rainfall with no year-to-year trend (1993–1999) followed by a four-year drought (2000–2003), a five-year wet period (2004–2008), and a two-year post-wet, no-trend period (2009–2010) (Table 1). In addition, a replicated plot-scale (2.5 m × 2.5 m) rainfall

Table 1. Mean annual air temperature and precipitation for each water year (1 October–30 September) at the Jornada Basin USDA LTER site averaged across six locations (three grasslands, three mesquite shrublands) and the 30-yr means (1981–2010) used to identify three climate periods (no trend, dry, wet) (Peters et al. 2014).

Year	Temperature (°C/yr)		Precipitation (cm/yr)		Period
1993	15.0	−	30	+	No trend
1994	15.7	+	15	−	No trend
1995	15.8	+	23	−	No trend
1996	16.2	+	21	−	No trend
1997	15.5	+	26	+	No trend
1998	15.0	−	15	−	No trend
1999	15.8	+	26	+	No trend
2000	16.2	+	20	−	Dry
2001	15.3	+	22	−	Dry
2002	15.8	+	15	−	Dry
2003	15.6	+	15	−	Dry
2004	15.5	+	27	+	Wet
2005	15.5	+	28	+	Wet
2006	15.6	+	34	+	Wet
2007	15.0	−	29	+	Wet
2008	14.8	−	33	+	Wet
2009	15.2	+	12	−	
2010	14.2	−	29	+	
30-yr mean	15.1		25		

Note: +/−: Yearly value was greater/less than the 30-yr mean.

manipulation experiment has been conducted since 2006 that provides complementary information on species-level and biogeochemical responses to altered precipitation (Gherardi and Sala 2015*a*, *b*). Manipulations consist of plots with rainout shelters to reduce rainfall by 50% or 80% to represent drought, and additional plots with irrigation to enhance rainfall by 50% or 80% to represent wet years (Gherardi and Sala 2013).

A drier Southwest, even without changes in the frequency of extreme precipitation or temperature events, is expected to influence the composition and structure of plant communities. First, as aboveground net primary production (ANPP) is reduced, the reproductive output of plant species will likely be reduced which will translate into lower inputs to the soil seed bank with direct impacts on granivorous animal species. Second, there is evidence that increasing aridity

will favor the ability of shrubs to access soil water resources at greater depths and time periods than grasses and to maintain growth during drought periods (Gherardi and Sala 2015*b*).

Desert rodents are an important consumer group whose dynamics are driven in part by bottom-up processes. Wet years with higher ANPP lead to increased abundance and biomass of rodents, but with a time lag of one year or more (Lightfoot et al. 2012). During dry periods, the biomass of desert rodents is primarily contributed by granivores (kangaroo rats, pocket mice), core species who are always present (Fig. 12). Hence, extended drought would not only reduce biomass of these rodents, and it also would alter the relative importance of granivore, folivore, and omnivore trophic groups. Moreover, if increased precipitation variability in the future promotes shrub dominance in the region (Gherardi and Sala 2015*b*), species composition of desert rodents will strongly shift (Lightfoot et al. 2012).

Both lower production of seeds and less frequent episodes of plant recruitment would have important consequences for ecosystem function and services. Lower plant cover and lower functional diversity would lead to higher rates of soil erosion by wind and water. Lower plant growth and fewer years of abundant plant growth would reduce inputs of organic matter to the soil, soil porosity, and soil water holding capacity to further limit plant recruitment, survival, and ground cover, exacerbating soil erosion by wind. A dustier Southwest in the future means that illnesses related to dust, such as pediatric asthma (Samoli et al. 2011) and Valley Fever (Leathers 1981), will also likely increase in an increasingly urbanized region (see Phoenix case study above).

Recently, a sequence of years with above-average amounts of precipitation led to unusual growth and recovery of perennial grasses in a threshold response that could not be predicted from precipitation amount in dry and no-trend years (Fig. 13) (Peters et al. 2012, 2014*b*). In upland grasslands, the production response resulted from a nonlinear increase in seed availability and production of recruits of *Bouteloua eriopoda* (Fig. 14), while in desertified shrublands, the grass production response was primarily related to a nonlinear increase in number of
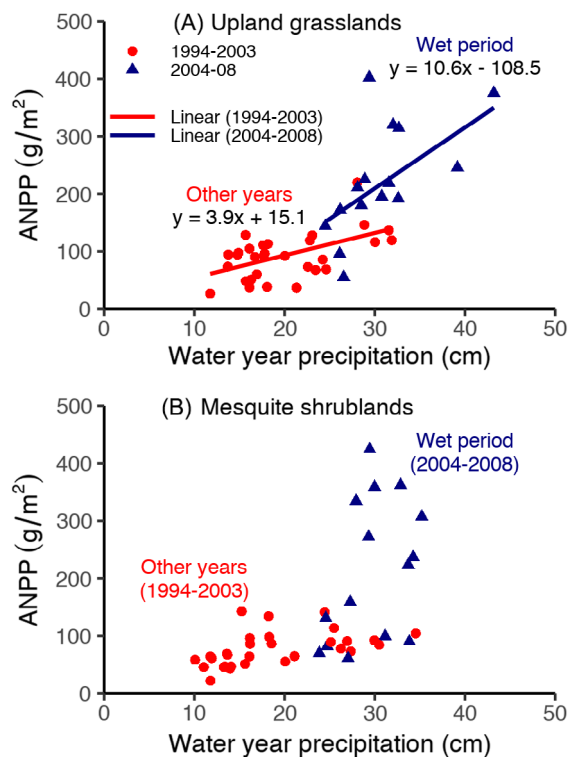
Fig. 12. Relationships between water-year precipitation (1 October–30 September) and aboveground net primary production (ANPP) at the Jornada Basin LTER site for data collected between 1994 and 2008: (A) upland grasslands, (B) mesquite shrublands. Regression lines, if significant, are shown for each of three time periods for each ecosystem type (no trend, dry period [1994–2003], wet period [2004–2008]). (From Peters et al. 2012.)

Sporobolus flexuosus recruits as the number of consecutive wet years increased (Fig. 15). These results suggest that a directional increase in rainfall as a result of global warming could drive desertified states past a threshold toward a higher productivity savanna ecosystem featuring both grasses and woody plants.

Wet periods that increase ANPP could also lead to lagged irruptions of desert rodents and an increased contribution to biomass from folivores (Fig. 12). The folivores include transient species (e.g., *Sigmodon hispidus*) that disappear from many observational sites on Jornada during droughts. Folivores are large contributors to rodent biomass following wet years, especially on mesquite shrublands (Fig. 12). More generally, a more mesic environment should reduce resource constraints on rodent consumers and increase the potential for top-down (predator) limitation of rodent biomass.

A more mesic region under similar precipitation variability and a similar vegetation state would lead to an increased occurrence of flooding events and increased connectivity by water by reducing the available storage capacity of hillslope and channel systems. If the additional precipitation is also delivered in larger, less frequent events under the same vegetation state, an even higher flooding potential would be expected, with recharge events anticipated in hillslope, channel, and playa ecosystems. However, erosion by aeolian processes and connectivity by wind would decrease, and local inputs of soil carbon would increase as herbaceous cover increases in interspaces between plants in desertified shrublands on sandy soils.

Over the past 150 yr, large areas of the American Southwest underwent rapid and profound state change from grasslands with shrubs to shrublands in response to drought and overgrazing by livestock. Long-term measurements at the Jornada LTER site first demonstrated the threshold nature of change in these systems and the importance of connectivity by wind and water to these changes. Recovery of grasses is limited despite exclusion of cattle and individual wet years. As the length of LTER observations and information from manipulative experiments continues to increase, we are beginning to understand the nonlinear processes causing hysteresis in vegetation community structure and composition.

In the American Southwest, the climate will continue to change in uncertain ways, and the long-term perspective available through the LTER program will provide insight into likely responses, either toward desertified shrublands or toward savannas and grasslands. These ecosystem state changes will depend on the magnitude and direction of change in underlying climate drivers interacting with soil properties, geomorphology, and connectivity by wind, water, and land use. Over a century of LTER and USDA research on the complexities of desert ecosystem dynamics that illuminated the importance of feedbacks, thresholds, nonlinearities,
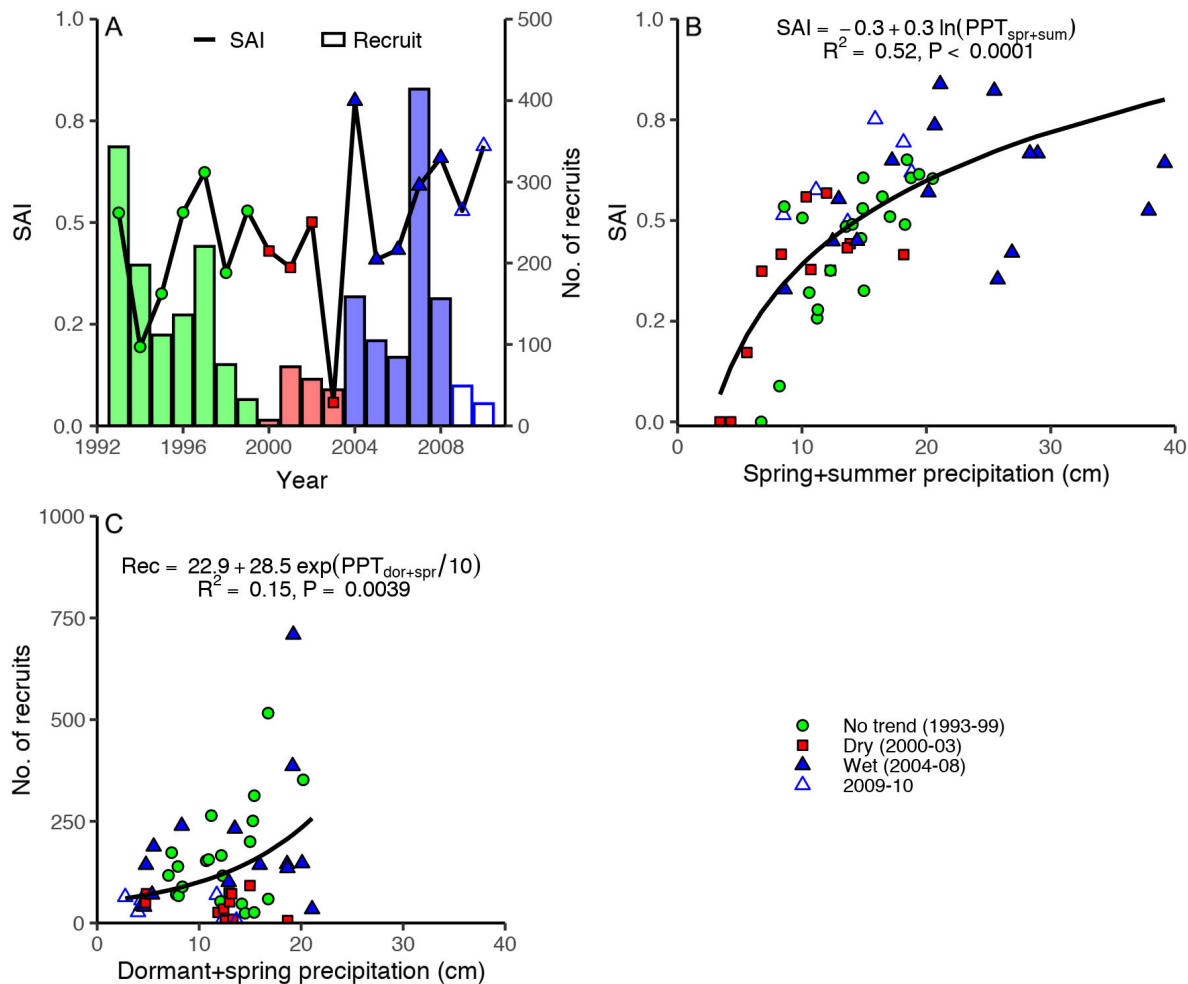
Fig. 13. Recruitment of *Bouteloua eriopoda* in Jornada grasslands: (A) mean seed availability (SAI) and mean number of recruits by stolons through time for three locations. Years within period shown by circles (no trend), rectangles (dry), and triangles (wet). For all years and locations, (B) SAI is positively related to spring and summer precipitation combined ($N = 54$), and (C) number of recruits is positively related to dormant and spring precipitation combined ($N = 54$). (From Peters et al. 2014*b*.)

hysteresis, and connectivity provides the foundation for understanding and predicting landscape dynamics in a non-stationary future.

Conclusions

The six research case studies presented here demonstrate the importance of physical connectivity to the biodiversity, structure, function, and services of ecosystems, as well as intellectual connectivity across disciplines to address our most pressing research questions and future challenges. Human-driven alteration of climate and changing land use have emerged as two major drivers of changing flows of organisms and materials that cascade to influence other ecosystem processes. In these case studies, the importance of connectivity is obvious across widely different ecosystems; three aquatic and three terrestrial, two very hot and two very cold. There is a clear need to consider multiple aspects of connectivity, from land-use legacies that interact with climate to alter the structure and function of contemporary ecosystems to analysis of how climate affects flows of resources and organisms between ecosystems both near and far.
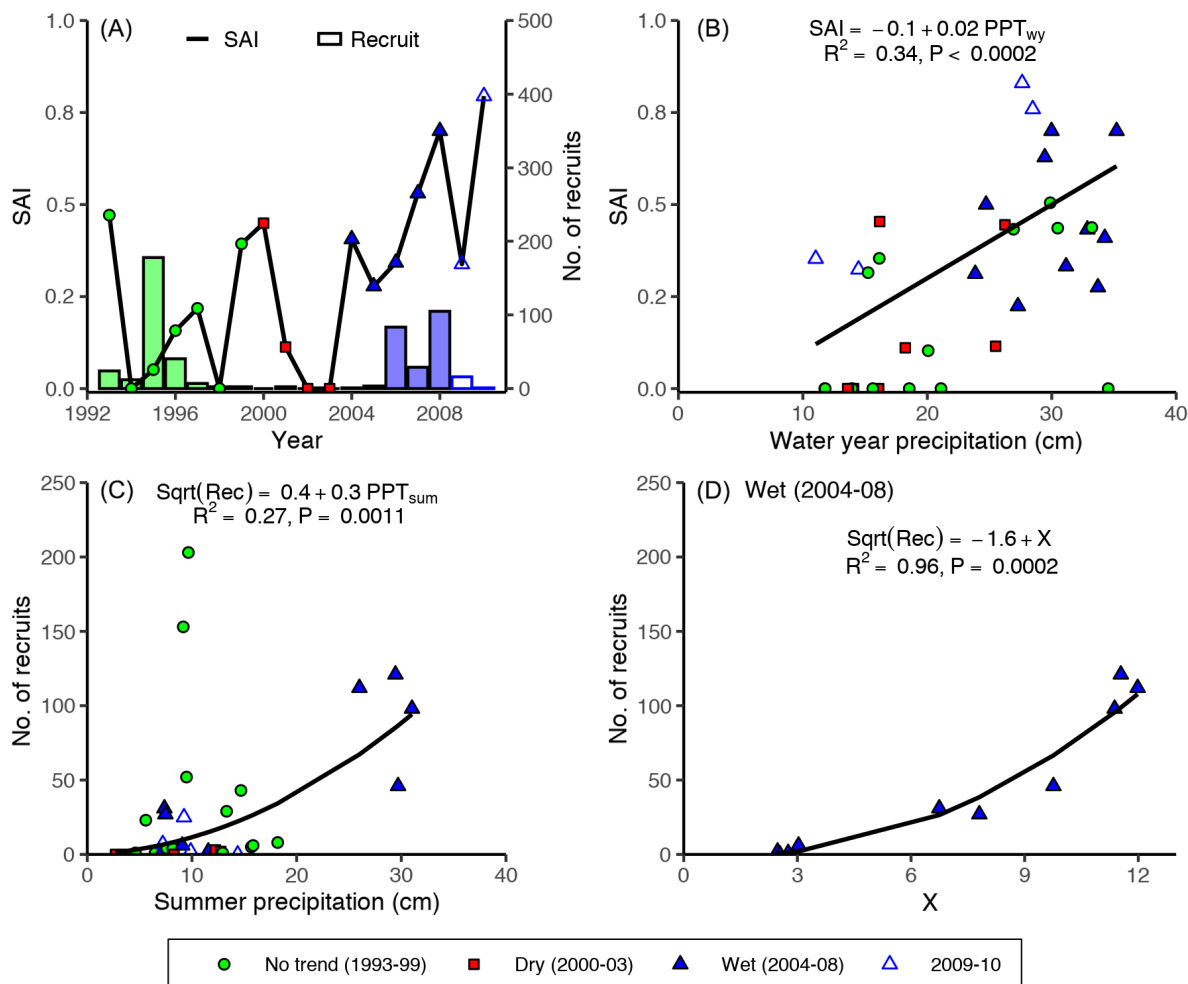
Fig. 14. Recruitment of *Sporobolus flexuosus* in Jornada shrublands: (A) mean seed availability (SAI) and mean number of recruits by seedlings through time for two locations. Years within period shown by circles (no trend), rectangles (dry), and triangles (wet). For all years and locations, (B) SAI is positively related to water-year precipitation ($N = 36$), (C) number of seedlings is positively related to summer precipitation ($N = 36$), and (D) in the wet period, the number of seedlings is related to summer precipitation (PPT_{sum}), seed availability two years previously ($t - 2$), and number of consecutive wet years: sqrt(recruitment) $= -1.6 + 0.1 \times PPT_{sum} + 9.6 \times SAI_{t-2} + 0.9 \times$ no. consecutive wet years ($N = 10$). In (C) and (D), regressions were conducted using square-root-transformed Y, but the regression lines are shown using back-transformed predicted values. (From Peters et al. 2014b.)

Long-term ecological research demonstrates that connectivity can sustain valuable ecosystem functions, such as the persistence of foundation species and their associated biodiversity. On the other hand, increased connectivity due to warming can lead to species range expansions and the introduction of undesirable species. Connectivity of organisms and materials is often highly variable over space and time, or driven by episodic events, and hence, long-term data—and modeling of future scenarios in the case of interconnected social–ecological ecosystems—are needed to isolate secular changes from background variability. Continued long-term studies are essential for addressing the complexities of connectivity. The diversity of ecosystems within
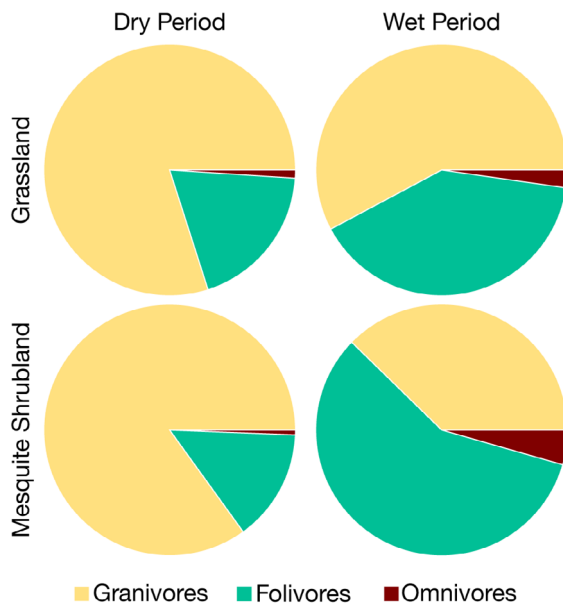
Fig. 15. Typical contribution of trophic groups to biomass of Chihuahuan Desert rodents following periods with below-average and above-average precipitation and annual net primary productivity (ANPP). (From Schooley et al. 2018.)

the LTER network is a strong platform for these studies.

Acknowledgments

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