Chapter 3

Cross-Site Comparisons of Ecological Responses to Climate and Climate-Related Drivers

M.D. Ohman and T.K. Kratz

Climate (the average and variability of weather conditions over a period of time) is a primary driver of ecological systems. Important climate and climate-related factors for ecosystems include precipitation, air and water temperature, ice cover duration, sea level, stream flow, solar radiation, and water clarity. These factors affect resources available to plants, animals, and microbes and act as environmental constraints on the suitable habitat for reproduction, growth, and survival of organisms. Changes in seasonal and annual climatic patterns can have important consequences for key ecosystem properties, such as species composition and diversity, phenology, migrations, trophic interactions, rates of nutrient cycling, and net primary production.

Long-term data are required to differentiate directional climate trends from short-term pulses and natural variability in climate. Globally over the past century, temperatures have warmed in the atmosphere, on land, in the ocean, and in the cryosphere (IPCC 2007). In addition to this background of progressive long-term change, there are multidecadal-scale variations associated with phenomena such as the Pacific Decadal Oscillation (PDO) and North Atlantic Oscillation (NAO), as well as interannual variations dominated by the El Niño-Southern Oscillation (ENSO).

Understanding ecological responses to climate change is difficult because of the interactions among climate drivers on these multiple time scales. In addition, ecological systems respond to multiple drivers (such as climate and land use change) simultaneously, and these responses are often nonlinear. It is often difficult to perform large experiments in which climate is manipulated in controlled ways. Thus, long-term observations of ecological systems are critical to improving our understanding as to how a wide range of ecological phenomena respond to changes in climate at timescales ranging from multiple years to decades and centuries (Greenland et al. 2003).

In this chapter, we illustrate the value of long-term data in testing two ecological hypotheses related to climate change for different ecosystems. The relationship between changes in climate, responses of ecosystems and their constituent populations, and the services that ecosystems provide is the subject of considerable contemporary research. We do not attempt a listing of the diverse hypotheses that are possible, but rather we illustrate the value of long-term data from a geographically dispersed network of research sites in testing hypotheses with different time scales of climate change: (1) interannual variations forced by ENSO and (2) longer term, multidecadal changes. In the case of ENSO, the examples illustrate the power to assess qualitatively different types of ecosystem responses to a common climate driver. Additional examples of ecological responses to climate can be found in Greenland et al. (2003). Graphs of long-term climate data for each site are shown in chapter 11.

Hypothesis 1: El Niño-Southern Oscillation (ENSO) Alters Populations and Food Webs in Both Ocean and Terrestrial Biomes

Characteristics of the climate driver. ENSO constitutes one of the major climate signals on Earth and has effects that can extend globally. El Niño refers to large, positive anomalies in temperature across the eastern tropical Pacific Ocean, while La Niña refers to negative temperature anomalies in the same region. Corresponding changes in the atmosphere are known as the Southern Oscillation, which arise from variations in the west-to-east Walker Circulation in the equatorial Pacific.

The Southern Oscillation Index is based on differences in atmospheric pressure between the eastern tropical Pacific (at Tahiti) and the western tropical Pacific (Darwin, Australia). A negative state of the SOI implies a weakened atmospheric high pressure zone in the eastern Pacific, diminished Walker Circulation, and weakened westward-flowing winds, which are accompanied by warm ocean El Niño conditions in the western Pacific. A positive state of the SOI implies an intensified atmospheric high in the eastern Pacific, stronger than normal westward flowing winds, and anomalously cool La Niña ocean conditions in the western Pacific.

In recent decades, ENSO has recurred about every 2-7 years. It has been suggested that the strength of the Walker Circulation, whose variations affect ENSO dynamics, has decreased approximately 3.5 percent in the past 150 years as a consequence of human-induced climate change through greenhouse gas emissions (Vecchi et al. 2006). Other evidence suggests equatorial ocean responses may differ from those in the atmosphere (Karnauskas et al. 2009). If changes do occur in the frequency of occurrence and magnitude of ENSOs, we can expect consequences for numerous ecological processes in diverse ecosystems.

ENSO has consequences for the Earth's climate far from the tropics because its effects can propagate through both the ocean and the atmosphere. From the eastern tropical Pacific, warm El Niño temperature anomalies move poleward along the eastern ocean margin in both the northern and southern hemispheres. ENSO-related changes of atmospheric circulation can extend to middle latitudes and even polar regions through long-distance atmospheric teleconnections. Combined ocean and atmospheric changes affect temperature, winds, sea level, and rainfall patterns—and therefore droughts and forest fires—in regions distant from the equator.

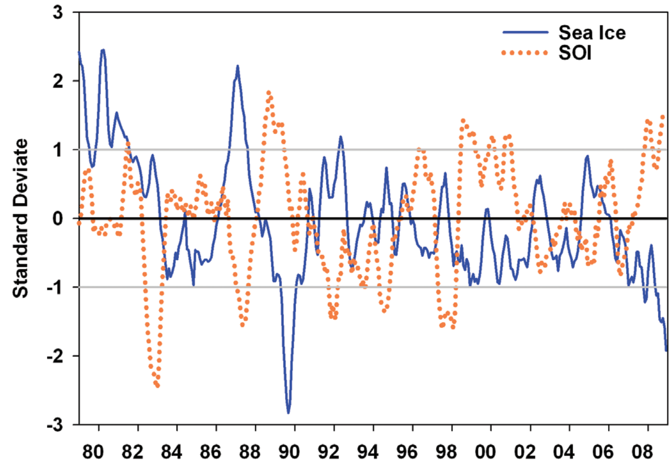

Figure 3-1. Normalized anomalies of a Sea Ice Index from the PAL LTER site (solid line) and the Southern Oscillation Index (SOI) (dashed line). (Adapted from Stammerjohn et al. 2008.)

Ecosystem Responses to ENSO

Adélie penguin foraging success in the Southern Ocean. Studies in the Palmer Station LTER site (PAL) on the Western Antarctic Peninsula have shown that interannual variations in sea ice extent are related to variations in ENSO, as reflected by the SOI (figure 3-1). A positive SOI during La Niña conditions is associated with decreased spatial coverage of sea ice, while a negative SOI during El Niño is associated with increased sea ice, principally through changes in the timing of sea ice advance and retreat (Stammerjohn et al. 2008). Such changes have important consequences for penguins and their primary prey, Antarctic krill.

The increased sea ice coverage during the El Niño phase favors Adélie penguins, but not the ice-avoiding Gentoo and Chinstrap penguins (Fraser and Hofmann 2003, Smith et al. 2003, Ducklow et al. 2007). Increased sea ice is associated with enhanced krill recruitment and therefore better foraging conditions for Adélies at their breeding colonies (Fraser and Hofmann 2003). In addition, Adélies are flightless and do not forage at night, so their ability to search the marine environment during polar winter is limited. Their foraging range and feeding success is constrained to particular regions ("hotspots") of the Western Antarctic Peninsula where krill patches recur and where prey availability is predictable over ecological time scales (decades to centuries) (Fraser and Trivelpiece 1996). If sea ice does not develop near these hotspots or its duration is too short, as typically occurs during the La Niña phase, then Adélie penguins cannot access key winter foraging areas, and their mortality increases (W. Fraser et al., unpublished data).

In addition to the relationship between ENSO and Adélie foraging success on an interannual scale, long-term changes in the frequency of occurrence of La Niña conditions have been associated with a precipitous decline in the Antarctic Adélies and an increase in the numbers of sub-Antarctic Gentoos and Chinstraps (figure 4-2) (Ducklow et al. 2007). This shift in dominant penguin species is resulting in state changes with important consequences for other parts of the ecosystem (McClintock et al. 2008).

Zooplankton trophic shifts off the Southern California coast. Food webs in the currents off the coast of California are strongly influenced by ENSO events via changes in both the ocean and the atmosphere. Kelp forest canopies are removed during strong winter ENSO storms, and the surviving plants become nutrient starved as nitrate-rich waters remain too deep in the water column to be accessible to the growing kelp (Dayton and Tegner 1984). Phytoplankton are also affected adversely, as vertical fluxes of nutrients into the euphotic zone appear to be reduced through a deepening of the region of elevated nitrate concentrations (Goericke et al. 2007), accompanied by a contraction of the area of coastal upwelling (Kahru and Mitchell 2000).

Such ENSO-related changes in nutrient supply and phytoplankton primary production are also reflected in reduced biomass of zooplankton (Chelton et al. 1982, Lavaniegos and Ohman 2007). Food web structure is also modified, as reflected in stable nitrogen isotopes of zooplankton from the California Current Ecosystem site (CCE). For three of four zooplankton species examined, the animals became isotopically heavier in the spring of major El Niño years relative to the spring of preceding and following years (figure 3-2). One of the two species of omnivorous copepods *(Calanus pacificus)* shows such an effect, while the other *(Eucalanus californicus)* does not because of interspecific differences in life history.

Both of the carnivorous chaetognath species show enrichment of the heavier nitrogen isotope of 1-2 per mil, which illustrates that the effects of ENSO are measureable at the level of primary carnivores. These isotopic shifts of zooplankton during El Niño conditions occur because of altered nitrogen sources for the phytoplankton at the base of the food web, with an apparent change in the nitrate supply relative to ammonium (Rau et al. 2003).

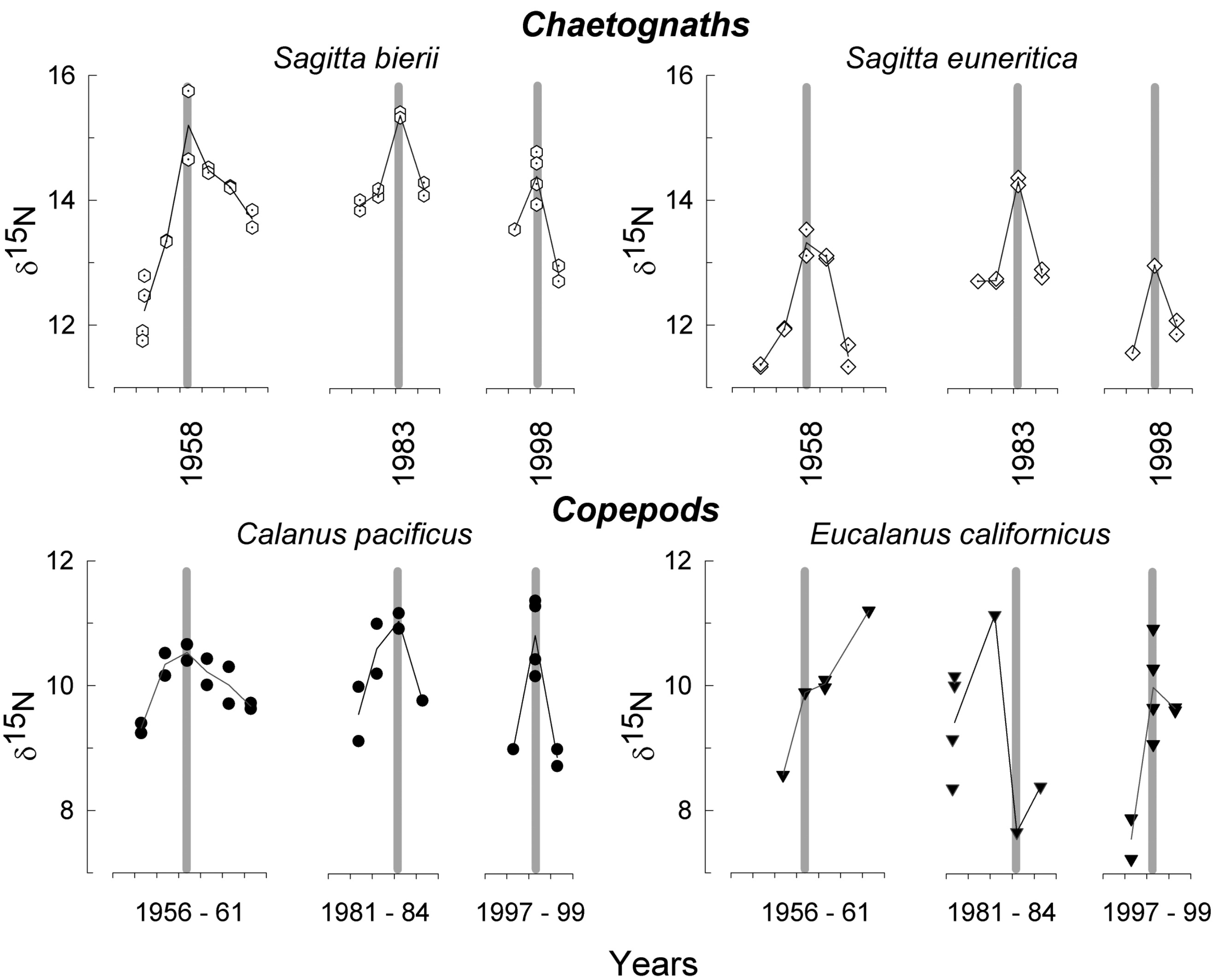

Figure 3-2. Springtime stable nitrogen (N) isotope content of four species of zooplankton from the CCE LTER region. Grey bars indicate major El Niño years (1958, 1983, 1998) (Rau et al. 2003). Reprinted with permission from Elsevier.

Hantavirus in deer mice from the southwestern desert. In a remarkable linkage between ENSO and human disease, Yates et al. (2002) documented the rodent-vectored hantavirus outbreak in the southwestern United States and its connection to El Niño. The primary vectors of the hantavirus are deer mice (*Peromyscus* spp.), whose populations have been studied at the Sevilleta LTER site (SEV) since 1989. During El Niños in 1992-1993 and 1997-1998, winter precipitation increased markedly, especially in the fall to spring period. Increased precipitation increased soil moisture content and primary production, and resulted in enhanced food supply for deer mice (Yates et al. 2002). An increase in population density of deer mice lagged the precipitation increase by one year, and was followed by an increase in density of virus-infected deer mice and resulting increase in incidence of the disease in humans after an additional 1-2 year lag (figure 3-3). Thus, ENSO-related changes in precipitation led to an expansion of numbers of infected mice and density-dependent increase of human infection.

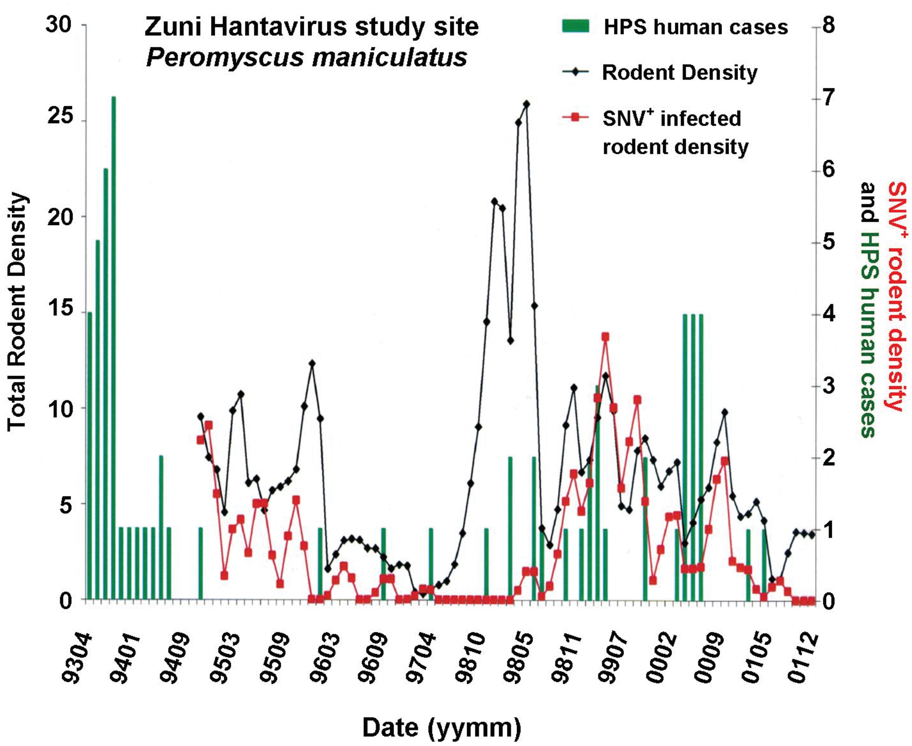

Figure 3-3. Densities of deer mice near Zuni, NM (black line), and densities of deer mice infected with Sin Nombre virus (SNV) at the same localities (red line). Human Hantavirus pulmonary syndrome (HPS) cases (green histograms) from the five counties surrounding Zuni and near the SEV LTER (Yates et al. 2002). Reprinted with permission from the American Institute of Biological Sciences.

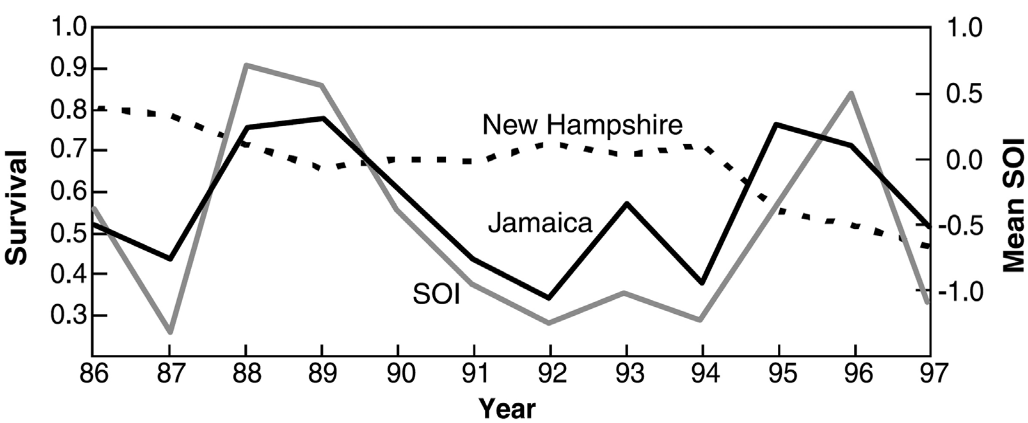

Figure 3-4. Black-throated blue warbler survival in winter in Jamaica (black solid line) is correlated with ENSO variations, as reflected in the Southern Oscillation Index (SOI, gray solid line) (Sillett et al. 2000). These songbirds breed in northeastern United States, including at the HBR in New Hampshire (dashed line). Reprinted with permission from AAAS.

Songbird survival in temperate and tropical forests. Many songbirds in the northeastern United States, including the Hubbard Brook Ecosystem Study LTER site (HBR), breed in temperate latitudes but overwinter in the tropics; thus an understanding of bird dynamics in the tropics is important to sites in the continental United States. Annual survival of the black-throated blue warbler in Jamaica is strongly associated with the Southern Oscillation Index (Sillett et al. 2000). Annual warbler survival estimated from mark-recapture analyses in Jamaica was low during El Niño conditions and high during La Niña (figure 3-4). The mechanism involved appears to be enhanced food availability in Jamaica during the wet winters of La Niña years (Sillett et al. 2000). Although annual survival of breeding warblers in New Hampshire was relatively constant through time (figure 3-4), ENSO affects blue warblers in the breeding season through increased body mass of fledglings during La Niña conditions, which can be associated with higher survival and fecundity of breeding birds (Sillett et al. 2000). The lack of a relationship between survival of birds in New Hampshire and changes in ENSO is probably due to many birds overwintering on islands without a strong climatic effect of ENSO (Sillett et al. 2000).

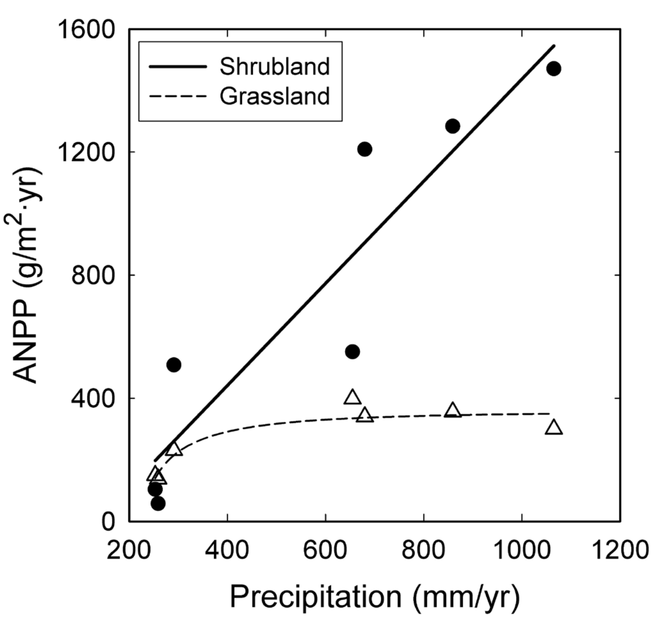

Figure 3-5. Relationship between aboveground annual net primary production (ANPP) and mean annual precipitation for shrublands is linear (solid line) across eight North American sites, including the Arctic (ARC), Jornada (JRN), Konza Prairie Biological Station (KNZ), Sevilleta (SEV), and Virginia Coast Reserve (VCR) sites. The relationship for grasslands (dashed line) peaks near 700 mm/year of precipitation, when nitrogen and light become limiting. (Redrawn from Knapp et al. 2008.)

Hypothesis 2: Gradual, Progressive Climate Change Can Elicit Marked Responses in Ecosystem Structure

Progressive climate change has led to gradual long-term changes in ecologically important aspects of the physical environment at many sites (chapter 11): Water temperatures have increased off the coast of California, ice duration has shortened in lakes in Wisconsin, sea level has risen along both coasts of North America, and streamflow has changed in places as diverse as Michigan, Massachusetts, and Florida. These gradual environmental changes have resulted in directional ecological responses, three of which we will illustrate here.

Shifting shrubland/grassland dominance with altered precipitation. Many ecological systems are highly responsive to climatic variability. Annual above-ground productivity of grassland ecosystems, for example, is related to annual precipitation. In a comparative study across eight grassland sites in North America, including five LTER sites, mean annual precipitation explains much of the variability in above-ground productivity (figure 3-5; Knapp et al. 2008). Across these grassland sites spanning a precipitation gradient from 250 to 1,100 mm/y, productivity increases until a threshold is reached as precipitation approaches 700 mm/y. At larger amounts of precipitation, production is limited by additional resources such as nitrogen and light. In contrast, shrublands show no evidence of saturated productivity over the same range of precipitation.

These results suggest that gradual changes in precipitation at the wet end of the gradient (for example, at KNZ) may have marked consequences for vegetation dominance such that an increase in rainfall would favor woody plant dominance over grasses. Shifts in dominance at the dry end (for example, at JRN) are more likely related to changes in seasonality of precipitation where an increase in winter precipitation would favor shrubs and an increase in summer precipitation would favor grasses (figure 4-1). These shifts in dominance have important consequences for ecosystem services, such as forage production, biodiversity, and air and water quality, that are provided by grasslands or shrublands to human populations.

Decline in pelagic tunicates with ocean warming. Long-term records of ocean temperatures and zooplankton biomass off the coast of California (CCE) have documented a long-term decline in biomass of pelagic tunicates called salps, along with a long-term increase in the temperature of the water column and its density stratification (the vertical density difference between surface and subsurface waters) (figure 3-6). While correlated with changes in temperature, the decline in salp biomass appears to be related to changes in ocean circulation rather than to ocean warming itself (Lavaniegos and Ohman 2007). This decline in biomass has implications for the vertical movement of carbon from the surface to deep ocean waters because salps have very high grazing rates and produce fecal pellets that sediment rapidly out of ocean surface waters. These changes in surface dwelling salps are thought to alter the “biological pump” of carbon into the deep sea: Lower biomass of salps may result in reduced flux of organic carbon to benthic organisms living on the deep sea floor (Smith et al. 2008).

Decline in grasshopper diversity with increased precipitation. An increase in annual precipitation in central Minnesota at the Cedar Creek LTER site (CDR) has been associated with a decline in grasshopper species richness (figure 3-7) (M. Ritchie et al., personal communication). These declines in richness appear to be related to a series of cooler, cloudier, wetter-than-normal summers in the past 15 years. The primary loss of species has been in the band-winged (Oedipodinae) and slant-faced (Gomphocerinae) subfamilies of grasshoppers, which apparently need warmer weather to develop and lay eggs during the relatively short

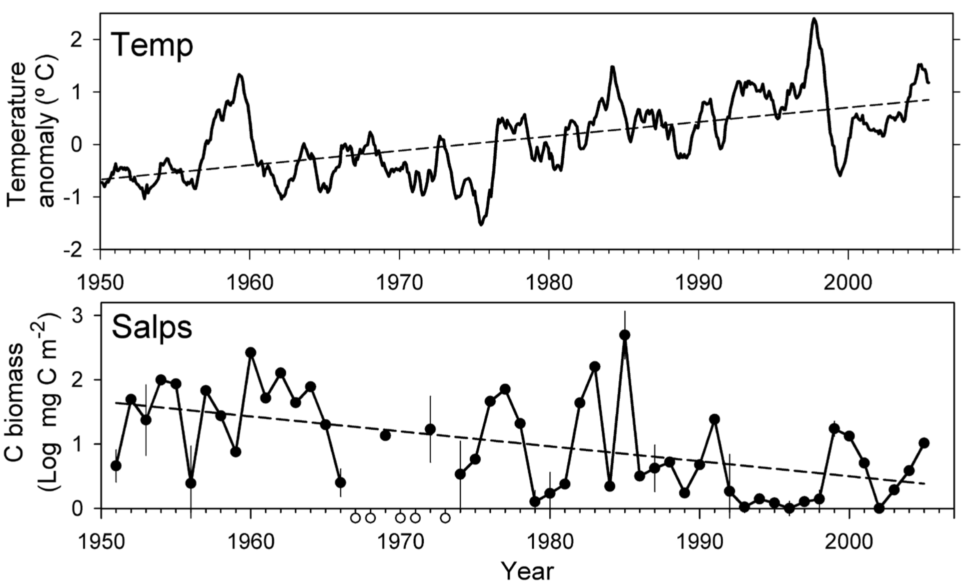

Figure 3-6. Top: Ocean temperature measured at the Scripps pier, California Current Ecosystem (CCE), over the past 5 1/2 decades (anomalies from the seasonal mean). (Data from http://cce.lternet.edu/data/.) Bottom: Decline in carbon (C) biomass of a group of pelagic tunicates known as salps, a zooplankton taxon whose grazing activity and fecal pellet production accelerate vertical transport of organic carbon into the deep sea. (Modified from Lavaniegos and Ohman 2007; data from http://cce.lternet.edu/data/.) Significant regression lines are shown in both panels (dashed lines).

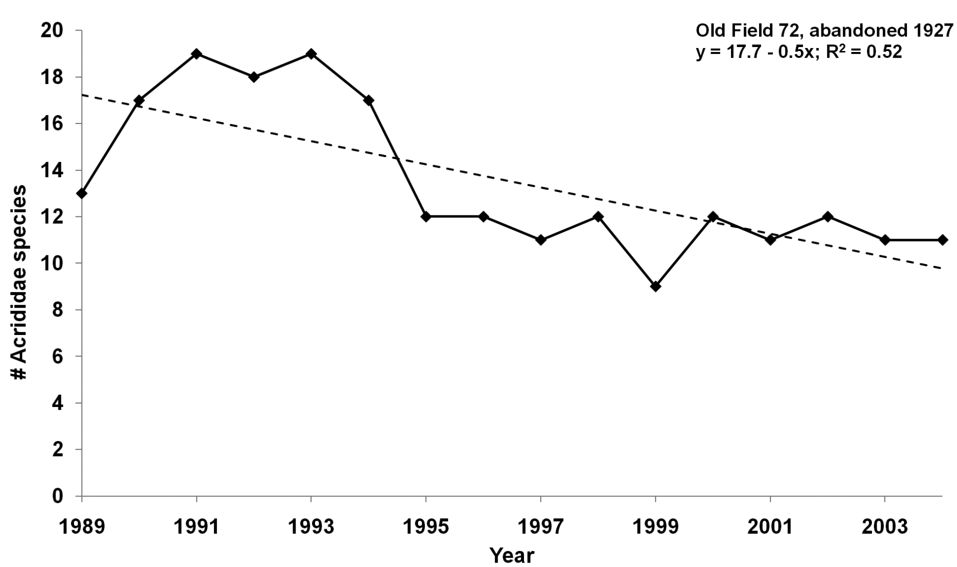

Figure 3-7. Decline of species richness of grasshoppers in the family Acrididae from old field 72 at the Cedar Creek site (CDR) over 15 years (M. Ritchie et al., personal communication). This decline parallels a longer-term increase in precipitation in the region. (Original data from http://www.cedarcreek.umn.edu/. Synthesized data from http://www.ecotrends.info.)

Minnesota summers. Accumulation of litter is also associated with cooler, wetter summers. Shading of the ground by litter may also slow egg development of these groups, leading to declines in their populations (Ritchie 2000).

Conclusions

Our changing climate leaves a footprint on ecological systems that at times may be subtle, but is long lasting. Resolving the climate footprint—a part of Magnuson's (1990) "invisible present"— requires sustained and standardized observational, experimental, and modeling programs, such as those developed and maintained at LTER and other long-term sites (Greenland et al. 2003). Although climatic drivers are often measured using standardized approaches (Greenland et al. 2003, WMO 2008), ecological responses to climate are more variable in both the types of responses measured (such as plant production and animal abundance) and in the attributes of the variable, such as sampling frequency (daily, weekly, peak growth), spatial scale of the sample unit (square meter, hectare, sweep nets), and taxonomic resolution (species, genera, family, functional group).

Recommendations for future research that would allow cross-site comparisons of ecological responses to climate and other global change drivers are provided in chapter 17. Expanded comparative studies across diverse biomes offer great promise for discerning characteristics of the climate footprint. These studies can also be used to tease out cause and effect relationships that are fundamental to developing the capacity for forecasting future trajectories of coupled human-natural ecosystems under different climate change scenarios.

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Chapter 4

Cross-Site Comparisons of State-Change Dynamics

D.P.C. Peters, W.R. Fraser, T.K. Kratz, M.D. Ohman, A. Rassweiler, S.J. Holbrook, and R.J. Schmitt

Changes in the state of a system—for example from grassland to shrubland or from dominance by one fish species to another species—with associated changes in other parts of the system, are often irreversible. These state changes are related to changing climatic conditions (chapter 11) interacting with human activities (MEA 2005b). State changes can lead to positive effects on ecosystems; but more frequently, such as with the invasion by an exotic species, the changes are negative and result in altered levels of biodiversity, shifts in rates of nutrient cycling, changes in air and water quality, and increased losses of soil and nutrients to wind and water erosion (Scheffer et al. 2001, Scheffer and Carpenter 2003).

Examination of the dynamics of state changes across a variety of ecological systems can identify common interactions among patterns and processes that can provide new insight into the drivers of these dynamics (Bestelmeyer et al. 2011). It is only through the use of long-term data that we can identify persistent changes in states, the drivers influencing these shifts, and potential reversals or modifications of shifts through time.

Here we illustrate common features of state changes for six systems with a diverse set of organisms (plankton, invertebrates, fish, plants, or penguins).

Vegetation state changes in deserts. In the American Southwest and throughout arid systems globally, large areas of land have converted from perennial grassland to shrubland over the past several centuries (Reynolds and Stafford Smith 2002). This state change is self-reinforcing as positive feedbacks between shrubs and soil properties allow continued shrub survival and promote grass mortality (Schlesinger et al. 1990, Rietkerk et al. 2004). The result is a discontinuous cover of shrubs and unvegetated areas that increases movement of soil and nutrients from bare areas to beneath shrub canopies. In arid systems where average annual precipitation is typically less than 300 mm, one consequence of this shift from grassland to shrubland is a reduction in above-ground net primary production (figure 3-5).

Although this process of desertification has been well studied (MEA 2005a), little is known about the conditions which affect rate and pattern of shrub dominance or variation in grass survival at patch to landscape scales (Peters et al. 2006). Researchers at the Jornada ARS/LTER (JRN) and Sevilleta LTER (SEV) sites have documented this shift using long-term observations (figure 4-1) and are using experimental manipulations to test the importance of biotic and abiotic processes to threshold behavior through time and across space (Peters et al. 2004, 2009).

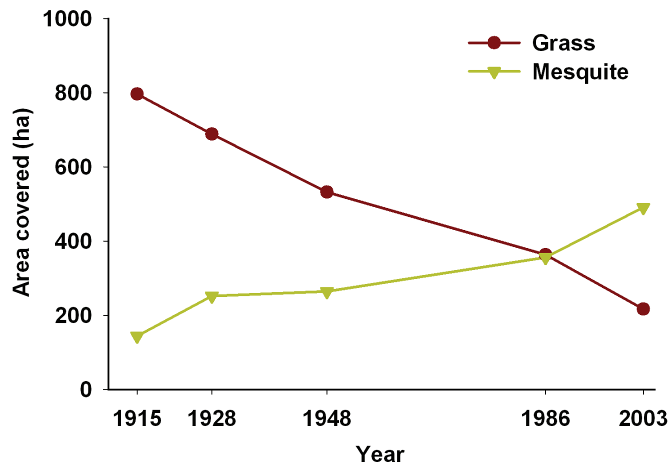

Figure 4-1. State change from grassland (brown) to mesquite shrubland (green) in the Chihuahuan Desert based on changes in area of each ecosystem type through time (Peters et al. 2004). Reprinted with permission from the National Academy of Sciences, USA.

Penguin dynamics in Antarctica. Along the rapidly warming western Antarctic Peninsula (Vaughan et al. 2003), southward climate migration is driving replacement of Adélie penguins by Gentoo and Chinstrap penguins (Ducklow et al. 2007, McClintock et al. 2008). Adélie penguins are a true polar species, with a life history that is critically dependent on the availability of sea ice, especially during winter (Fraser et al. 1992, Ainley 2002). In contrast, the other two species originate in sub-Antarctic latitudes and are ice-intolerant (Fraser et al. 1992, Williams 1995). The population trends shown in figure 4-2 are unprecedented, with the paleo-record indicating that neither Gentoo nor Chinstrap penguins have occupied the region over the past 700 years (Emslie et al. 1998). The changes in penguin abundance and species

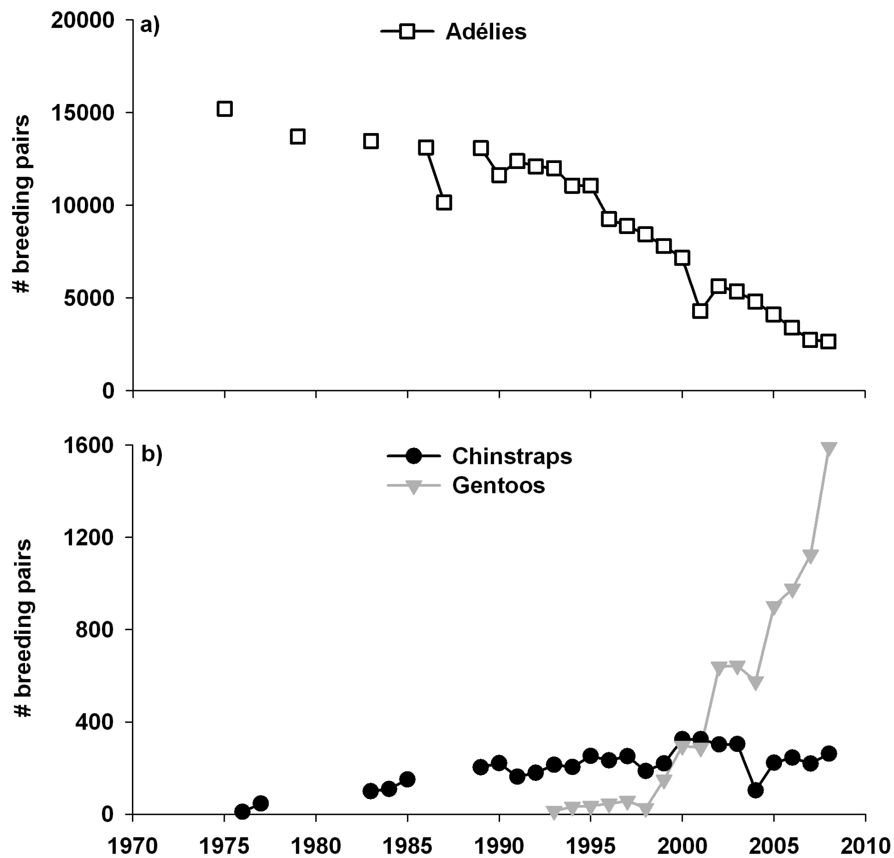

Figure 4-2. State change based on number of breeding pairs of birds from dominance by (a) Adélie penguins, a polar species, to (b) dominance by the ice-intolerant Gentoo and Chinstrap penguins in Antarctica. (Updated from McClintock et al. 2008.)

composition near Palmer Station LTER (PAL) reflect a reduction in the extent and duration of sea ice cover in the area (Ducklow et al. 2007), which is related to the positive Southern Oscillation Index during warm El Niño conditions (figure 3-1).

Fish dynamics in Wisconsin lakes. Similar state changes have been observed in lakes in Wisconsin (figure 4-3). The non-native rainbow smelt became established in Sparkling Lake in the mid 1980s and caused major changes in the lake's fish community (Hrabik et al. 1998, Wilson and Hrabik 2006). Cisco were extirpated by smelt predation on juveniles. Yellow perch also have been greatly reduced because young-of-year smelt out-compete young-of-year yellow perch for prey. Recent declines in rainbow smelt catch per unit effort may be attributed to a harvesting program intended to reduce abundance of this harmful non-native species. It is unclear whether these changes are irreversible. Scientists from the North Temperate Lakes LTER (NTL) are conducting a decade-long experiment that combines manual harvesting of smelt with enhanced stocking and regulatory protection of its predators to reduce smelt to low numbers or possibly remove them from the lake. It is unclear whether the abundance of cisco (if reintroduced) or yellow perch will increase when smelt abundance is experimentally reduced.

Plankton dynamics in the Pacific Ocean. Along the coast of southern California, variations in plankton populations are closely linked to long-term changes in physical conditions in the ocean environment. A

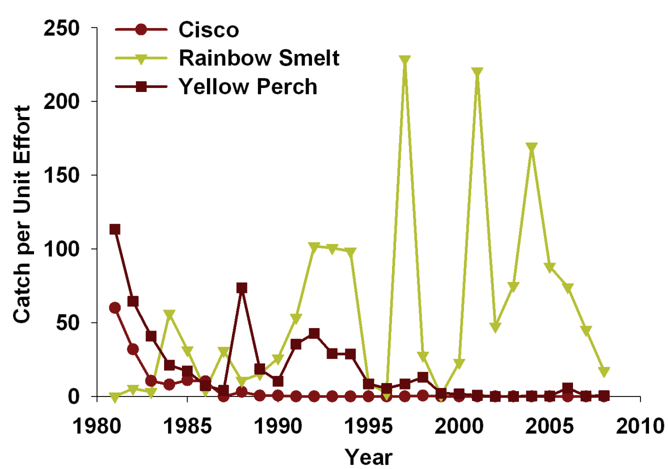

Figure 4-3. State change in lakes in Wisconsin based on fish catch data from dominance by native cisco and yellow perch to dominance by the introduced rainbow smelt. (Updated from Hrabik et al. 1998, Wilson and Hrabik 2006.)

relatively abrupt change occurred in the mid 1970s in sea surface temperature (figure 3-6) (reflected by the Pacific Decadal Oscillation (PDO) index in figure 4-4), with accompanying changes in several members of the plankton assemblage. For example, a subtropical species of krill *(Nyctiphanes simplex)* increased in abundance in the mid 1970s (figure 4-4). Other types of suspension-feeding zooplankton known as salps, one group of which typically enters the study area from higher latitudes, decreased abruptly in biomass at this time (Ohman and Venrick 2003). Following the major El Niño of 1997-98, there was a decrease in sea surface temperatures in the northeastern Pacific Ocean with accompanying reversals of the changes in some plankton populations.

The nodal points of these ecosystem transitions are associated with changes in ocean circulation, but the persistence of the altered communities for two to three decades at a time appears to be related to biotic responses. Whether these ecosystem changes represent cyclical variations is under investigation by the California Current Ecosystem LTER (CCE) site.

Subtidal dynamics off the Pacific Coast. Rocky reefs are known to exhibit sudden changes in state in which one type of benthic community is replaced by another. Scientists at the Santa Barbara Coastal LTER (SBC) have documented a particularly dramatic example of this shift on shallow subtidal reefs at Santa Cruz Island: The density of a small filter-feeding sea

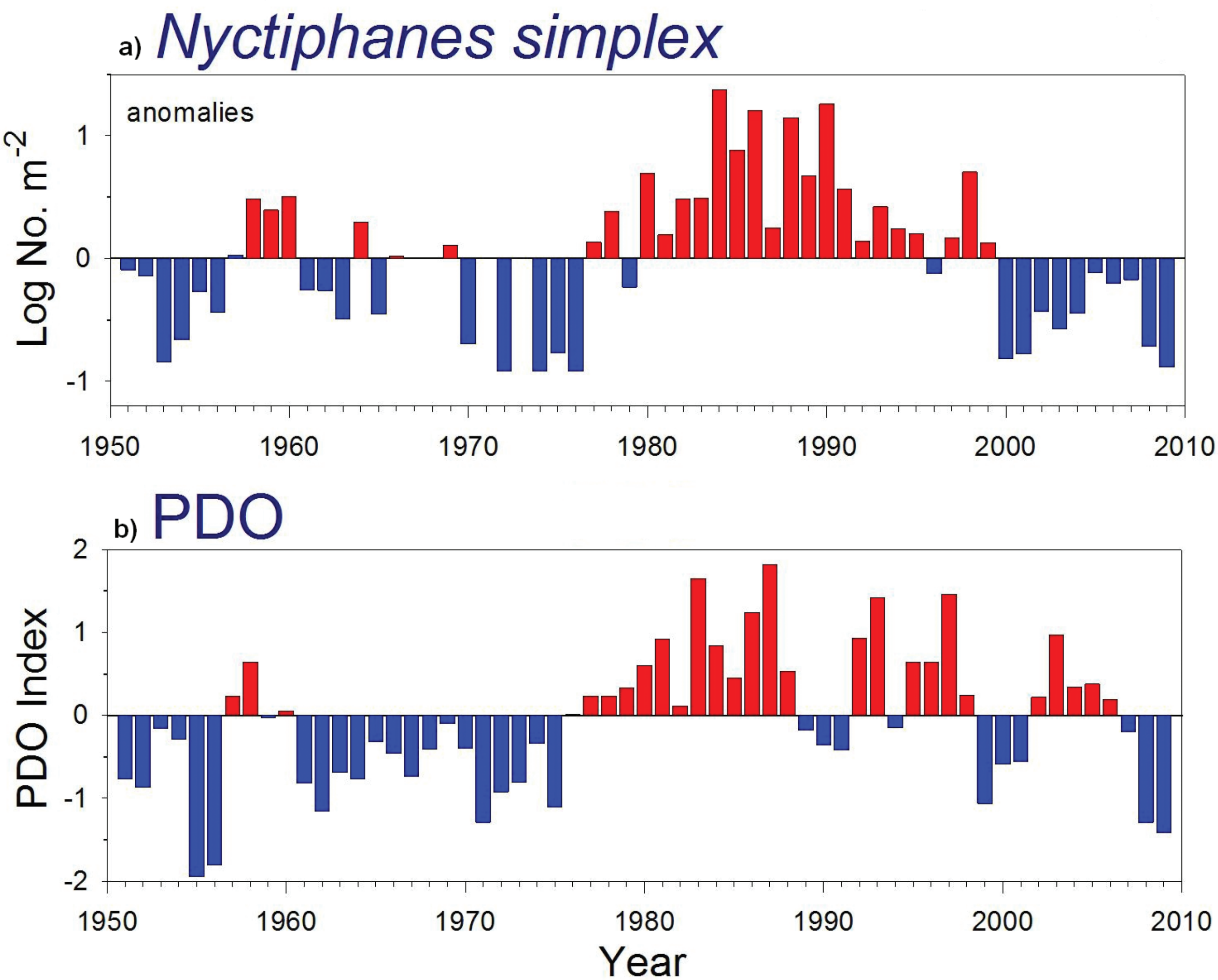

Figure 4-4. Long-term variability in the northeastern Pacific Ocean off the coast of southern California: (a) anomalies of springtime abundance of the euphausiid *Nyctiphanes simplex* and (b) annual averages of the Pacific Decadal Oscillation (PDO) index. (M. Ohman, updated from Brinton and Townsend 2003.)

cucumber, *Pachythyone rubra,* increased from near zero to thousands per square meter (figure 4-5). This change occurred within 2 years and resulted in *P. rubra* covering more than 90 percent of the bottom at many sites (Rassweiler 2008). Manipulative experiments show that *P. rubra* competes for space with understory macroalgae, which had dominated these sites prior to the increase in sea cucumber density. For more than a decade, macroalgae were unable to recover at these sites, in part because sea cucumbers consume algal spores in the water column.

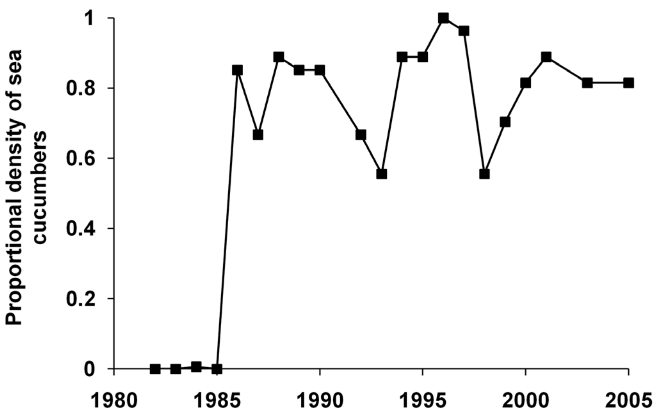

Figure 4-5. State changes in subtidal reefs off the coast of southern California. Sea cucumber biomass increasing over time. (Redrawn from Rassweiler 2008.)

Once the filter feeders reach a high enough abundance, they can reduce settlement rates of macroalgal spores to levels that are low enough to prevent reestablishment of macroalgae. Shifts from an algal-dominated state to one dominated by invertebrate filter feeders represents a major change in the trophic structure of the benthic food web, as energy is derived from captured plankton instead of from primary production by macroalgae. The decline in macroalgae has reduced the abundance of a wide variety of organisms that use the algae for food and shelter, including small crustaceans, which are a key food resource for many reef fishes.

Shifts in coastal fish assemblages in the Pacific Ocean. Similar to the dynamics of plankton along the coast of southern California, communities of rocky reef organisms in the same region underwent dramatic changes in response to the abrupt shift from the cool phase to the warm phase of the PDO in the mid 1970s. This climate shift brought warmer, nutrient-poor surface waters to nearshore regions, as well as increases in the intensity and frequency of El Niño Southern Oscillation episodes. Composition of reef fish assemblages changed in response to this abrupt shift in physical conditions of the nearshore ocean environment. For example, at coastal sites near Los Angeles, CA, dominance of the assemblage shifted from cold-affinity, northern species to warm-affinity, southern species following the abrupt warming of surface waters (figure 4-6). In addition, by the mid 1990s abundance of nearly all fish species had declined by an average of 69 percent (Holbrook et al. 1997, Brooks et al. 2002).

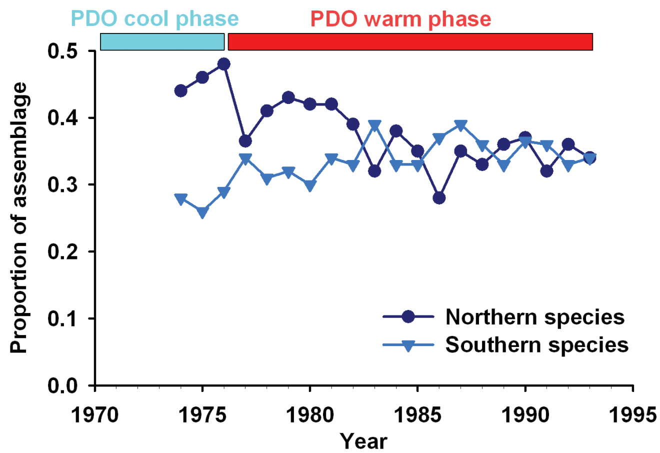

Figure 4-6. Temporal patterns in composition of the fish assemblage on reefs in the Southern California Bight. Shown are the proportions of the annual total species present that were northern species (cold water affinity: circles) and southern species (warm water: triangles). (Redrawn from Holbrook et al. 1997.)

The lower productivity of the coastal marine ecosystem was also accompanied by large effects on population abundance and reef trophic structure. At the SBC study sites on Santa Cruz Island, CA, declines of a similar magnitude were observed for several linked trophic levels in a model food web (several species of surfperches [Pisces: Embiotocidae], the standing stock of their crustacean prey, and the biomass of understory macroalgae on which the prey reside) (Holbrook and Schmitt 1996, Holbrook et al. 1997). The SBC is exploring whether observed changes in composition of the fish assemblage and in trophic structure of the community represent reversible phases driven by cyclical climatic variation.

Conclusions

These examples clearly show the effect of global environmental change (warming, invasive species, altered trophic structure) on the abundance and distribution of dominant and subordinate species in aquatic, marine, and terrestrial systems. In many cases, environmental drivers have shifted to the point that current conditions are leading to threshold changes in species abundance within communities and are altering species range distributions both regionally and globally. However, this era of rapid environmental change is only beginning to be manifested in species responses. Thus, researchers will continue to need long-term data to quantify and predict the nonlinear system responses expected in the future.

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Chapter 5

Patterns of Net Primary Production Across Sites

A.K. Knapp, M.D. Smith, D.P.C. Peters, and S.L. Collins

Net primary production (NPP) is a fundamentally important and commonly measured ecosystem process that provides an integrative estimate of energy capture and flow into systems and consequently of the energy available for use by other trophic levels. A wide range of productivity levels occurs globally (figure 5-1) with high temporal dynamics among sites (chapter 14). In this brief overview, we discuss approaches to estimating NPP, highlight site-specific trends in productivity, and provide examples of past synthetic analyses across space and time. We focus on aboveground components of NPP for reasons explained below.

Methods of Measuring and Estimating NPP

In terrestrial ecosystems, NPP includes both aboveground (ANPP) and belowground (BNPP) components. Data and analyses are much more common for ANPP because measuring belowground components is technically difficult (Fahey and Knapp 2007). In general, ANPP in terrestrial systems can be directly measured via destructive harvest or estimated with nondestructive (for example, allometric) techniques. Data in this book include both approaches and, because the units of NPP are usually grams of dry mass (or carbon) per unit area per unit time (usually per year), comparisons across ecosystems are facilitated. In addition to the challenges associated with measuring BNPP, estimating ANPP in forests and NPP in aquatic systems often require techniques that use much different spatial and temporal scales than what is employed in ecosystems dominated by herbaceous plants. For a recent review of the most commonly used and accepted methods of estimating both ANPP and BNPP, see Fahey and Knapp (2007).

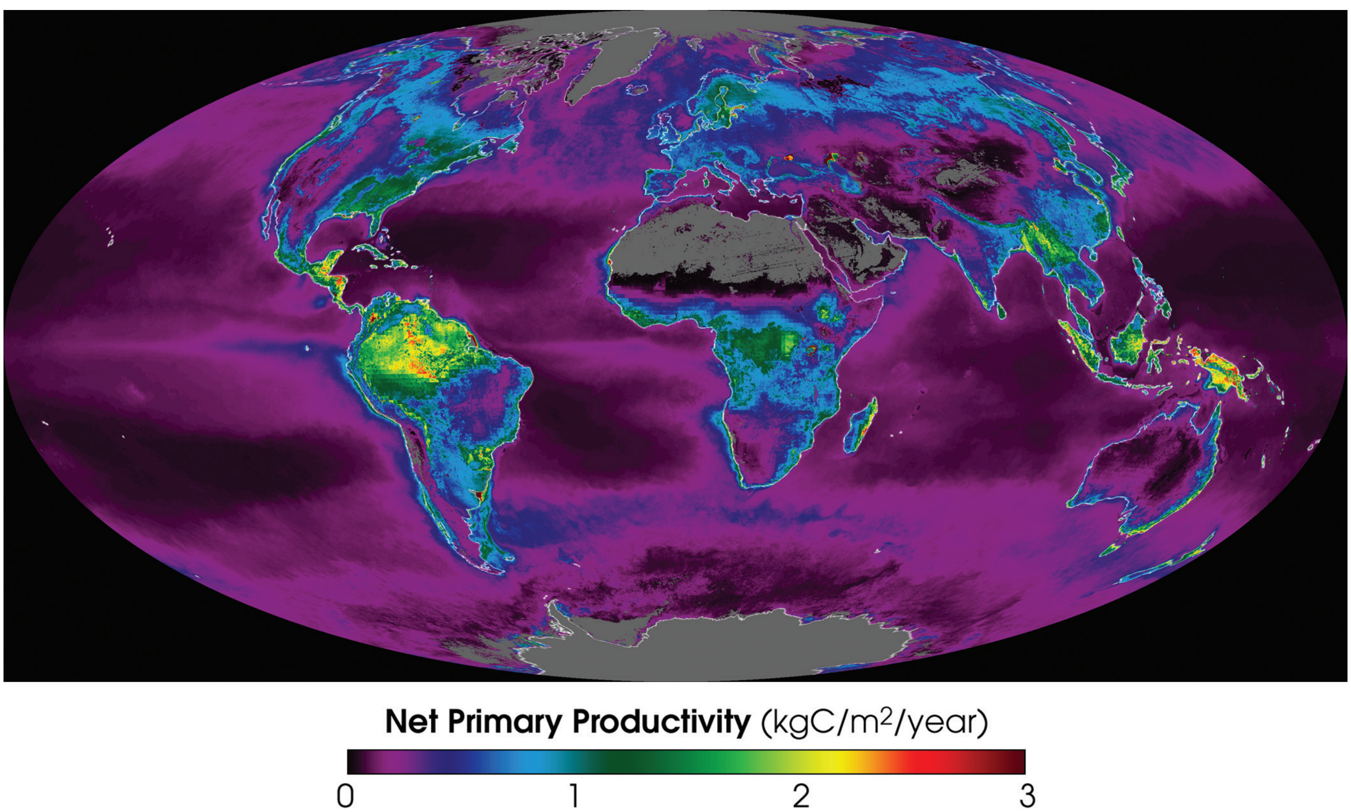

Figure 5-1. Global patterns in annual average net primary production on land and in the ocean in 2002. The yellow and red areas show the highest rates, 2 to 3 kilograms of carbon per square meter per year. The green, blue, and purple shades show progressively lower productivity. (Map from NASA Goddard Space Flight Center, http://science.hq.nasa.gov/oceans/system/climate.html.)

Temporal and Spatial Trends in ANPP

For many sites, both increasing and decreasing trends in ANPP are evident over time (figures 14-1 to 14-4) and are often a consequence of disturbance regimes or changes in plant community composition. In many sites, spatial variation among locations within a site can overwhelm temporal variation (figure 5-2). However, strong interannual variation in ANPP over time is not always the rule; instead, trends in ANPP (either positive or negative) can be quite consistent from year to year (figure 5-3). Additional trends in ANPP, surrogates for NPP, and aquatic productivity are included in chapter 14.

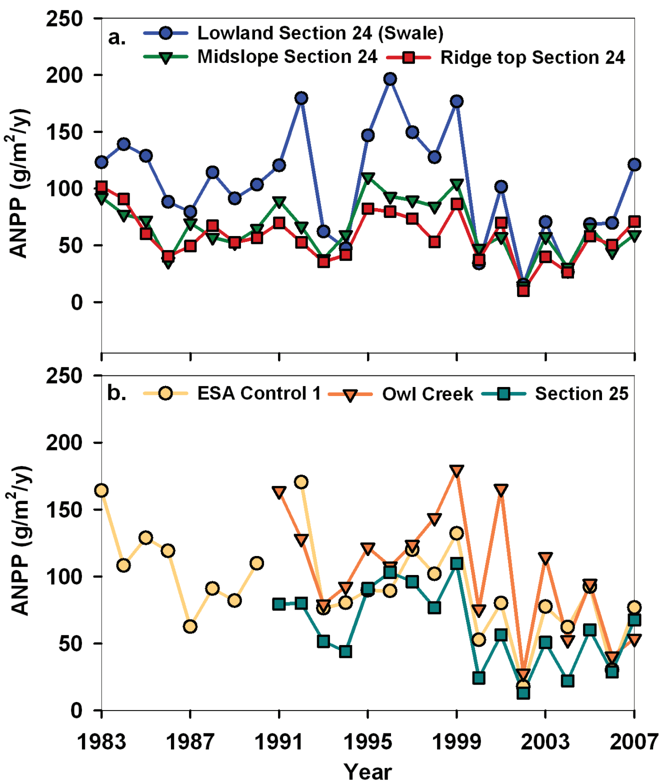

Figure 5-2. Patterns of aboveground net primary production (ANPP) for the Shortgrass Steppe (SGS) from 1983 to 2007 for 6 locations based on topographic position and soil texture from high sand (Owl Creek) to low sand (Pasture 25). (Original data from http://sgs.cnr.colostate.edu/; synthesized data from http://www.ecotrends.info.)

Cross-Site Synthetic Analyses

One of the advantages of the EcoTrends database is that it facilitates more comprehensive synthetic analyses of NPP data across space and time. The determinants of differences among sites in NPP quantity and dynamics have long been of interest to ecologists (Rosenweig 1968, Webb et al. 1978). More recent analyses have

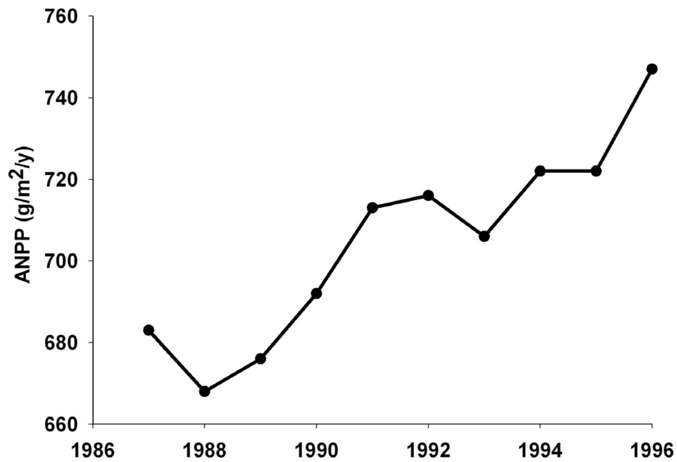

Figure 5-3. Pattern of aboveground net primary production (ANPP) for a mixed deciduous forest site at the Hubbard Brook Ecosystem Study (HBR) site from 1987 to 1996. (Original data from http://intranet.lternet.edu/cgi-bin/anpp.pl; synthesized data from http://www.ecotrends.info.)

begun to take advantage of long-term data across sites (Knapp and Smith 2001, Huxman et al. 2004). These analyses have provided key insights into the relative roles of biotic versus abiotic drivers of dynamics as well as elucidating where and when biogeochemical versus climatic factors underlie patterns of NPP across biomes. For example, the strong role that precipitation plays in determining ANPP across grassland sites is clearly evident in a multisite analysis (figure 5-4) (Muldavin et al. 2008). Across a broader range of terrestrial ecosystems, differential sensitivity to mean annual precipitation appears with other limitations (temperature or biogeochemistry) becoming more important in more mesic and productive ecosystems (figure 5-5) (Huxman et al. 2004).

Biotic constraints on ANPP, such as vegetation composition or meristem limitation, can also explain patterns across sites. Lauenroth and Sala (1992) pointed out a space versus time discrepancy when comparing the temporal relationship between ANPP and precipitation at an individual site compared with the same relationship based on ANPP and precipitation across sites (spatial vs. temporal trends, figure 5-6). The shallower slope of the relationship at any one site reflects site-specific vegetation constraints on the capability of the ecosystem to respond to changes in precipitation. A similar pattern can be seen for a broader range of sites (figure 5-5). Shifts in plant species composition within a site, due to woody plant encroachment or invasion of shrubs into grasslands, can dramatically change ANPP at that site (with no change in environmental conditions) as well as alter patterns of ANPP across sites (Knapp et al. 2008).

Another manifestation of how vegetation structure can influence ANPP responses to changes in precipitation was demonstrated by Knapp and Smith (2001) in a multisite synthetic analysis of long-term ANPP data. The interaction between meristem density (low in xeric ecosystems and high in mesic ecosystems) and interannual variability in precipitation (high in xeric ecosystems and low in mesic ecosystems) resulted in a pattern where the greatest interannual variability in ANPP (CV in figure 5-7) was in grasslands.

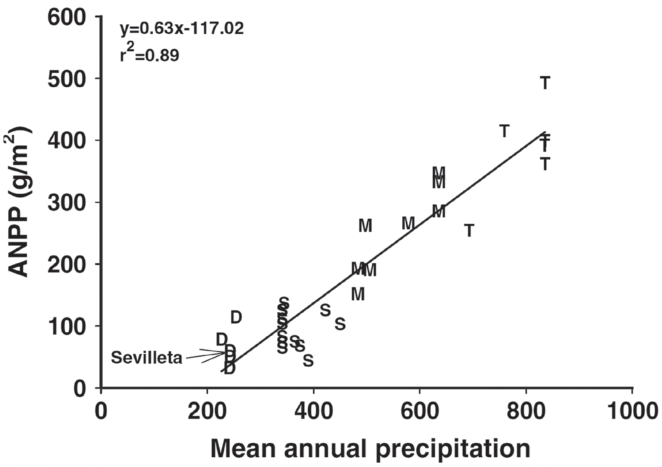

Figure 5-4. Regional comparison of aboveground net primary production (ANPP) and long-term mean annual precipitation for four grassland types: D = desert grassland, S = shortgrass steppe, M = mixedgrass prairie, T = tallgrass prairie (Muldavin et al. 2008). The Sevilleta site is identified. Reprinted with permission from Springer Science+Business Media.

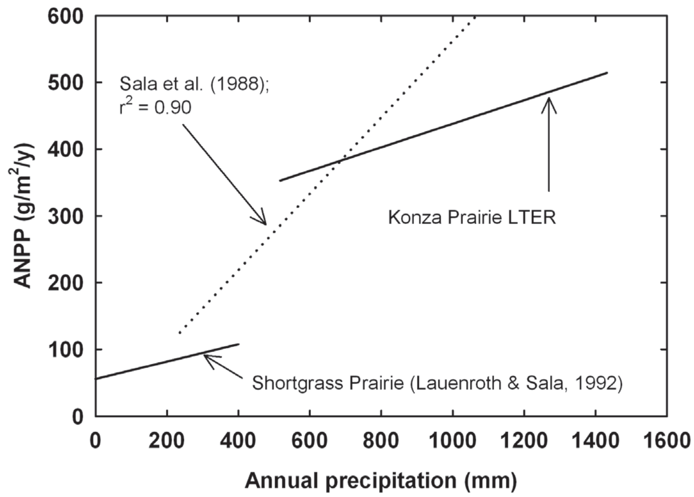

Figure 5-6. Aboveground net primary production (ANPP) has a different relationship with mean annual precipitation for sites located across a rainfall gradient (dashed line) compared with the relationship between ANPP and precipitation in each year for two sites (solid lines): the Shortgrass Steppe (SGS) site (Sala et al. 1988, Lauenroth and Sala 1992) and the Konza Prairie Biological Station (KNZ) site (Knapp et al. 1998). Reprinted with permission from Oxford University Press, Inc.

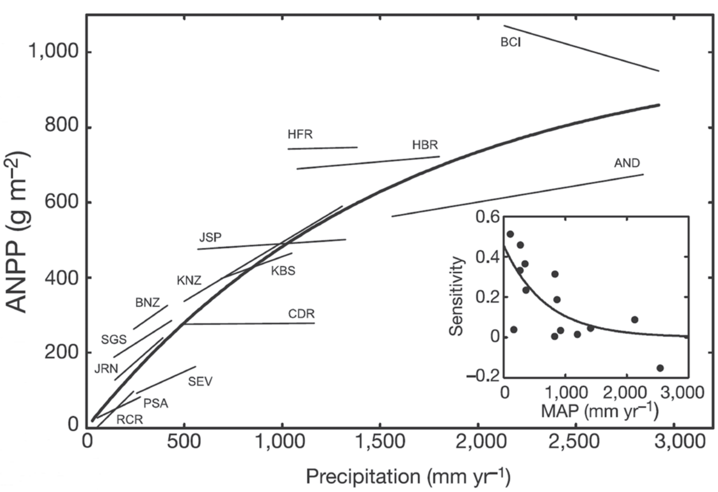

Figure 5-5. Between-year variation in aboveground net primary production (ANPP) across a precipitation gradient for 14 sites. Site-specific relationships developed using linear regression (Huxman et al. 2004). The overall relationship (bold line) shown for all sites: ANPP = 1011.7 x (1 – exp[-0.0006 x PPT]); $r^2 = 0.77$; $P < 0.001$. Inset shows site-level slopes of ANPP versus annual precipitation as a function of mean annual precipitation (MAP). Reprinted with permission from Macmillan Publishers Ltd.

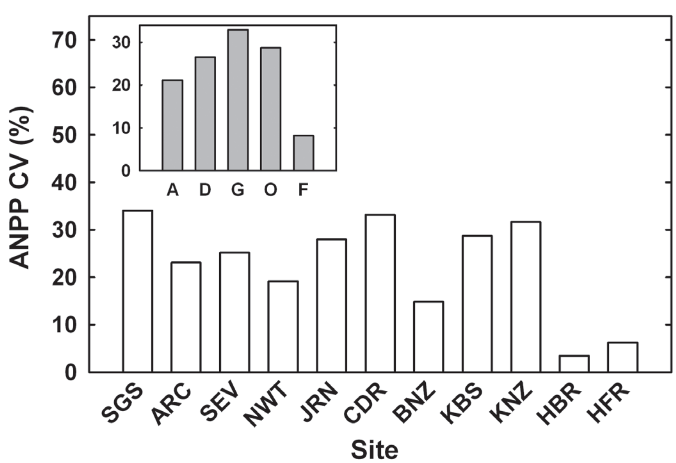

Figure 5-7. Comparison of the temporal coefficient of variation (CV) in aboveground net primary production (ANPP) for 11 sites. Inset shows CV data combined by biome type: A = arctic and alpine sites, D = desert sites, G = grassland sites, O = old fields, F = forest sites (Knapp and Smith 2001). Reprinted with permission from AAAS.

Future Analyses

In a changing world where both global and local changes in climate and nutrient deposition are affecting resources that influence NPP (chapters 11, 12), a re-assessment of past studies and assumptions is warranted, and many questions remain to be addressed (Smith et al. 2009):

- How do the dynamics and amplitude of change in NPP vary across a broad range of ecosystems?
- What are the key drivers of NPP change and dynamics? Is there convergence among ecosystems to a few key drivers?
- How can we more directly compare patterns and controls of NPP in terrestrial and aquatic systems?
- How do ecosystems vary in their sensitivity to their drivers, and is there predictive value in this sensitivity?

Conclusions

Understanding patterns and controls of NPP have been a long-standing challenge for ecological research. This challenge remains a core research area for many sites. As the number of comparable long-term datasets across ecosystems grows, answers to these and other key questions about NPP will be possible in the future.

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Chapter 6

Cross-Site Comparisons of Precipitation and Surface Water Chemistry

C.T. Driscoll, P.M. Groffman, J.M. Blair, A.E. Lugo, C.M. Laney, and D.P.C. Peters

The biogeochemistry of ecosystems involves the transport or cycling of elements (such as sulfur, carbon, nitrogen, calcium) and compounds (such as water) through the biotic (plants, animals, microbes) and abiotic (soils, atmosphere) components. All elements and compounds cycle through the Earth's system, although at different rates and by different pathways that depend on their chemical characteristics and the extent to which they are utilized by organisms.

Cycling involves both inputs to and losses from different pools or standing stocks and the transformations of major and trace elements (figure 6-1). Inputs include weathering from rocks and minerals and deposition from the atmosphere (wet in precipitation and dry as gases or particles). Losses can occur either through gaseous emissions to the atmosphere or drainage below the soil surface or from land to ocean. Pools include the accumulation of elements in the soil, sediments, and vegetation of an ecosystem. Important internal transformations of elements include litter inputs, mineralization of organic matter, uptake of nutrients by vegetation, and the retention or release of material in soil or sediments.

Ecologists measure these pools and fluxes to learn critical information about the functioning of ecosystems. Because the time for a molecule to be completely transported through an ecosystem may be decades to millennia, long-term data provide one of the few means to estimate how ecosystems use and respond to changes in inputs of nutrients and toxic substances. Long-term data can characterize the average size and variability in ecosystem pools and the rates of flow among pools. Monitoring biogeochemical indicators provides useful insights on the response of ecosystems to chronic change, such as in climate or land use, the introduction of invasive species, or changes in air pollution, and short-term disturbances such as fire or climatic events including hurricanes, ice storms, and droughts. Many important ecosystem services, such as the supply of clean air and water, ecosystem productivity, and carbon sequestration, are closely coupled to the biogeochemistry of ecosystems.

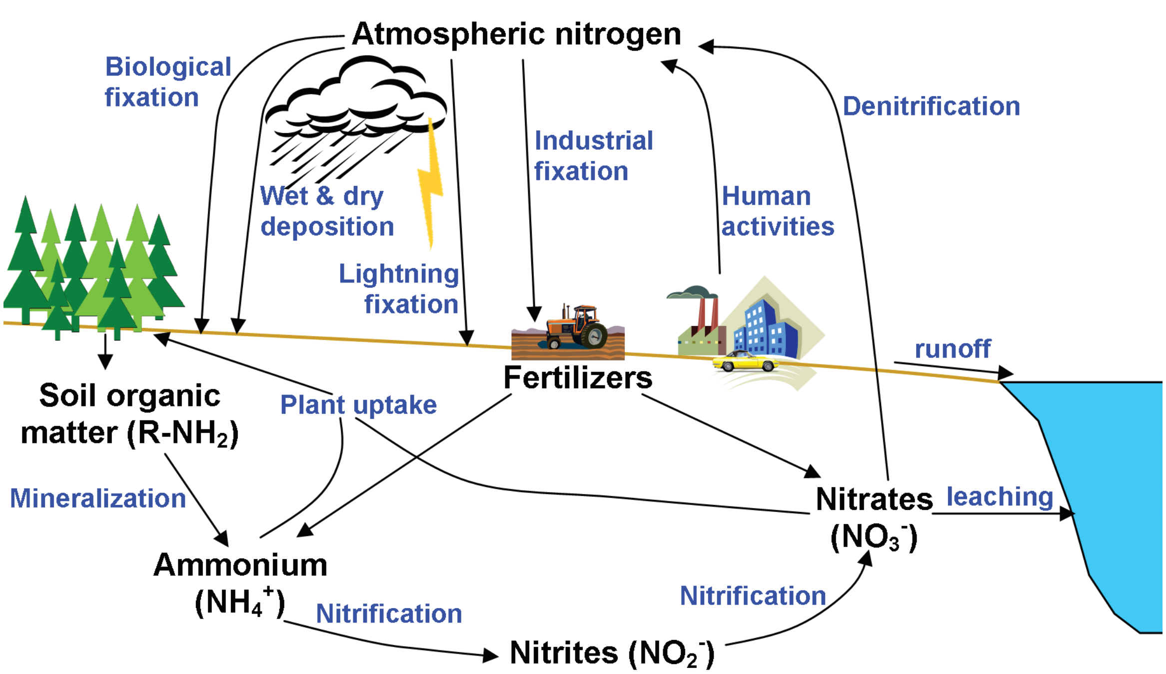


Figure 6-1. Nitrogen cycling through the Earth system involves inputs for wet deposition (in rainfall) and dry deposition (in dust particles and gases), as well as direct human activities such as application of fertilizer. Inputs to the atmosphere come from fossil fuel emissions and gaseous emissions from the soil. Nitrogen also can be exported from land to water bodies through leaching, deep drainage, and runoff. Nitrogen is a major nutrient for plants, animals, and microbes.

Over the past 150 years, marked changes have occurred in atmospheric emissions from human sources and deposition in precipitation across the United States (chapter 12). These changes have been driven by industrialization, human population increases, land-use change, and since the early 1970s, Federal Government controls on industrial and vehicle emissions. Air pollution through atmospheric deposition can influence ecosystem structure and in turn alter ecosystem functioning and services. Atmospheric deposition influences terrestrial ecosystems—including soil chemistry, vegetation nutrient cycling, and species health and distribution—and aquatic ecosystems—including surface water chemistry (chapter 12) and aquatic productivity, density, and composition (chapter 14).

A number of interesting and society-relevant hypotheses can be tested using long-term biogeochemistry data collected from a number of sites located in different ecosystem types and climatic regimes. In this chapter, we use data from chapter 12 to test two hypotheses related to patterns in biogeochemistry across EcoTrends sites and elements:

- Patterns in atmospheric deposition over the past 20 years are different for the eastern and western parts of the United States.
- Changes in atmospheric deposition are related to changes in human population density for some sites.

We test these hypotheses using chemical measurements in wet deposition (nitrate, ammonia, sulfate). To help interpret the patterns and trends in precipitation chemistry, we used sulfur dioxide, nitrogen oxide, and ammonia emission data compiled by the U.S. Environmental Protection Agency (EPA) (www.epa.gov/air/data/geosel.html).

Hypothesis 1. Patterns in Atmospheric Deposition Over the Past 20 Years Are Different for the Eastern and Western United States

In support of our hypothesis, total sulfur dioxide and nitrogen oxide emissions were higher through time for the region of the United States east of the Mississippi River than in the western region (figure 6-2). These patterns are consistent with higher population density on average in the eastern than the western parts of the country (figure 8-1, chapter 13). Emissions of sulfur dioxide are largely associated with coal-fired electric utilities located in the East (Dennis et al. 2007) that contribute sulfate to precipitation. Emissions of nitrogen oxides are largely due to a combination of electric utilities and transportation sources, resulting in nitrate in precipitation. Ammonia emissions are higher in the West than in the East, and are largely associated with agricultural activities (Driscoll et al. 2003).

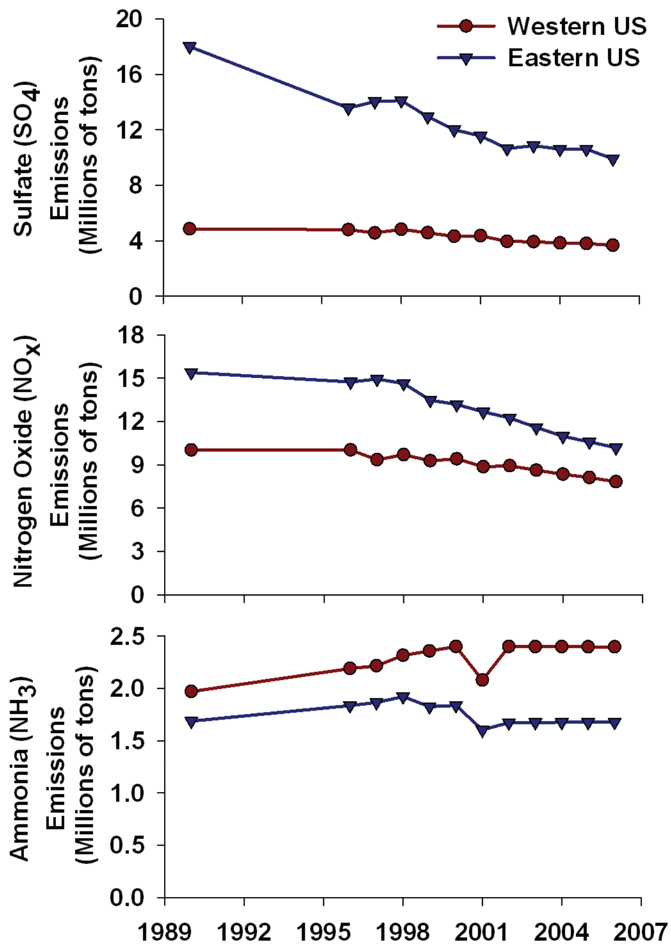


Figure 6-2. Annual atmospheric emissions of sulfur dioxide, nitrogen oxides, and ammonia for the eastern (east of the Mississippi River) and western States from 1990 to 2006 (www.epa.gov/air/data/geosel.html).

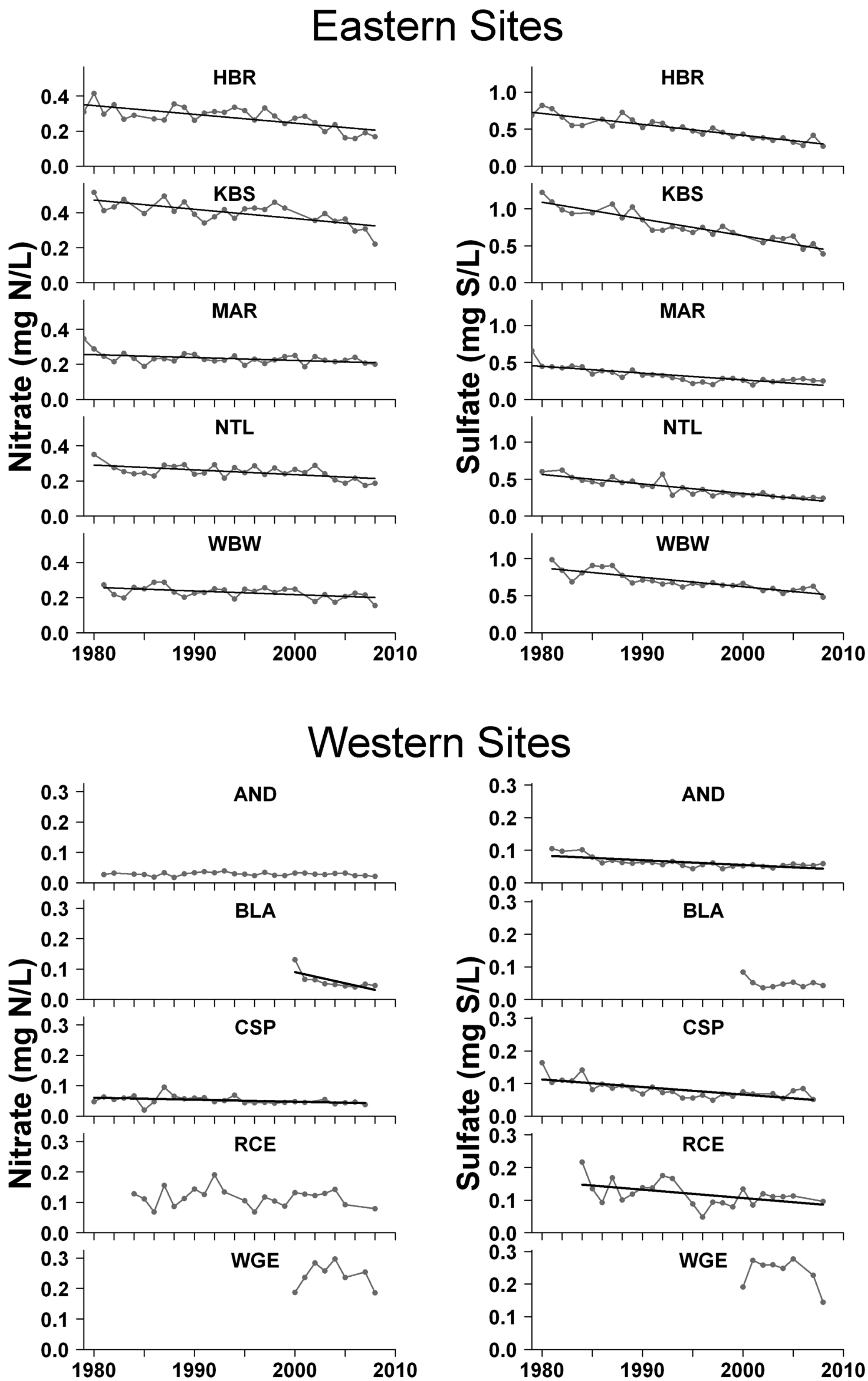
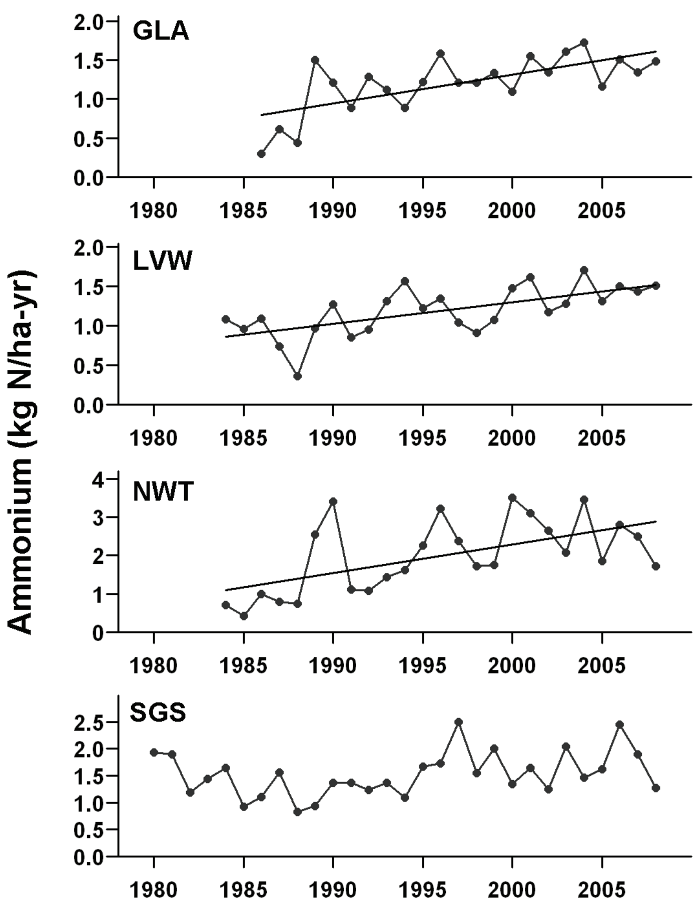


Figure 6-3. Change in annual volume-weighted concentration of nitrate and sulfate in precipitation at five eastern (upper panel: HBR, KBS, MAR, NTL, WBW) and five western sites (lower panel: AND, BLA, CSP, RCE, WGE). (Original data from Internet home pages—see table 1-1—and http://nadp.sws.uiuc.edu/. Synthesized data from http://www.ecotrends.info.)

The temporal trends in sulfate and nitrate concentrations in precipitation also reflect emission trends regionally. In the East, considerable effort has been made to control sulfur dioxide and nitrogen oxide emissions from electric utilities through the 1990 Amendments of the Clean Air Act and the Nitrogen Oxide Budget Trading Program (Dennis et. al. 2007). These control efforts have resulted in significant decreases in sulfate and nitrate concentrations in precipitation in eastern EcoTrends sites in both forests (HBR, MAR, NTL, WBW) and grasslands (KBS) (figure 6-3, top). In contrast, emissions of nitrogen oxides and sulfur dioxide in the West are either decreasing at a lower rate or not changing (figure 6-2). This limited change in trends through time is reflected by patterns in nitrate concentrations in precipitation for several forest (AND, BLA, CSP) and aridland (RCE, WGE) sites in the West (figure 6-3, bottom). These patterns are likely associated with increasing human development and associated transportation emissions, as well as less aggressive emission controls in the West than in the East.

In general, ammonia emissions have not changed appreciably for either region (figure 6-2) as a result of limited changes in agricultural activities. These trends in nitrogen emissions suggest a pattern of increasing importance of ammonium in the future as a percentage of total atmospheric nitrogen deposition if nitrogen oxide emissions continue to decrease.



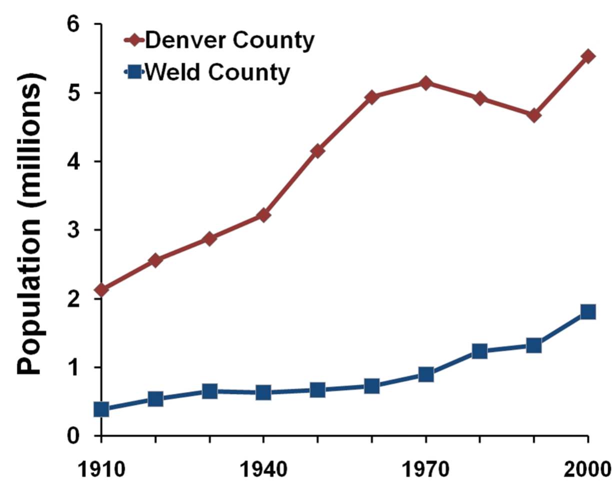


Figure 6-4. Left panel: An increase in ammonium deposition (kg/ha-yr) at three upslope Rocky Mountain locations (GLA, LVW, NWT) and no trend at a grassland site (SGS). Right panel: Patterns in nitrogen deposition for mountain sites reflect high rates of population increase in metropolitan Denver (represented by Denver County), the main source of nitrogen in rainfall in spring and summer. The county of the grassland site (Weld) also increased in population, but the source of nitrogen deposition is rainfall from surrounding agricultural land and rangeland. (Original data from Internet home pages—see table 1-1, http://nadp.sws.uiuc.edu/, and http://www.census.gov. Synthesized data from http://www.ecotrends.info.)

Hypothesis 2. Changes in Atmospheric Deposition Are Related to Changes in Population Density for Some Sites

Sites in the Rocky Mountains show a different trend in nitrogen deposition than other sites in the West, and these patterns are related to location rather than to ecosystem type (figure 6-4 left panel). For three high-elevation sites in the central Rockies, ammonium (and nitrate, not shown) deposition has increased through time (GLA, LVW, NWT). These sites are located upslope to the west of the Denver metropolitan area along the Front Range of the Rocky Mountains where human population density has been rapidly increasing (figure 6-4, right). Spring and summer moisture at these mountain sites is influenced mainly by westerly upslope storms from the Front Range; these storms provide an important source of atmospheric nitrogen deposition (Burns 2003). Thus, a rapid increase in density of humans may explain, at least in part, the higher nitrogen deposition rates in the mountains. In contrast, the lack of a trend in ammonium (or nitrate) for grasslands at lower elevations east of the mountains (SGS) likely reflects the long distance and easterly location of this site away from the influence of the major cities along the Front Range.

Conclusions

Human activities have greatly altered patterns in atmospheric deposition over the past 20 years. Effects of these activities vary regionally and across the continent as a result of variation in factors such as human population density, energy and agricultural production and use, atmospheric circulation and sources of rainfall, and government regulation. Cross-site comparisons of long-term data provide new insights into these spatial patterns.

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Chapter 7

Cross-Site Comparisons of Ecological Responses to Long-Term Nitrogen Fertilization

S.L. Collins, K.N. Suding, and C.M. Clark

Atmospheric pollution, as either wet or dry deposition, is changing through time for many ecosystems (chapters 6, 12). The long-term effects of these changes on ecosystem structure and function are not well understood, in particular for reactive nitrogen in the forms of nitrate (NO_3) and ammonium (NH_4). Reactive nitrogen is an essential nutrient that limits net primary production in most terrestrial and some aquatic ecosystems (Vitousek and Howarth 1991, Elser et al. 2007). Atmospheric nitrogen deposition is considered one of the major drivers of diversity loss in ecosystems (Sala et al. 2000), though land-use change remains the most important factor.

Given that human activity has doubled available nitrogen (Vitousek et al. 1997) along with other key resources (such as phosphorus) and that net primary production is increasing globally (Nemani et al. 2003) with variable patterns in time and space at specific sites (chapters 5, 14), a more mechanistic understanding of the relationship between nitrogen availability, productivity, and species diversity is needed.

The following key questions remain unanswered:

- How do increasing resources other than nitrogen affect productivity and species diversity?
- What are the mechanisms that can cause diversity to decline as productivity increases?
- Does an increase in productivity directly or indirectly through other environmental variables (such as pH) affect species diversity?
- How do microbial communities and processes respond as resource availability increases?
- Can plant functional trait responses provide a mechanistic understanding to the relationship between productivity and diversity?

Long-term observational and experimental data are needed to address these important research questions. For example, a long-term nitrogen fertilization study at the Cedar Creek LTER site in Minnesota (CDR) provides an interesting example of both threshold changes in species abundance and loss of diversity with addition of resources. In this experiment, about 10 g/m of nitrogen has been added annually to an abandoned agricultural field since 1982. Species diversity declined rapidly in response to nitrogen fertilization, whereas diversity in control plots fluctuated from year to year in response to interannual changes in precipitation. Consequently, the abundance of a non-native annual C_3 grass, *Agropyron repens,* increased relatively rapidly while the abundance of a long-lived clonal C_4 bunchgrass, *Schizachyrium scoarpium,* decreased relative to controls (figure 7-1). Thus, chronic environmental change can cause rapid, nonlinear transitions in local distribution and abundance of plant species.

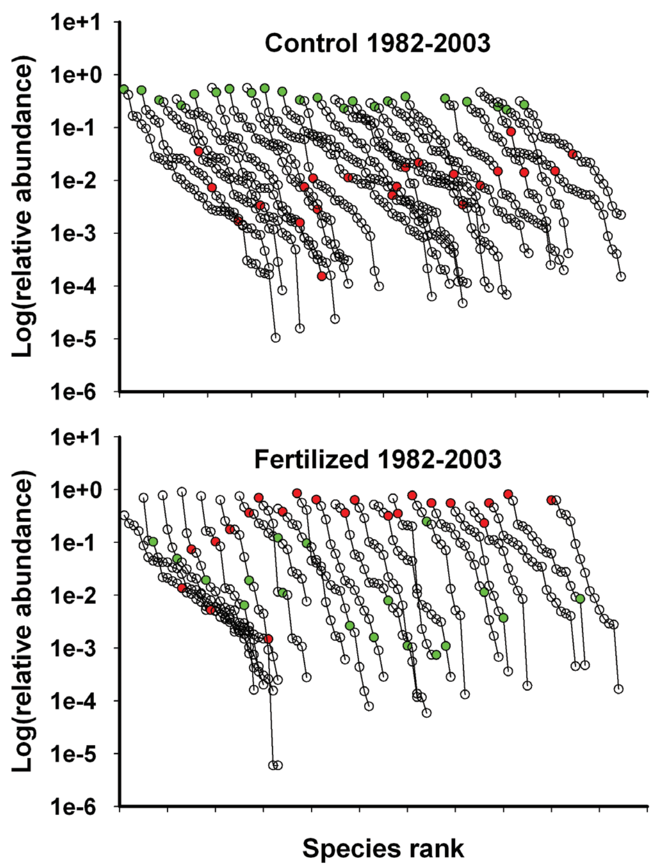

Figure 7-1. Annual rank-abundance curves for (a) control and (b) fertilized plots at the Cedar Creek Ecosystem Science site (CDR) for Field C from 1982 to 2003 show the relative ranking of a late successional, perennial C_4 grass *(Schizachyrium scoparium)* (green filled circles), and an early successional, annual C_3 grass *(Agropyron repens)* (red filled circles) (Collins et al. 2008). The curves show how the ranks of *Schizachyrium* and *Agropyron* remain relatively constant in control plots, but they rapidly reverse order in fertilized plots. Reprinted with permission from the Ecological Society of America.

Extrapolating cause and effect relationships from one ecosystem to another is often challenging, whereas multisite analyses of similar fertilization experiments across systems can provide greater generality. In a multisite analysis of plant community responses to experimental addition of nitrogen (100 kg/ha in most cases), plant species richness declined by about 30 percent and aboveground net primary production (ANPP) increased by about 50 percent across a range of sites with different initial productivity potentials (figure 7-2). This loss of diversity also occurs along natural productivity gradients (Stevens et al. 2004). Despite these common responses across sites and systems, the mechanisms causing this decline in diversity as productivity increases are still being debated, and long-term responses have not been evaluated.

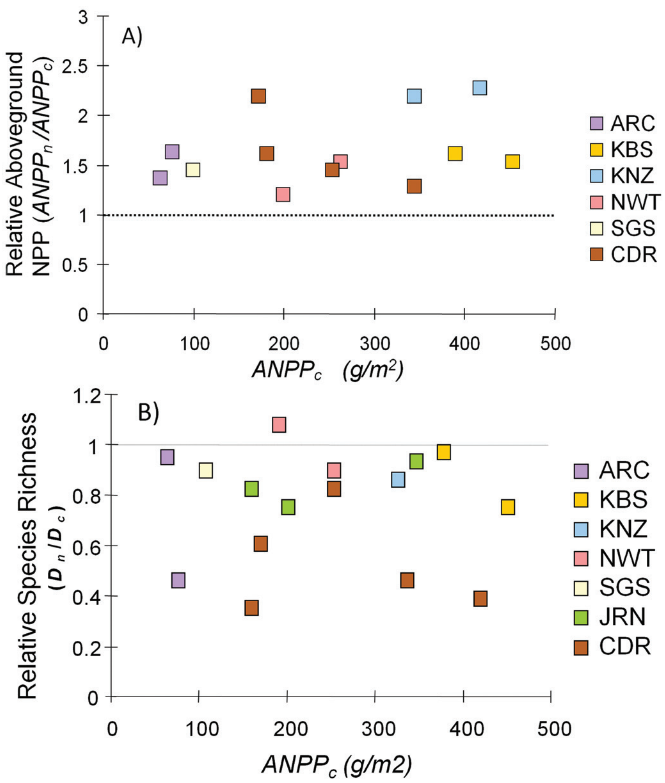

Figure 7-2. Response ratios for the last year of data for seven grassland sites receiving long-term N additions of 9 to 13 g/m^2/yr. (A) $ANPP_n$ in fertilized plots over $ANPP_c$ in control plots versus mean $ANPP_c$ of control plots. (B) species richness in fertilized plots (D_n) over species richness in control plots (D_c) versus mean $ANPP_c$ of control plots. Dashed lines indicate a response ratio of 1, meaning the N fertilization plots show no difference from control plots. (Redrawn from Gough et al. 2000.)

Functional traits may provide mechanistic insights into a plant community's response to fertilization (Bai et al. 2004). Species traits reflect evolutionarily derived strategies for resource capture and interspecific interactions, which influence community structure and ecosystem processes (Diaz and Cabido 2001). An analysis of more than 900 species responses from 34 nitrogen fertilization experiments across North America showed that both trait-neutral mechanisms (for example, rarity) and trait-based mechanisms (such as plant height) operated simultaneously to influence diversity loss as production increased (Suding et al. 2005). Thus, rarity, species identity, and functional traits affect species responses to increasing productivity in long-term nitrogen fertilization experiments. Because these responses may be highly dependent on context, they challenge our ability to predict how communities will change as the amount of reactive nitrogen continues to increase globally.

Conclusions

Human activities have greatly altered the nitrogen cycle. As a consequence, net primary production has increased globally and biodiversity has decreased in many herbaceous plant communities. Trait-based analyses may provide insight into the mechanisms behind biodiversity loss in response to increased nitrogen availability. Long-term studies are needed to document these patterns under variable climatic conditions.

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Chapter 8

Long-Term Trends in Human Population Growth and Economy Across Sites

C.G. Boone, T.L. Gragson, and J M. Grove

Human activities play profound roles in ecosystem dynamics, both directly through land use change, spread of invasive species, and increases in air and water pollution and indirectly through increases in atmospheric carbon dioxide (CO_2) and trace gases that modify climate and weather patterns. Rapid growth in the global human population during the last century, from 1.6 billion in 1900 to 6.7 billion in 2008, has increased demands for resources with subsequent effects on biotic (plants, animals, microbes) and abiotic (soils, atmosphere, water) properties of ecosystems. These changes in ecosystem properties result in modifications to the goods and services provided to humans. Thus, a feedback loop exists between human populations and their environments that makes it imperative that trends in human populations be examined as both a key driver to changes in ecosystems, and as a key responder to changes in those same systems.

Although human population is rising globally, the distribution is not uniform and varies spatially, even across the United States (figure 8-1). The Eastern United States is more heavily populated than the West, although parts of the West have experienced some of the highest rates of increase over the past 50 years (chapter 13). In particular, between 1990 and 1998, the Phoenix metropolitan area grew faster—a 31-percent rate of increase—than any other metropolitan area in the United States. (National average rate was 8.7 percent.)

Figure 8-1. Night lights show spatial variation in human population density across the United States. (Http://veimages.gsfc.nasa.gov//1438/land_lights_16384.tif.)

These increases in human populations throughout the country influence the ecological dynamics of research sites adjacent to urban areas as well as noncontiguous sites. Many research sites in this book were originally located in relatively pristine areas with low direct human impacts. As human populations have increased through time, housing and urban developments are moving closer to these formerly pristine areas. Although most research sites allow restricted or limited access to the public, the spread of native and exotic plants and animals from residential areas to nearby research areas is difficult to control. In addition, human activities upslope or upwind of research areas can influence those ecosystems through the transport of seeds, particulates, chemical compounds, water, soil, and nutrients by water, wind, and animals. This transport of materials can occur locally from a nearby city (figure 6-4) or over large distances, such as sediment loads from the upper Mississippi River deposited in the Gulf of Mexico.

Thus, we need to understand how human populations are changing in demographic and socioeconomic variables that directly influence nearby research sites. We also need to know the broader context of change in these variables across the country and how these changes influence patterns in migration and economic policies that can influence noncontiguous areas. Comparing human population and economic variables through time and across space (chapter 13) for the same set of sites where detailed ecosystem properties are measured (chapters 11, 12, 14) provides an opportunity to directly link these important elements of coupled human-natural systems.

In this chapter, we illustrate the value of long-term data in testing two important hypotheses related to spatial variation in trends in coupled human-natural systems and present a case study of cross-site comparisons made possible with population and economic data from different locations across the country. Long-term graphs of human population and economy data by site are in chapter 13.

Hypothesis 1. Tree Canopy Cover and Socioeconomic Status Are Positively Correlated in Both Urban and Suburban Counties

Tree canopy cover in both urban and suburban areas is largely a function of human population density, socioeconomic status, and lifestyle preferences. Although ecosystem properties such as water or soil nutrients can be limiting factors, these limits can be overcome through human intervention, including infrastructure, such as amendments to soil and irrigation, and management regimes including fertilizer application. These interventions along with maintenance of trees and available land for planting require resources. We hypothesize that variability of canopy cover in urban and suburban neighborhoods is explained primarily by the demographic and socioeconomic characteristics of those neighborhoods (Troy et al. 2007). A complementary hypothesis is that present-day canopy cover is a function of past socioeconomic characteristics of neighborhoods and that a “lag effect” can be detected through appropriate analysis of historic census data. Both long-term ecological data on canopy cover and human economic data collected by a suite of sites can be used to test this hypothesis (Boone et al. 2009).

Hypothesis 2. Health-Related Ecosystem Services Follow an Inverted U Relationship

Environmental conditions that affect human health, such as air pollution, are significantly affected by changes in the economy. We hypothesize that as the economy transitions from agriculture to manufacturing, either in locations or over time, air pollution will worsen. By contrast, as the economy shifts from manufacturing to a service economy, air quality will improve. The same inverted U relationship (known as the Environmental Kuznets Curve) is expected to develop with increases in income per capita. This hypothesis could be tested using air quality data obtained as the number of EPA nonattainment days per year for criterion air pollutants or as atmospheric deposition data in chapter 12 combined with economic data in chapter 13.

Case Study: Patterns in Human Population Growth Across the Country

Prior to this project and book, patterns in human population and economy variables had not been systematically examined for ecological research sites. Historically, most sites focused on collecting ecological data. In 1994, two LTER sites, NTL and CWT, were funded to incorporate a regional human dimension. In 1997, two LTER sites, BES and CAP, were funded as coupled human-natural systems with objectives directly related to studying human systems as part of the ecological system. More recently, the LTER Network published a document that describes a critical need for coupled human-natural systems research at all LTER sites (LTER 2007). This new direction for the LTER Network reflects an increasing recognition that humans are an integral part of all ecological systems. Thus, effects of both direct drivers (such as land use) and indirect drivers (such as climate change) of human systems on their environment must be studied in addition to studying feedbacks from ecological systems to human systems.

As a first step in studying these coupled systems, we examine spatial variation in trends in human populations with a focus on the percentage of the population that is urban. Although the United States in general is becoming more urban (Brown et al. 2005), we expect that the rate of change in urbanization varies across the country. We also acknowledge that some parts of the country are less urbanized than others. We selected six sites in different parts of the country to illustrate spatial variation in demographic change. Three of these counties were mostly urban in 2000: Santa Barbara, CA; Maricopa, AZ; and Miami-Dade, FL. The population data obtained from the U.S. Census Bureau show that these counties had very different patterns in the rate of change in urbanization through time (figure 8-2). Miami-Dade county in the southeastern United States, where the FCE LTER site is located, was more than 60 percent urban by 1920, whereas counties in the West became urbanized later: Santa Barbara County (SBC LTER) by 1930 and Maricopa County (CAP LTER) by 1950.

Three other counties were selected that were less than 80 percent urban in 2000—Dona Ana, NM; Grafton, NH; and Weld, CO (figure 8-3). These counties had similar rates of change until 1970 even though they are in different parts of the country. The increase in the populations of Doña Ana County (JRN LTER) and Weld County (SGS LTER) starting in 1970 reflects the migration of people from the north and west to the moderate climate of the Southwest and the Front Range of the Rocky Mountains. The county in New Hampshire surrounding the HBR LTER site remains mostly rural. These differential patterns in urbanization provide a template and stratification for future studies that link human populations with their environment.

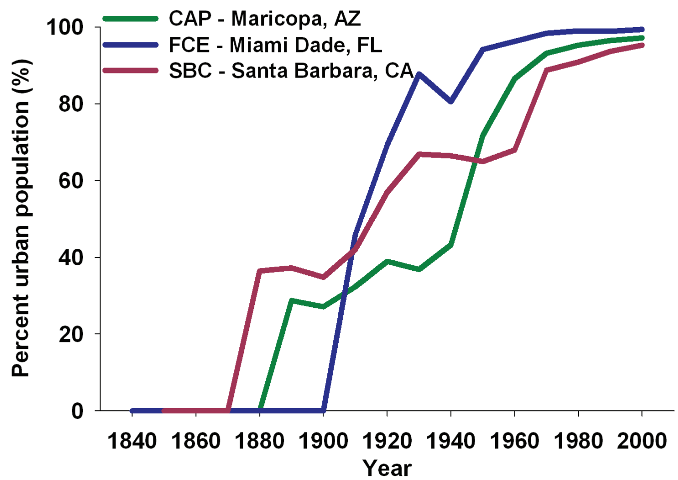

Figure 8-2. Percentage of the population in each county that was urban in each year of the U.S. census for three counties associated with LTER sites that are currently nearly 100 percent urban: Central Arizona-Phoenix (CAP), Florida Coastal Everglades (FCE), and Santa Barbara Coastal (SBC). (Original data from http://www.census.gov. Synthesized data from http://www.ecotrends.info.)

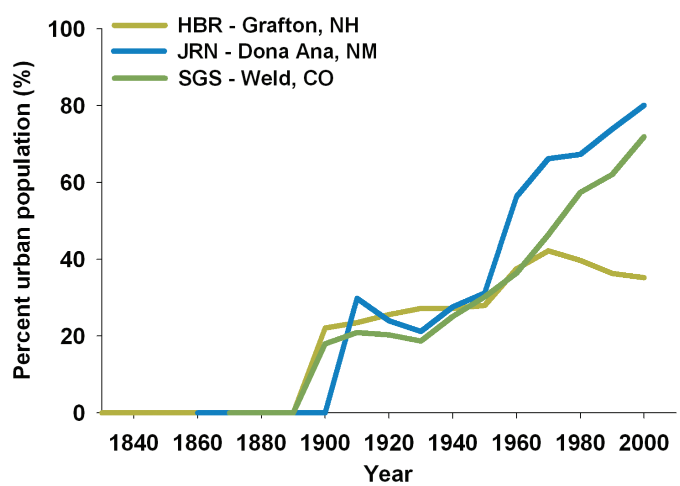

Figure 8-3. Percentage of the population in each county that was urban in each year of the U.S. census for three counties associated with LTER sites that are currently less than 80 percent urban: Hubbard Brook Ecosystem Study (HBR), Jornada (JRN), and Shortgrass Steppe (SGS). (Original data from http://www.census.gov. Synthesized data from http://www.ecotrends.info.)

Summary

Since 1920, the majority of the human population of the United States has lived in urban areas. In the past few decades, urbanization rates have been particularly rapid in the West. Timing of growth affects the nature of urban expansion across the country because of the variation in policies, availability of technologies, and cultural norms that dominate over time. Especially since World War II, urban growth has been characterized by low-density development on the periphery of cities. This urban expansion can have direct effects on surrounding ecosystems through land use change and indirect affects through resource consumption, nutrient transport, and waste generation. In turn, alterations to ecosystem structure and function can affect availability of ecosystem services and human outcomes and behavior. Therefore, integrating human and ecological systems is critical to understanding the feedbacks and linkages that affect both and to develop better management systems.

Long-term demographic data are valuable for testing variations in social-ecological systems across space and time. We hypothesize that variation in vegetation cover in urban areas reflects demographic characteristics more than biophysical limits and that past demographics may be better predictors of vegetation, especially tree canopy cover, than present population characteristics. Long-term census data coupled with ecological data could be used to test the Environmental Kuznets Curve hypothesis, that as the economic base shifts from agriculture to manufacturing to services, air quality will worsen then improve. Variability across LTER sites through time provides a rich dataset for testing socioecological dynamics.

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Chapter 9

Disturbance Regimes and Ecological Responses Across Sites

D.P.C Peters, A.E. Lugo, F.S. Chapin III, A.J. Tepley, and F.J. Swanson

A disturbance is defined as a discrete event with the capacity to alter the structure, functioning, and species composition of an ecosystem (White and Pickett 1985). A number of different disturbances that affect ecosystems fall into four major classes: climatic, physical, biotic, and anthropogenic (figure 9-1). The effects of a particular disturbance event depend on its duration (short or acute vs. chronic or long-term) and intensity, how large an area it affects, the state of the ecosystem at the time of disturbance (whether the system is mature or young, in active growth, or dormant), and the frequency of return of the disturbance. Some disturbances occur frequently but at low intensity, such as annual fires that move quickly through forest understories. Some are very infrequent but of high intensity, such as volcanic eruptions or category 5 hurricanes. And others exhibit a wide range of frequency and intensity combinations, such as the size and frequency of landslides on forested landscapes.

Figure 9-1. Examples of four classes of disturbance based on the type of driver. Top left: Physical—wildfire in Alaska, Bonanza Creek Experimental Forest (BNZ), photo by F. Chapin. Top right: Climatic—hurricane in Puerto Rico, Luquillo Experimental Forest (LUQ), photo by N. Brokaw. Bottom left: Biotic—salt cedar invasion along the Rio Grande, Sevilleta (SEV), photo by J. Thibault. Bottom right: Anthropogenic—housing development abutting desert in the Phoenix metropolitan area, Arizona, Central Arizona-Phoenix (CAP), photo by CAP photo gallery.

Disturbances affect ecosystems in almost limitless ways and extend beyond the initial effects that are usually visible to the human eye. A cascade of effects involving the functioning, restructuring, and other changes (succession) in an ecological system follows the immediate visible effects of the disturbance. As an example, figure 9-2 shows a 60-year record of structural changes in a subtropical wet forest in Puerto Rico (LUQ) following the passage of a hurricane 10 years before data collection began followed by two more recent hurricanes (Drew et al. 2009). Both the trend (increase, then decrease) and magnitude of change depend on the response variable. These dramatic long-term changes in tree density, biomass, and species diversity and evenness were accompanied by equally significant changes in nutrient cycling, species composition, primary productivity, and rates of mortality and regeneration (Lugo 2008, Drew et al. 2009).

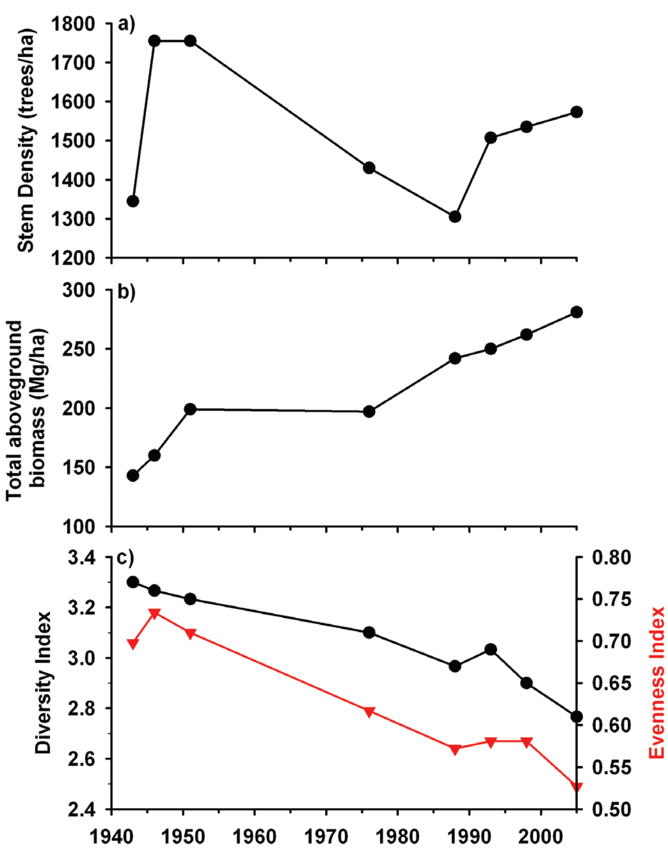

Figure 9-2. (a) Tree stem density; (b) total aboveground biomass (leaves and wood); and (c) Shannon-Weiner plant species diversity (black line) and overall evenness index (Pielou's J) (red line) of trees through time in Puerto Rico, following a hurricane in 1930, Luquillo Experimental Forest (LUQ). Two additional hurricanes influenced forest dynamics: Hugo in 1989 and Georges in 1998 (Drew et al. 2009). Modified with permission from Interciencia.

For many disturbances, long-term data are needed to unravel their effects. A long return interval between disturbance events requires a long period of study to capture multiple events. However, the field of ecology is a recent historical development that spans about 100 years, and the simultaneous monitoring of ecosystem structure and functioning has less than 50 years of experience. Moreover, the focus of this activity has been on a few ecosystem types. Thus, the scientific opportunity to understand how events with recurrence intervals of greater than 100 years affect ecosystem processes has been very limited.

Two circumstances complicate the study and understanding of the effects of disturbances on ecosystems. First**,** interactions between different disturbance events can create greater effects than each disturbance alone, or these interactions can mask the effects of individual events. As an example, fires often follow hurricanes, and fires can be followed by debris flows. When one disturbance event follows another, determining what effects to attribute to each event is difficult. In some cases, it can even be difficult to identify the disturbance that resulted in the dramatic effects on an ecological system. For example, in 2001-2002, the salt marshes of coastal Georgia (GCE) experienced a sudden dieback that affected large patches (up to 240 ha) of both salt marsh cord grass *(Spartina alterniflora)* and black needlerush *(Juncus roemerianus)* (Ogburn and Alber 2006). A number of hypotheses have been advanced to explain the dieback, which was associated with an extreme drought (Silliman et al. 2005, Alber et al. 2008). To date, no single factor has been unambiguously linked to all dieback events, and it is possible that multiple factors interacted to produce dieback at different sites. Plant densities have increased at affected sites, but at varying rates—some sites appear to have fully recovered while others still have sparse vegetation (figure 9-3).

Second, the number, spatial extent, and frequency of occurrence of disturbance events are changing as a result of human activity. These activities can have both direct and indirect effects on ecosystems (chapter 8). For example, frequency and intensity of fires are increasing in some areas, likely as a result of human activity that includes increasing temperatures (figure 9-4) (Kasischke and Turetsky 2006). The increase in frequency of major storms along the Atlantic coast (Hayden and Hayden 2003), with consequences for shoreline location, may also be related to climate change (figure 9-5) (Harris 1992, Shao et al. 1998). Trends in climate for each site are shown in chapter 11.

Ecologists have the dual challenge of understanding the effects of natural and anthropogenic disturbances on ecosystems and at the same time understanding how changing ecological systems can modify the characteristics of subsequent disturbances. Of particular interest are the effects of disturbances on the services that society requires to sustain human populations and economies and the conservation of species assemblages and ecosystems.

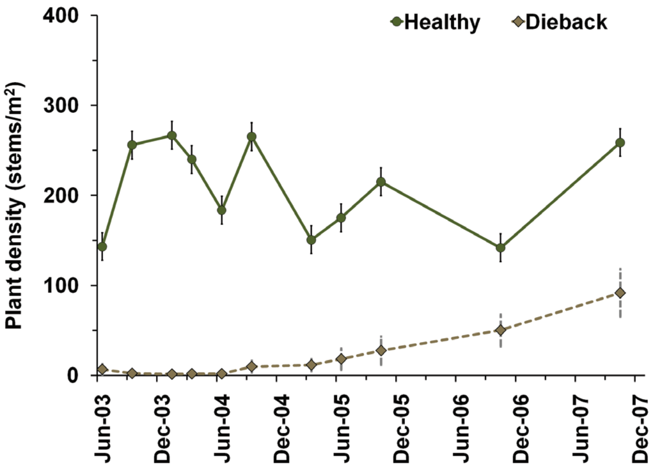

Figure 9-3. Regrowth of *Spartina alterniflora* at a marsh dieback site in coastal Georgia (GCE). Samples collected at dieback (dashed line) and nearby healthy (solid line) areas (Alber et al. 2008). Reprinted with permission from Elsevier.

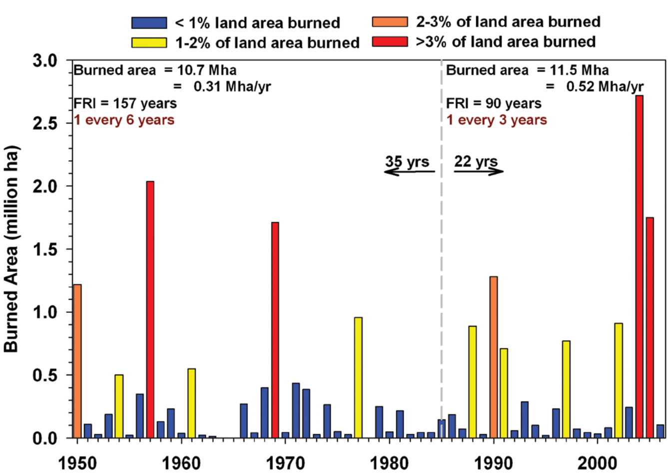

Figure 9-4. Area burned in North America's northern forest, which spans Alaska and Canada, tripled from the 1960s (Fire Return Interval [FRI] 1 every 6 years) to the 1990s (FRI 1 every 3 years). Two of the three most extensive wildfire seasons in Alaska's 56-year record, based on area burned, occurred in 2004 and 2005; and half of the largest fire years have occurred since 1990. Modified from Kasischke and Turetsky 2006.

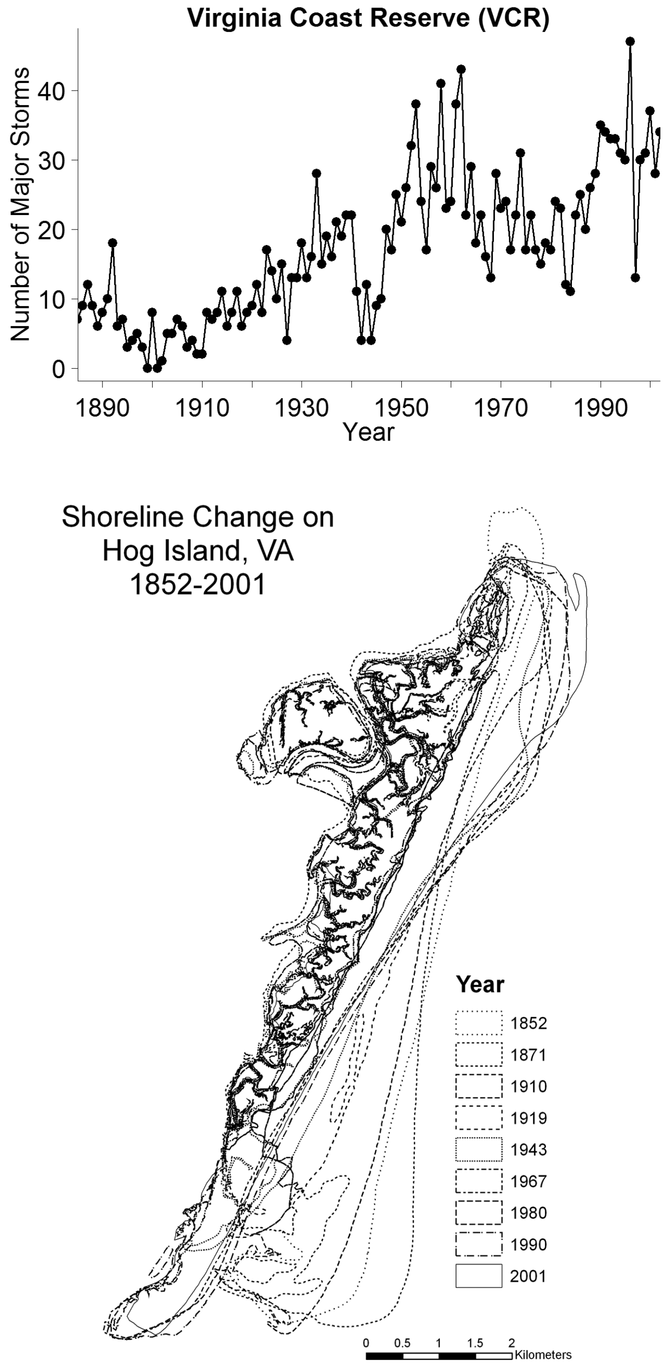

Figure 9-5. Number of major storms along the coast of Virginia, Virginia Coast Reserve (VCR), has increased since 1950 (top: modified from Hayden and Hayden 2003; data from http://amazon.evsc.virginia.edu) with associated changes in the shoreline of Hog Island, VA (bottom: modified from Harris 1992, Shao et al. 1998). Over 90 percent of the current upland area on Hog Island is newly deposited since the late 1800s. Data compiled based on historical maps (1852-1919), aerial photos (1943-1990), and satellite imagery (2001).

In this chapter, we first present characteristics of disturbances and then discuss ecosystem responses for each of four major classes of disturbance. Because specific disturbance events vary among sites and ecosystem types, we use examples from a variety of sites to illustrate the importance of long-term data in unraveling the role of disturbances in ecosystem dynamics. Quantitative cross-site comparisons are currently not possible for many types of disturbance as a result of nonstandardized methods of data collection, archiving, and retrieval (chapters 16, 17), although recently a framework was developed to "unpack" the drivers and responses associated with disturbance events to allow cross-site comparisons (Peters et al. 2011).

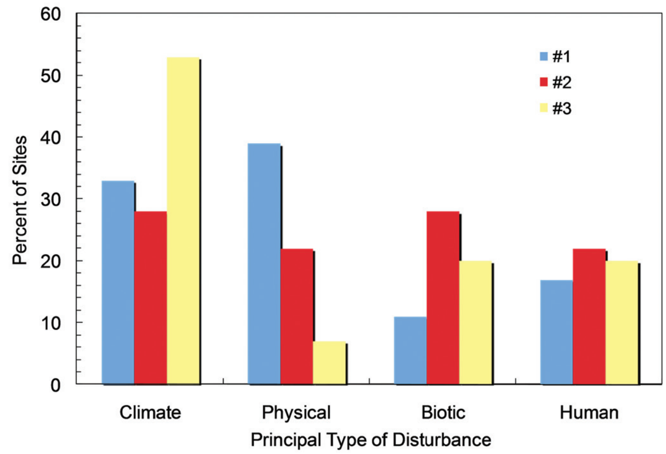

Figure 9-6. In a survey of lead scientists from the 26 LTER sites, physical and climatic disturbances were identified as the most important classes at their site (ranked #1). All four disturbance classes were equally important as the second most important type (ranked #2) (Peters et al. 2011).

Disturbance Characteristics

Each of four major classes of disturbance (climatic, physical, biotic, and anthropogenic) can have different effects on ecosystems. For example, windstorms are climatic disturbances that mechanically alter the structure of forests and transfer biomass from the forest canopy to the soil surface where it can be processed by microorganisms. In contrast, wildfires are physical disturbances that consume organic matter and release ash plus carbon dioxide gas into the atmosphere. Another class of disturbance includes those that affect ecosystems biologically, such as insect attacks on trees or defoliation by herbivores. Anthropogenic (human-caused) disturbances include the clearing of trees or cultivation of agricultural land as well as atmospheric warming and ozone pollution.

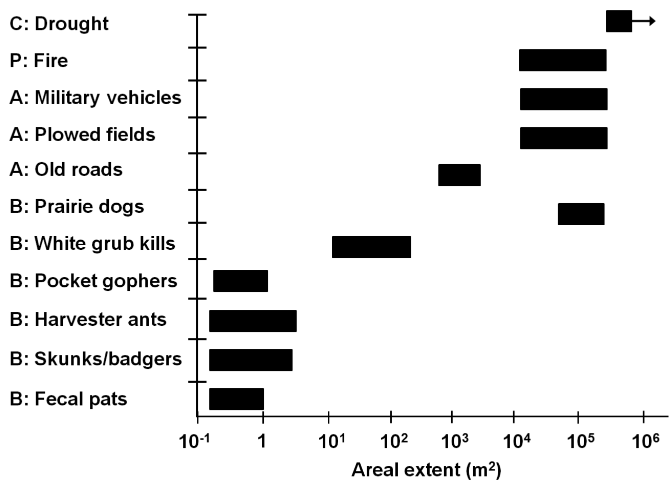

Figure 9-7. The disturbance regime in the Shortgrass Steppe (SGS) consists of all four types of disturbances that vary in spatial extent: C, climatic; P, physical; A, anthropogenic; and B, biotic. Modified from Peters et al. 2008.

In general, physical and climatic disturbances are the most important classes driving dynamics at many sites (figure 9-6) (Peters et al. 2011). However, the disturbance regime of a site can include all four classes, each with a characteristic spatial extent and frequency of occurrence (figure 9-7) (Peters et al. 2008). At some sites, climatic disturbances (like hurricanes or drought) are the most prevalent class, with multiple disturbance events occurring through time at a site (figure 9-8).

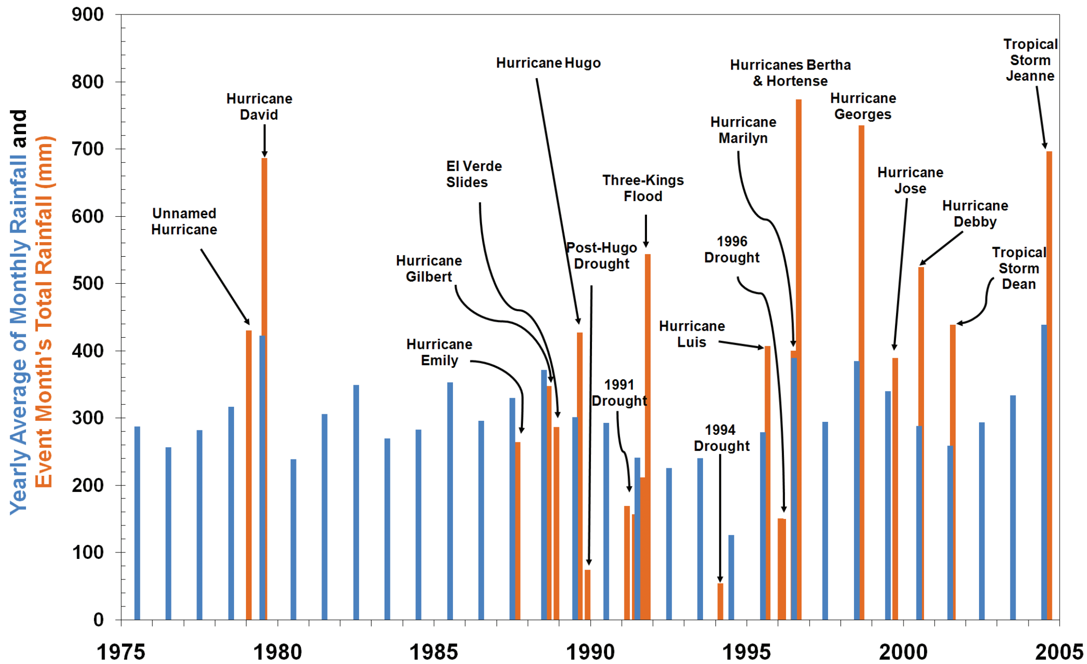

Figure 9-8. Multiple disturbance types often occur at one site as parts of the disturbance regime, for example, at Luquillo Experimental Forest (LUQ). However, physical disturbances (hurricanes) are the most prevalent at LUQ. Data from W. McDowell, D. Schaefer, A. Estrada-Pinto, A. Ramírez, and National Climatic Data Center. (http://www.ncdc.noaa.gov.)

Ecosystem Responses by Disturbance Class

Climatic Disturbances

Extremely high or low conditions of climatic drivers can have profound effects (chapters 3, 11). In many cases, the resulting disturbance is a combination of extreme events of multiple climatic drivers. Hurricanes are extreme climatic events with high wind speeds of more than 33 m/s, storm surges over 1.0 m, barometric pressure under 908 millibars, and variable rainfall sustained over several days in one location. Hurricanes move across landscapes to influence large areas. In the United States, the most frequent, intense hurricanes occur along the Atlantic Coast, moving northward from the Gulf of Mexico or Florida to the Northeastern States.

Long-term data show that hurricanes are more frequent and more intense in Puerto Rico (LUQ) than in New England (HFR) because storms decrease in intensity as they move across land (figure 9-9). Both locations have had periods with more events than others, although these events did not occur during the same period (1950-1960 at HFR; 1890-1900 at LUQ) (Boose 2003). This spatial variation in occurrence shows that hurricanes do not follow the same tracks across land and water every time.

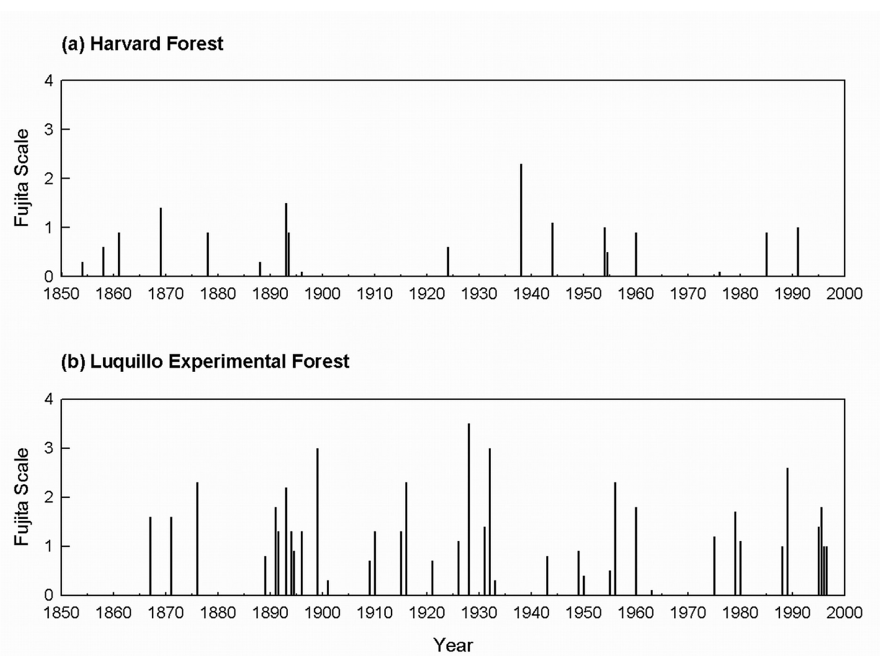

Figure 9-9. Years in which hurricanes occurred at two sites and their intensity based on the Fujito scale in which larger numbers are more intense events: (a) Harvard Forest (HFR) in the north-eastern United States and (b) Luquillo Experimental Forest (LUQ) in Puerto Rico (Boose 2003). Reprinted with permission from Oxford University Press.

The effects of hurricanes need to be examined within the context of other disturbances that affect an ecosystem. In Puerto Rico (LUQ), these other disturbances include high rainfall events due to passage of storms or frontal systems as well as droughts and landslides (figure 9-8). Populations of plants and animals respond in a variety of ways to these different events (figure 9-10). Snails maintain high population numbers during periods of frequent disturbance. Frogs increase after a hurricane with the creation of microsites for reproduction, but decrease rapidly during droughts. Shrimp in streams have an upward, although variable, trend, in spite of the disturbance regime, while birds showed lag responses to disturbance events.

Drought is another kind of climatic disturbance that affects many systems. A drought occurs when precipitation is sufficiently lower than average that ecological systems are affected. Low precipitation is often accompanied by high temperatures, low relative humidity, and low cloud cover such that a definition of drought needs to encompass multiple climatic variables. Indices such as the Palmer Drought Severity Index (PDSI) can be used to determine the beginning and end of a drought as well as its severity (chapter 11).

Drought occurs throughout the United States and globally, although its frequency and intensity vary regionally. In the Great Plains, the drought of the 1930s and the resulting Dust Bowl are often cited as the most extreme drought impacts over the past several centuries. In contrast, the 1950s drought was of longer duration and more extreme intensity in the Southwest, with major impacts on system dynamics. In southern New Mexico (JRN), the historically dominant perennial grass black grama *(Bouteloua eriopoda)* died out on most (64 percent) research quadrats (1 m^2)

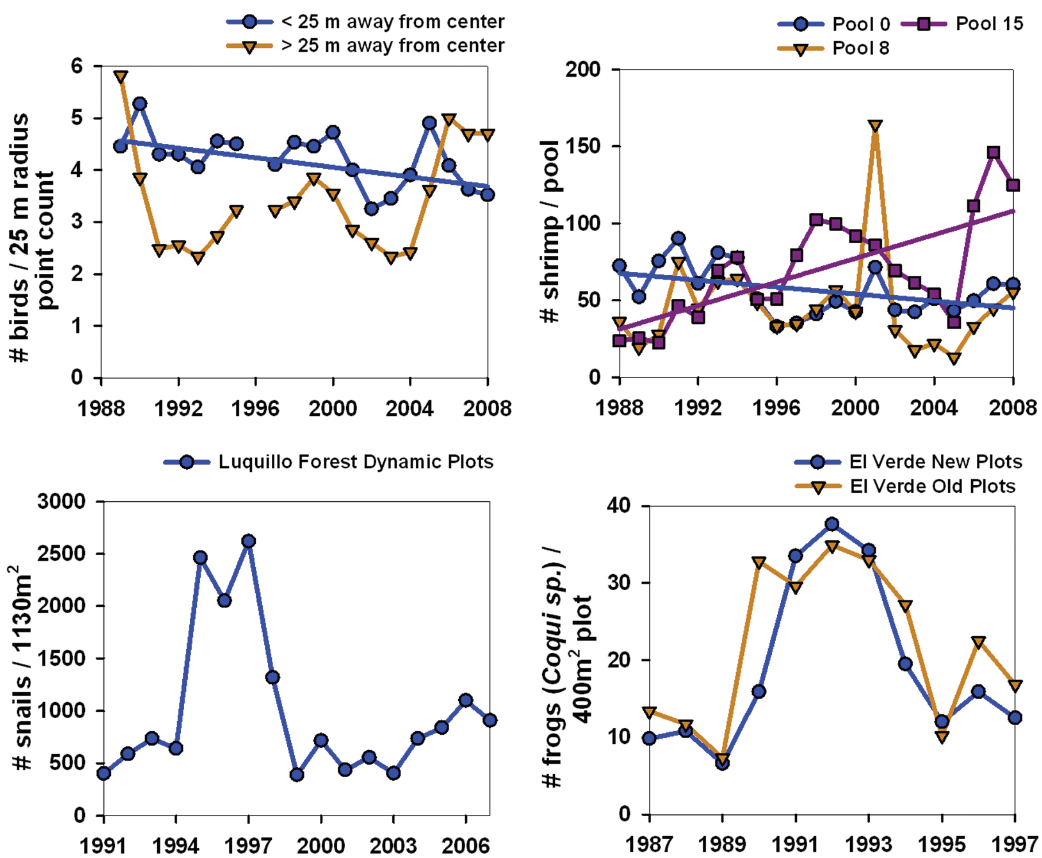

Figure 9-10. Response of different groups of organisms following multiple disturbance types in a forest in Puerto Rico. Data from R. Waide for birds, T. Crowl for shrimp, C. Bloch for snails, and L. Woolbright for frogs.

either during or shortly after the 1950s drought (figure 9-11). However, this species went locally extinct on 21 percent of research quadrats prior to that drought, probably because of a drought in the early 1900s in combination with livestock overgrazing (Peters et al. 2006). Persistence of this species to at least 1979 on 15 percent of the quadrats reflects spatial variation in vegetation dynamics that cannot be explained by broad-scale drivers such as drought and grazing.

Global warming, the increase in air and water temperatures, is a climatic disturbance that results from increases in carbon dioxide and other greenhouse gases in the atmosphere resulting from human activities (IPCC 2007). Increasing temperatures are an example of a chronic disturbance over a long period as compared to acute disturbances (events discrete in time). Ecological systems can respond to global warming in a number of ways. One effect of global warming is a shift in species distributions or abundances with changes in conditions for recruitment, mortality, and prey availability (figure 4-2). For example, glaciers are being lost in the Rocky Mountains as temperatures increase (figure A1-58).

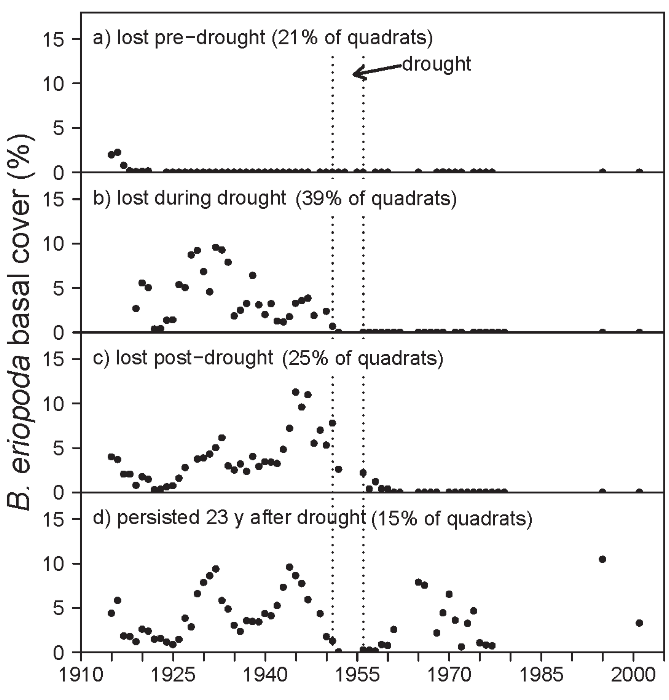

Figure 9-11. Black grama (*Bouteloua eriopoda*), the dominant perennial grass of upland grasslands in the Chihuahuan Desert, went locally extinct on most (64 percent) research quadrats (1/m^2) either during (b) or shortly after (c) the 1950s drought. However, this species went locally extinct on 21 percent of research quadrats prior to the drought (a) and persists to at least 1979 on 15 percent of the quadrats (d) (Peters et al. 2006). Reprinted with permission from the American Institute of Biological Sciences.

Physical Disturbances

Changes in abiotic conditions, such as soils, nutrients, and water have consequences for biotic responses. Wildfires, wave height in oceans, and landslide debris flows are good examples.

Wildfires remove aboveground plant biomass and result in the release of particulates to the atmosphere and addition of carbon and nitrogen to the soil. Fires occur across a range of intensities and spatial extents with variable effects on ecosystem dynamics. Fires are common features in grasslands and tundra with sufficient biomass to carry a fire and in forests where crown fires and understory fires are possible.

In the tallgrass prairie of Kansas (KNZ), fires induce pulses in the density of flowering stems of an important warm-season grass, big bluestem *(Andropogon gerardii)* (figure 9-12). Plant species composition

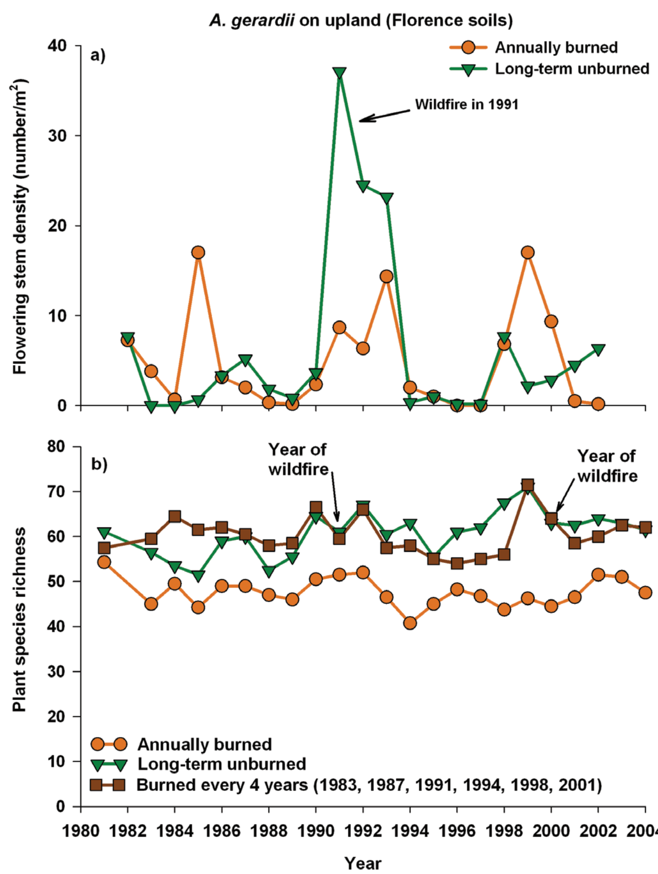

Figure 9-12. Wildfire in tallgrass prairie results in (a) a pulse in flowering stem density of *Andropogon gerardii*, an important perennial grass (data source: KNZ-PRE022; http://www.konza.ksu.edu; updated from Hartnett and Fay 1998), and (b) a decrease in plant species richness when it is burned annually compared with less frequent burns (updated from Knapp et al. 1998; http://www.konza.ksu.edu.)

is also affected by fire frequency. Annually burned watersheds have lower species richness than unburned or 4-year-burned watersheds (Hartnett and Fay 1998).

Much longer time periods for recovery can be required in some systems. In a semiarid grassland in central New Mexico (SEV), wildfire effectively limited invasion by the native shrub creosotebush *(Larrea tridentata)* (figure 9-13) (Parmenter 2008). Some plants were killed by fire, and the heights of remaining plants were reduced. It took 12 years for shrub height to recover to prefire levels.

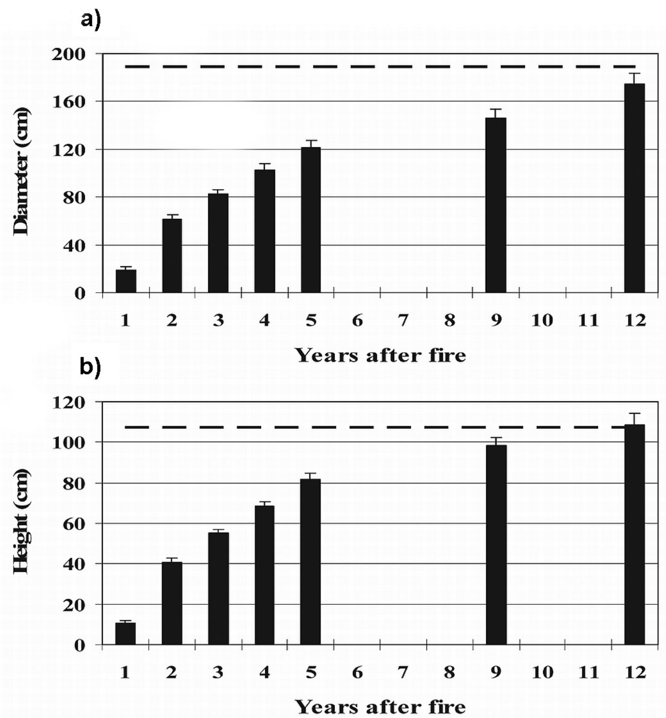

Figure 9-13. Diameter and height of *Larrea tridentata* (creosotebush), a common shrub in the Chihuahuan Desert, following fire at the Sevilleta (SEV) (Parmenter 2008). Twelve years' recovery was required before plants reached prefire height. Reprinted with permission from Allen Press Publishing Services.

Wildfire can also interact with other drivers in many systems. In coniferous forests of the Pacific Northwest (AND), centennial-scale variation in fire occurrence reflects climatic variability and human influences. Fire-history studies in western Washington and Oregon found two periods of extensive fires (the late 1400s to about 1650, and about 1800 to about 1925) (Weisberg and Swanson 2003). The increase in fire in the 19th century coincides with herding, logging, and mining by settlers, and the low abundance of fire throughout the 20th century corresponds to active fire suppression. Annual area burned in the 20th century also corresponds to climate, in particular the Pacific Decadal Oscillation (PDO) (Trouet et al. 2006). Warm phases of the PDO bring warmer-than-average winters with little snow, which may lead to long fire seasons with relatively low soil and fuel moisture.

Fire-history data (including establishment dates for 1,030 Douglas-fir trees in 124 stands) collected in the central western Cascades of Oregon (AND) suggests that the PDO also may have contributed to variation in the fire regime prior to the 20th century (Tepley 2010). Douglas-fir is a relatively shade-intolerant species whose regeneration depends on disturbances such as fire that open the canopy. In two large watersheds, major pulses of establishment by Douglas-fir were initiated during extended warm phases of the PDO (figure 9-14a, yellow bands) when tree-ring width was reduced, a likely indication of drought (Tepley 2010). As a result, 87 percent of Douglas-fir establishment dates fell in the intervals 1480-1610 and 1780-1940 (figure 9-14b), corresponding to previously identified periods of region-wide extensive fire. The correspondence of widespread establishment by this disturbance-dependent species with probable periods of drought during extended warm phases of the PDO suggests that the PDO may be an important factor in synchronizing widespread fire across the region.

Along coastlines, wave height shows high seasonal variability with storms that influence the standing crop of giant kelp (figure 9-15). Loss of giant kelp increases as wave height and storm intensity increase (Rassweiller et al. 2008).

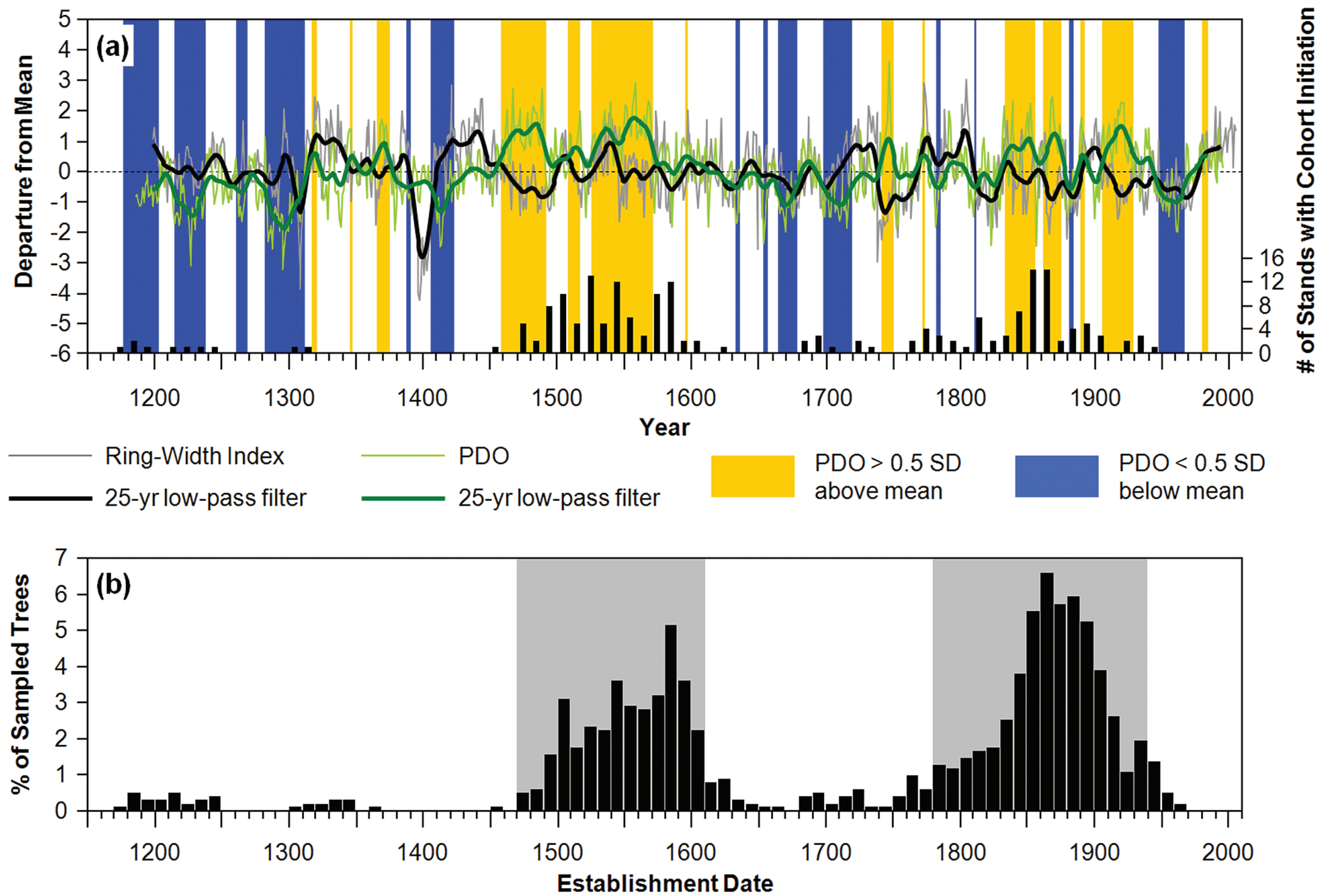

Figure 9-14. Comparison of (a) a tree-ring width chronology for some of the oldest Douglas-fir trees sampled in the central western Cascades of Oregon and a reconstruction of the Pacific Decadal Oscillation (PDO) (Tepley 2010). Yellow and blue shadings indicate extended warm and cold phases of the PDO, respectively. The histogram in the lower part of (a) shows the number of stands that recorded probable fire in that decade, based on an abrupt pulse of establishment. (b) Histogram of establishment dates for 1,030 Douglas-fir trees sampled at 124 stands in 2 watersheds, each totaling about 240/km. Gray shading indicates periods of abundant establishment that corresponds with regionwide periods of extensive fire (Tepley 2010).

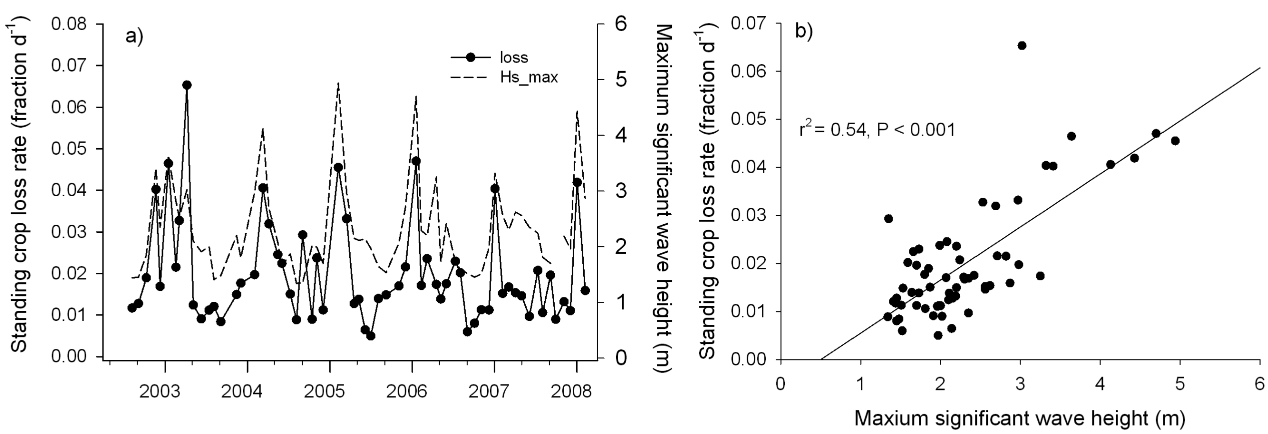

Figure 9-15. Wave disturbance and loss of kelp biomass off the coast of California, Santa Barbara Coastal (SBC). (a) The fraction of the standing crop of giant kelp lost per day each month at Mohawk Reef and the maximum significant wave height (Hs_{max}) during the monthly sampling interval. (b) The vast majority of kelp biomass lost episodically during winter when large waves remove entire plants, resulting in a strong positive relationship between the loss rate of kelp and maximum significant wave height. The lifespan of individual fronds is about 3 to 4 months, and the loss of fronds on surviving plants occurs continuously throughout the year. Wave data from NOAA Station 46053, E. Santa Barbara. Kelp data from Rassweiler et al. (2008).

Biotic Disturbances

Pest and pathogen outbreaks on plants and animals, and activities of animals that kill plants, as by burrowing, trampling, or herbivory are an important type of biotic disturbance. For example, feeding on the roots of perennial grasses by the larvae of june beetles (white grubs) resulted in patches of high mortality of the dominant grass (blue grama, *Bouteloua gracilis*) in 1977 at the SGS site in northern Colorado as compared with undisturbed areas (figure 9-16). Recovery of vegetation on grub-killed areas grazed by cattle and ungrazed areas were similar through time, in that perennial forbs dominated the patches in the first 3 years and were important components for the 14-year time period (Coffin et al. 1998).

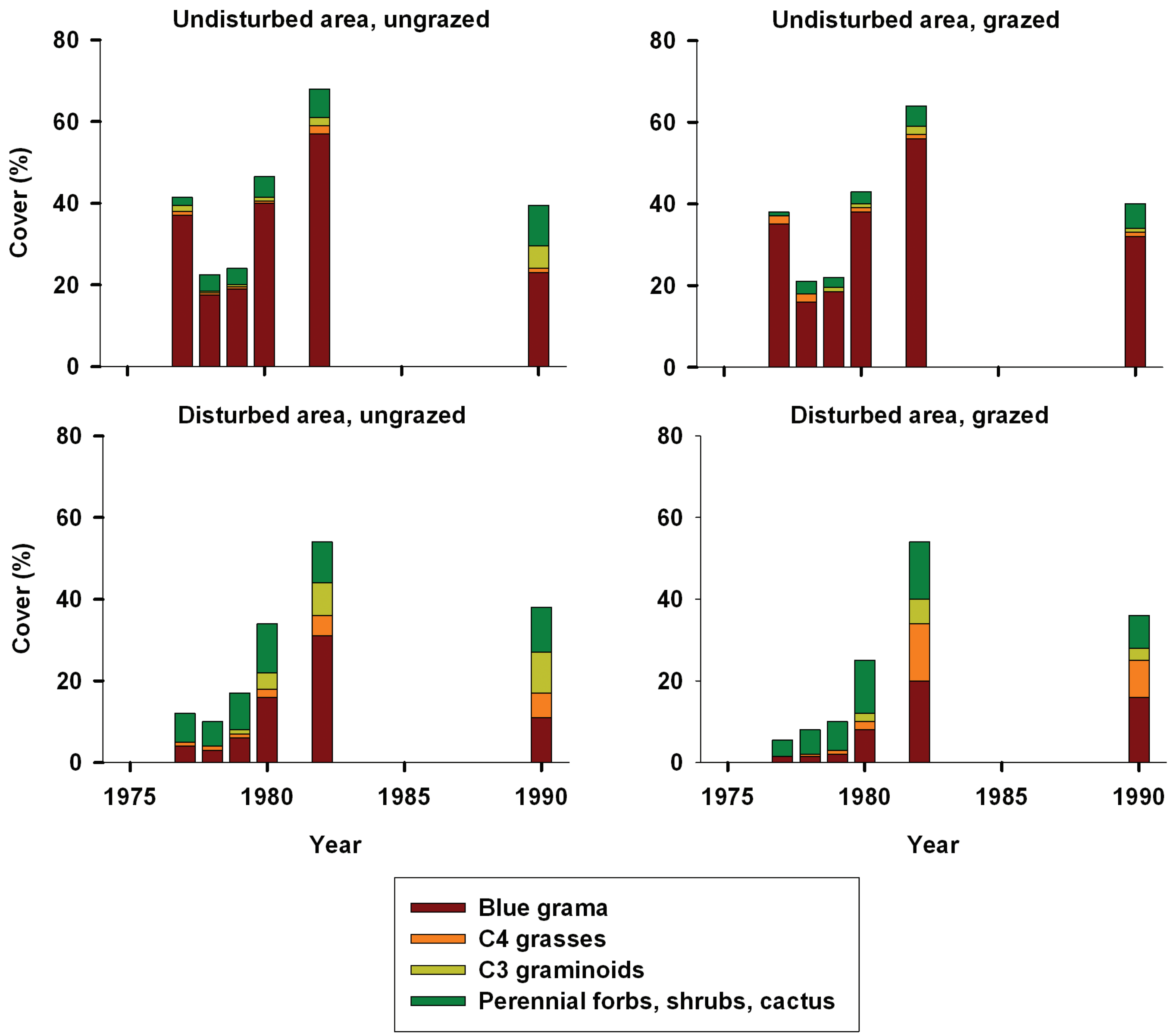

Figure 9-16. Recovery of vegetation at a shortgrass site (SGS) following plant mortality by the larvae of june beetles, a biotic disturbance, in 1977. Disturbed areas had greater percentage cover of perennial forbs and nondominant grasses compared with undisturbed areas that were primarily dominated by the warm-season perennial grass *Bouteloua gracilis* (blue grama). Areas grazed by cattle and adjacent ungrazed areas had similar patterns through time. Redrawn from Coffin et al. 1998.

A very different system, the coral reefs of French Polynesia (MCR), is experiencing a similar biotic disturbance as a result of a crown-of-thorns sea star outbreak that is killing live coral (figure 9-17). Comparison of permanent quadrats in 2006 and 2008 show the loss of coral over time. These biotic disturbances have important consequences for persistence of coral reefs, especially in combination with increasing ocean temperatures.

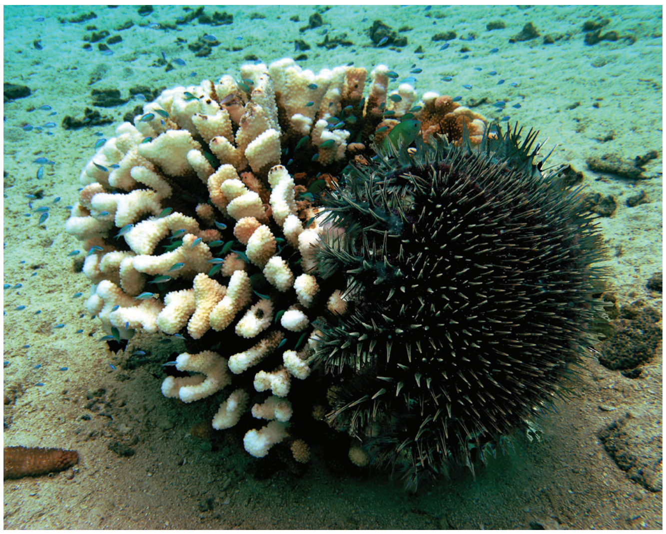

Figure 9-17. Crown-of-thorns sea star feeding on a live coral. Coral reefs of French Polynesia, Moorea Coral Reef (MCR), are experiencing a large crown-of-thorns sea star outbreak, which has decreased the cover of live coral on the reef from about 60 percent to less than 10 percent (P. Edmunds, unpublished data). Reprinted with permission from MCR.

Invasive species, either natives that expand their geographic distribution or introduced species that are transported from another region or continent, are increasingly recognized as disturbance agents. A well-documented example of the expansion of native plants is shrub encroachment into perennial grasslands in the American Southwest over the past 150 years. The expansion of shrubs is likely a result of overgrazing by livestock combined with herbivory by rabbits and extreme periodic droughts every 50-60 years. One approach to studying the recovery of perennial grasses is to remove livestock, rabbits, and shrubs from an area and then monitor vegetation as weather varies between drought and nondrought periods. In the Chihuahuan Desert, these studies show a time lag of 30-plus years before the dominant black grama responds following shrub removal; two other grass species have more variable responses (figure 9-18) (Havstad et al. 1999).

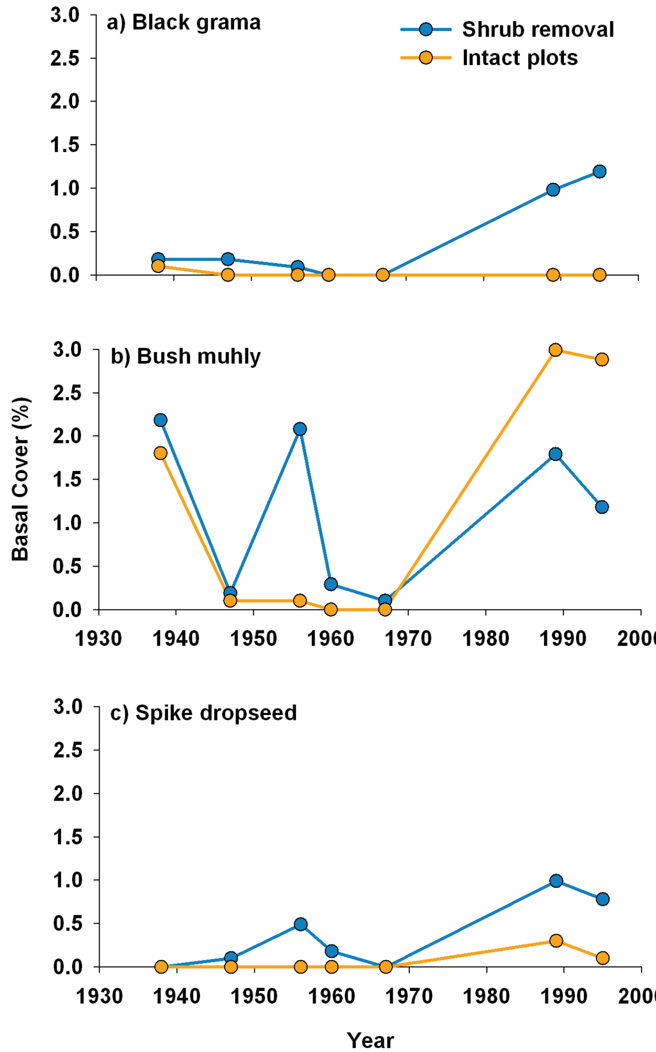

Figure 9-18. Basal cover of (a) black grama, (b) bush muhly, and (c) spike dropseed following shrub removal (blue) and on intact plots (orange) at a site in the northern Chihuahuan Desert, Jornada (JRN) (Havstad et al. 1999). Reprinted with permission from Elsevier.

Disease can make populations more vulnerable to disturbance. In the coastal bays of Virginia (VCR), populations of eelgrass *(Zostera marina)* once blanketed the seafloor and covered nearly 10,000 ha of Hog Island Bay. These populations were weakened in the early 1900s by a pandemic disease, marine slime mold “wasting disease.” In 1933, a large hurricane caused local extinction of the seagrass (Orth et al. 2006). Recovery did not begin until 1998. The time lag in recovery was due to the long distance to source populations and the limited dispersal potential of seagrass seeds. Restoration efforts by seeding since 2007 have resulted in 20 hectares of expanding seagrass meadows in Hog Island Bay. Adjacent coastal bays now have 570 hectares of seagrass meadows from restoration that began in 2001.

Anthropogenic Disturbances

Human activities have direct and indirect effects on the biota (Grimm et al. 2008b). Changing land use patterns are a direct influence. In Phoenix, AZ, (CAP) the land has been converted from mostly desert and agricultural land in 1912 to mostly urban starting in 1995 (figure 9-19) (Knowles-Yánez et al. 1999). Recreational areas have also increased over the past 25 years. Similar trends in increasing urban population are seen globally (Grimm et al. 2008a) and throughout the American Southwest (figure 9-20a) (Havstad et al. 2009). Land previously valued for livestock production is now being sold for housing developments at much higher prices than their value as rangeland. The result is that livestock density has decreased since 1950 for much of this region (figure 9-20b) (Havstad et al. 2009). The consequences of shifting lifestyles on ecosystem services, such as demands for high quality and quantity of water, biodiversity, air quality, and food production, are the subject of current research in many regions of the United States (Havstad et al. 2007, Sylvester and Gutmann 2008).

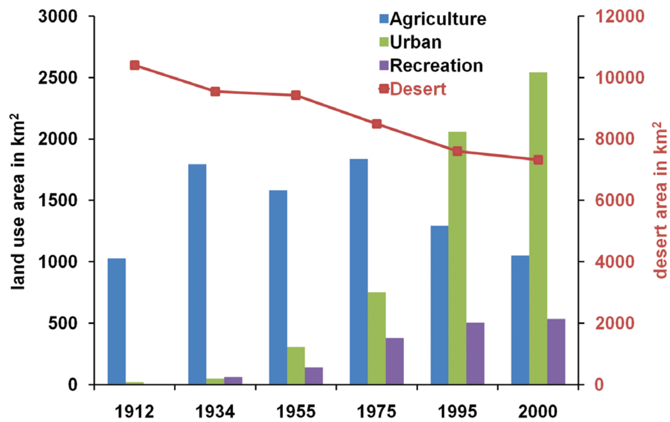

Figure 9-19. Over the past century, land in the Phoenix area, Central Arizona-Phoenix (CAP), has been converted from desert to agriculture, and ultimately to urban use. Data from Knowles-Yánez et al. (1999).

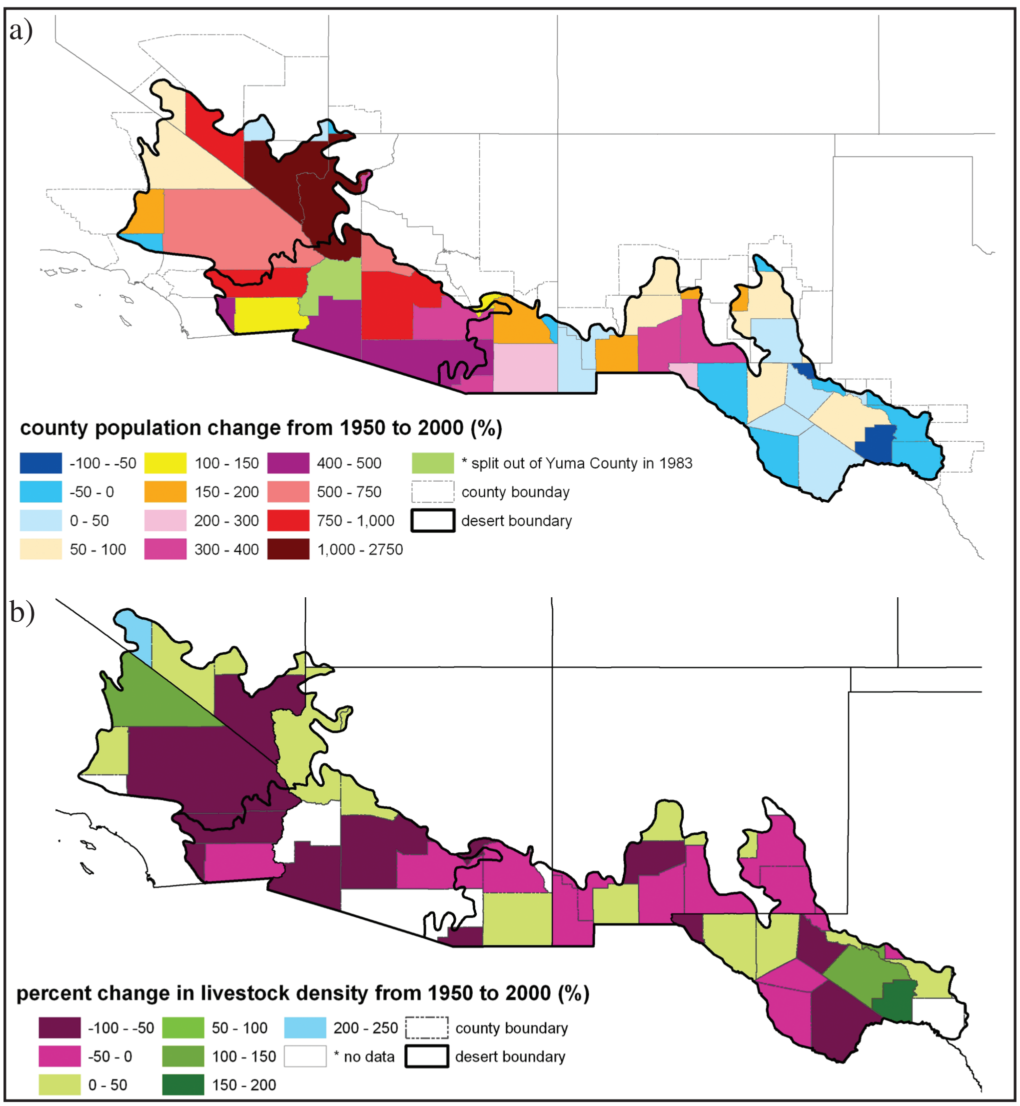

Figure 9-20. (a) Change in population as a percentage of the total from 1950 to 2000. (b) Change in livestock numbers by county for U.S. Bureau of Land Management allotments or districts between 1950 and 2000 for the United States Southwest (Havstad et al. 2009). Reprinted with permission from ASA-SSSA-CSSA.

Conclusions

Data available for a variety of sites where long-term responses to disturbance events are being monitored illustrate the complexity of these ecological phenomena. The information underscores the fact that ecosystems are continuously changing in response to complex disturbance regimes rather than to single events. Usually a particular event, such as a hurricane, fire, or species invasion, draws the attention of the public and ecologists; but invariably, when the response to the event is studied in detail, one finds that ecosystem responses are influenced by previous disturbances and interactions with others factors that make it very difficult to attribute cause and effect. Clearly, large-scale, multiple-site experiments are needed to further unravel the relationship between disturbance and ecosystem response.

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Chapter 10

Cross-Site Studies "By Design": Experiments and Observations That Provide New Insights

J. Yao, O.E. Sala, and D.P.C. Peters

In many cases, cross-site comparisons from similar experiments, often with different questions and designs, are conducted after the studies are completed to address new questions that require multiple sites. Here, we describe cross-site studies that are "by design" in which the questions, experimental layout, methods, and measurements included multiple sites from the beginning. Broad-scale questions and patterns can be addressed explicitly in these studies because the experiment or observation network was designed for comparisons among sites that are distributed spatially across one or more environmental gradients. The same design and methods of sampling allow powerful comparisons to be made without assumptions about differences in plot size, number, or sampling frequency and intensity on the results. However, these studies also have limitations:

- All sites need a similar experimental design, which can limit the types of questions that can be addressed.
- These studies typically involve large amounts of resources (time, personnel, supplies) that can limit the number of samples collected.
- Time and travel involved can also often limit graduate student involvement.
- Collaborators are needed at different sites for site selection and design details and to conduct the sampling and interpret the results.
- These studies often take longer to get started because of the coordinated efforts required by many people.

Cross-site studies are well suited to addressing large-scale questions that cannot be adequately addressed with local studies because of the uncertainties associated with extrapolation of results from one site to a much broader area. There has been a recent increase in the interest for large-scale ecological questions driven by the need to predict the consequences of global change on ecosystem functioning (IPCC 2007). Another independent demonstration of the increasing interest in regional- and continental-scale ecology is the emerging National Ecological Observatory Network (NEON) project that will be deployed throughout the continental United States (http://www.neoninc.org).

The objectives of this chapter are to present examples of the kinds of questions and results that require a priori cross-site experiments or observations and to describe new insights provided by these studies that would not have been possible with cross-site comparisons conducted from existing studies.

There are two types of cross-site studies described below: experimental manipulations of drivers or system properties and observations or monitoring of natural or managed ecosystems located along environmental gradients.

Experimental Manipulations of Ecosystems

Ongoing or Completed Cross-Site Experiments

Temperature manipulations. Global warming is occurring as a result of elevated concentrations of carbon dioxide and other greenhouse gases in the atmosphere (IPCC 2007). Regions of particular concern for increasing air temperatures are the Arctic and Antarctic, where ecosystems are dominated by cold-adapted plants and animals. The International Tundra Experiment was designed to study how ecosystems in arctic and alpine tundra respond to experimental warming (http://www.geog.ubc.ca/itex). At present, the project includes 50 sites from 13 countries (including three LTER sites) located in Antarctica (MCM), Asia, Australia, Europe, and North America (NWT, ARC). Each site follows standard protocols for experimental design. Response variables include those at the individual level (for example, height and cover of plants) and at the community level (for example, plant species richness). In one key result, canopy height and cover of deciduous shrubs and graminoids increased with elevated air temperature, and cover of mosses and lichens decreased; species richness and evenness decreased (figure 10-1) (Walker et al. 2006).

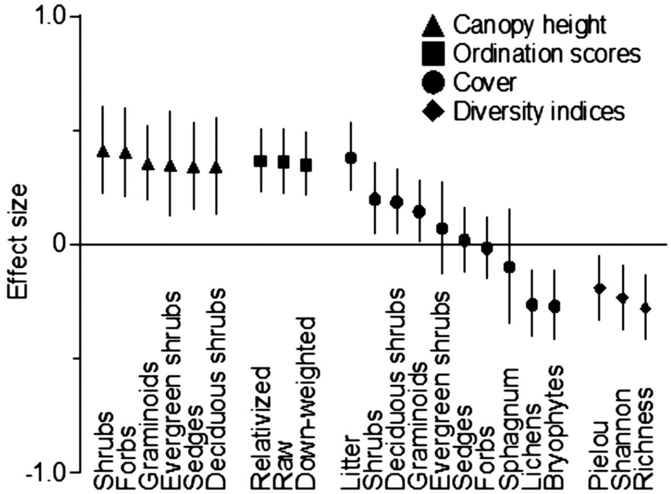

Figure 10-1. Effects of elevated air temperature on alpine and arctic tundra plants at 11 International Tundra Experiment (ITEX) sites. The mean effect size and the 95 percent confidence interval were obtained from meta-analyses of 22 variables (Walker et al. 2006). Reprinted with permission from the National Academy of Sciences, USA.

CO_2 manipulations. Effects of increasing atmospheric carbon dioxide (CO_2) on ecosystems is being studied using the Free Air CO_2 Enrichment technology that has been adopted by 30 sites in 16 countries in Australia, Asia, Europe, and North America, including one LTER site (CDR) (http://public.ornl.gov/face/). The technology allows plant and ecosystem responses to elevated CO_2 concentration to be studied under natural conditions. Examples of response variables include plant photosynthesis and respiration and plant and soil nitrogen and carbon dynamics (Nösberger et al. 2006). Recent analyses from four sites showed that the forest's net primary production (NPP) increased at a median of 23 percent at an elevated CO_2 concentration (550 ppm) compared to forests growing under current CO_2 concentration (figure 10-2a) (Norby et al. 2005). The increase in NPP at the lower end of production was due to an increase in the ability of plants to absorb more light, as measured by Absorbed Photosynthetically Active Radiation (APAR), while the increase in NPP at the higher end was due to increase in plants' efficiency in using light (figure 10-2b).

Nutrient manipulations in streams. The Lotic Intersite Nitrogen Experiment (LINX) was designed to examine how hydrodynamic, chemical, and metabolic characteristics of streams control nitrogen uptake, retention, and cycling through the experimental addition of a stable isotope of nitrogen (^{15}N) (http://www.biol.vt.edu/faculty/webster/linx/). Ten U.S. sites participated in LINX 1 (1996 to 2001). During LINX 2 (2001-2006), effects of land use on nitrogen cycling

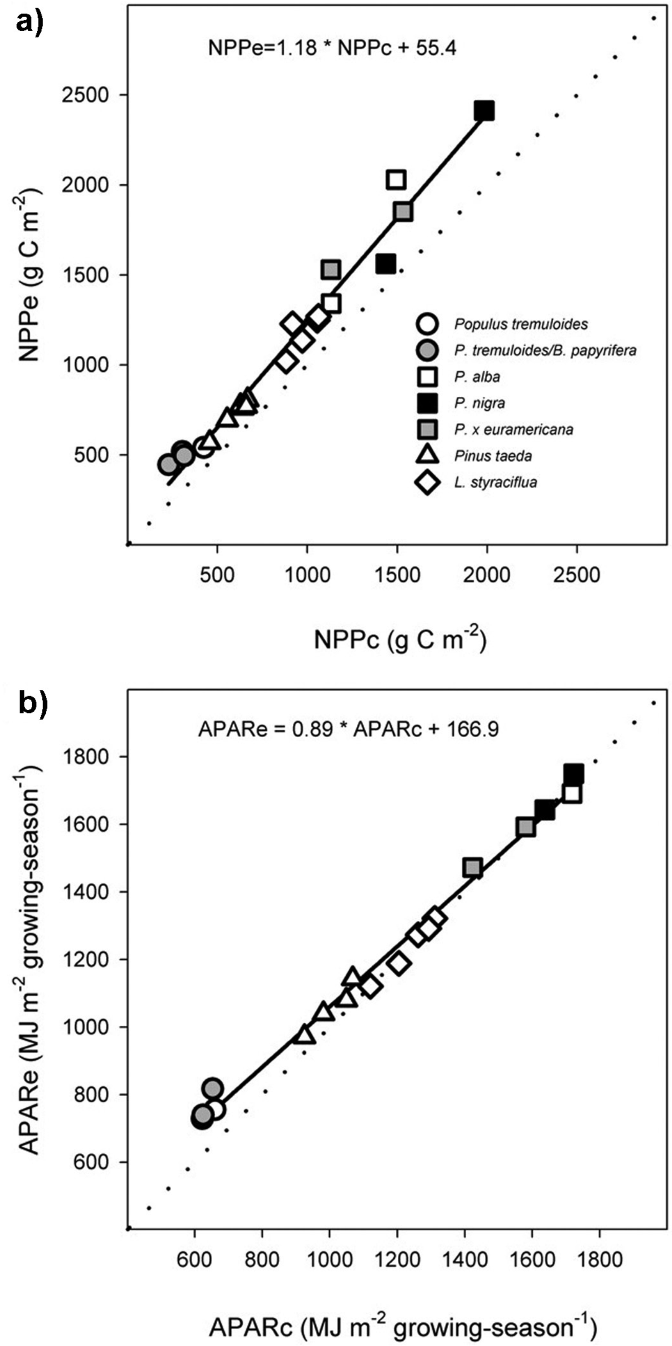

Figure 10-2. Effect of elevated CO2 concentration on forest primary production of seven species at four sites using Free Air CO_2 Enrichment (FACE) technology (Norby et al. 2005). (a) Comparison of forest net primary production at elevated (550 ppm, NPP_e) and current CO_2 concentrations (376 ppm, NPP_c). Regression: $R^2 = 0.97$, $p<0.001$, slope is significantly different from 1. (b) Comparison of absorbed photosynthetically active radiation at elevated ($APAR_e$) and current CO2 concentrations ($APAR_c$). Regression: $R^2 = 0.99$, $p<0.001$, the slope is significantly different from 1. Reprinted with permission from the National Academy of Sciences, USA.

were examined across 72 streams at 9 U.S. sites. Each site measured nitrogen uptake and denitrification rates as well as potential explanatory variables including physical, chemical, and biological characteristics of a stream and rates of stream metabolism by algae and microbes. Streams from agricultural and urban areas were found to contain higher concentrations of nitrate (NO_3^-) than streams from areas with vegetation typical of the biome (figure 10-3a) (Mulholland et al. 2008). The rates of total biotic nitrate uptake, one of two ways of nitrogen removal in streams, were higher in streams from agricultural and urban areas (figure 10-3b), stimulated by the increased nitrate concentrations. However, the nitrate uptake efficiency decreased with increasing nitrate concentration.

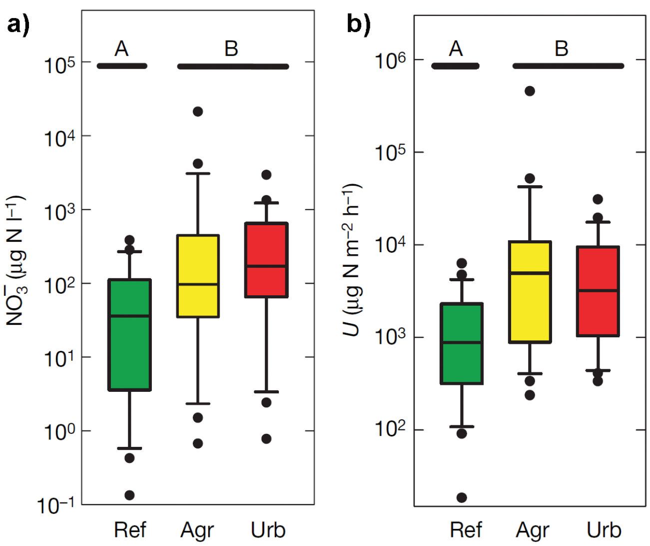

Figure 10-3. Nitrogen in streams located in different areas in the LINX2 project (Mulholland et al. 2008). (a) Nitrate (NO_3^-) concentration. (b) Total biotic nitrate uptake rate. Ref: streams in areas with vegetations typical of the biome; Agr: streams adjacent to agricultural practices; Urb: streams in urban areas. Reprinted with permission from Macmillan Publishers Ltd.

Animal removal. Removal of animals combined with monitoring of environmental variables has been used to investigate interactions among components of ecosystems that show similarities across sites. For example, results of removing seed-eating rodents or ants from desert shrublands were compared with removal of insect herbivores in a tree-dominated system (Brown et al. 2001). Each system was monitored for over 20 years; data recorded included variable precipitation. In the desert site (Portal, AZ), interactions were found among precipitation, food supply, and rodent populations. At the forest site (Sunset Crater, AZ), complex dynamics emerged from the interactions among abiotic stress, dominant tree growth and morality, keystone herbivores, and other trophic levels (Brown et al. 2001).

These results were used as the basis for an ongoing study at three sites in the Chihuahuan Desert: Sevilleta LTER (SEV), Jornada Basin LTER (JRN), and Mapimi Biosphere Reserve near Durango, Mexico (D.C. Lightfoot, unpublished data). The project was initiated in 1993 to experimentally determine how small mammals affect Chihuahuan Desert ecosystems, either grasslands or shrublands, and how small mammals are affected by climate change (http://tierra.unm.edu/projects/chihuahuan-desert-small-mammal-exclosure).

Litter manipulation. Litter decomposition is an important ecosystem process in which biochemical molecules in plants are broken down by microorganisms and made available in simpler forms for uptake by other organisms. The Long-Term Intersite Decomposition Experiment Team (LIDET) studied the effects of substrate quality (species and type of litter) and climate on long-term decomposition and nitrogen accumulation in litter (http://andrewsforest.oregonstate.edu/research/intersite/lidet.htm). Twenty-eight sites from seven biomes, including 15 LTER sites, followed the same methods. Response variables included litter mass, total nitrogen, lignin, and cellulose in material remaining in litter bags. Results during a 10-year period found that net nitrogen immobilization and release from leaf litter in six of the seven biomes depended strongly on initial nitrogen concentration in litter but did not depend on climate, other litter qualities, or local site characteristics (Parton et al. 2007). At high initial nitrogen concentration in leaf litter (1.98 percent), net nitrogen immobilization was close to 0; nitrogen release started when about 60 percent of the mass remained in a litter bag (figure 10-4a). At low initial nitrogen concentration (less than 0.39 percent), net nitrogen immobilization was high, and nitrogen release started when about 40 percent of the mass remained in a litter bag (figure 10-4d).

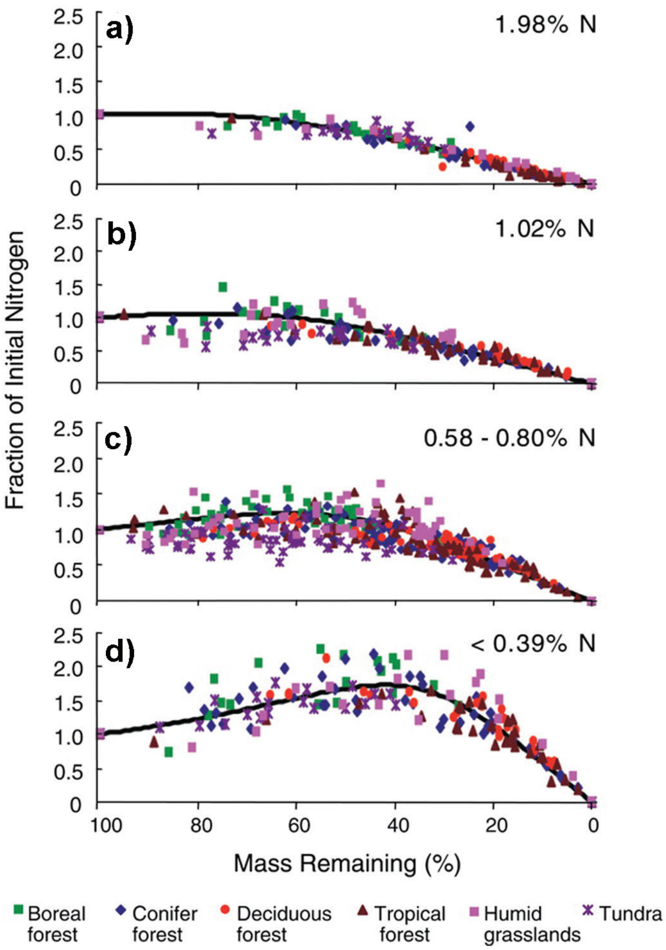

Figure 10-4. Pattern of nitrogen (N) immobilization and release from the LIDET study depends on the initial N concentration of leaf litter, shown as percentage in the upper right corner of each panel (Parton et al. 2007). N immobilization refers to the conversion of N from inorganic (usable by plants and microbes) to organic form (not usable). N release refers to the conversion of N from organic to inorganic form. Values of fraction of initial N > 1 indicate N immobilization while values < 1 indicate N release. Reprinted with permission from AAAS.

Biodiversity manipulations. Long-term studies that manipulated species richness in grasslands at the CDR LTER site found that aboveground net primary productivity (ANPP) and biomass increase as species richness (biodiversity) increases (Tilman et al. 1997, 2001, Reich et al. 2004, Fargione et al. 2007, Fornara and Tilman 2009). Similar biodiversity manipulations were conducted in Europe for eight sites in the Biodiversity and Ecological Processes in Terrestrial Herbaceous Ecosystems (BIODEPTH) project. Results confirmed the patterns found at CDR: ANPP increased as plant species richness increased at seven sites. The effect of biodiversity on production became stronger over time at most sites (Hector et al. 1999, Spehn et al. 2005). However, comparisons across ecosystem types have shown that the relationship between productivity and richness can take a variety of forms (Mittelbach et al. 2001).

New or Developing Cross-Site Experiments

Nutrient additions in grasslands. Nutrient Network is being designed to study the effects of nutrient (nitrogen, phosphorus, and potassium) additions in grasslands (http://nutnet.science.oregonstate.edu/). The research questions are:

- How general is current understanding of productivity-diversity relationships?
- To what extent are plant production and diversity co-limited by multiple nutrients in herbaceous-dominated communities?
- Under what conditions do grazers or fertilization control plant biomass, diversity, and composition?

All sites follow the same experimental protocol and collect similar data (Adler et al. 2011). The project started in 2009 with 52 sites in eight countries in Africa, Asia, Australia, Europe, and North America, including six LTER sites (AND, CDR, KNZ, NWT, SEV, SGS).

Anthropogenic manipulations in streams. A stream experimental and observational network (STREON) is part of the emerging NEON program. This study is expected to examine effects of nutrient loading, species losses, and hydrologic change on the structure and functioning of streams (http://www.neoninc.org/science/experiments). All sites will follow the same experimental protocols. Natural hydrologic events (flood and drought) will be recorded. Biological variables and other variables related to material flux and rates of nutrient transformations and metabolism are expected to be measured (Dodds 2008).

Rainfall manipulations. Rainfall is the most important determinant of ANPP in grasslands, steppes, and deserts (Sala et al. 1988). Manipulations of rainfall are often used to study how systems may respond in the future under altered rainfall regimes (IPCC 2007). Most rainfall manipulations require expensive installations that constrain the spatial extent of the manipulation, the number of replications, and the power of the experimental design (Hanson 2000). An inexpensive rainout shelter design (Yahdjian and Sala 2002) has recently been adopted in many locations around the world, from South Africa and Patagonia to the Alaskan Tundra (figure 10-5), including three LTER sites (JRN, SGS, ARC). These experiments use the same method to manipulate incoming precipitation, although there is not a formal network of rainfall manipulations. Future synthesis of results is expected to provide unique insights into the response of ecosystems to water availability along gradients of temperature and precipitation.

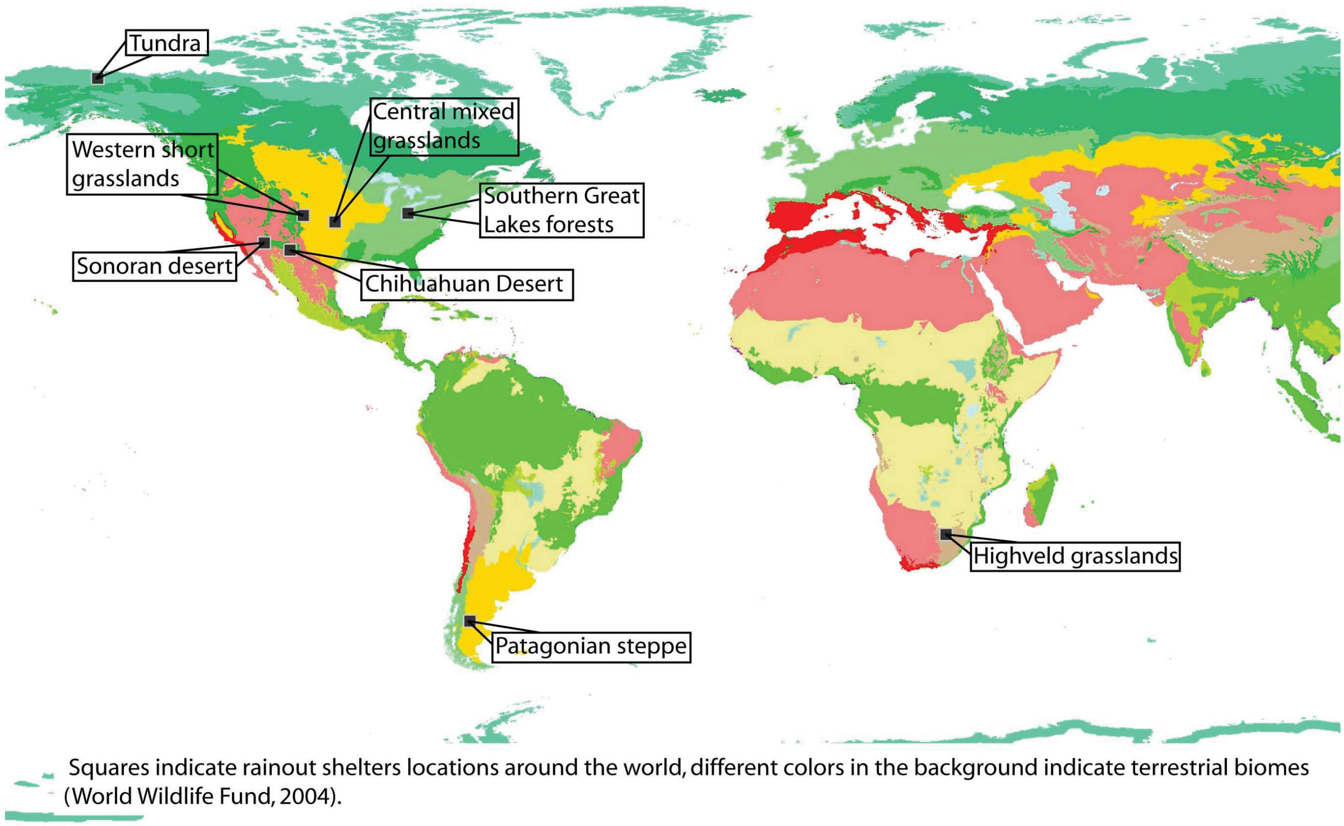

Figure 10-5. Sites using the rainout shelter design of Yahdjian and Sala (2002).

Monitoring of Ecosystems

Ongoing Monitoring Networks

Observations of the environment, such as climate (http://www.ncdc.noaa.gov), atmospheric chemistry (http://nadp.sws.uiuc.edu/NADP/), and human populations (http://census.gov) have been made in the United States over the past century or longer. Data from these networks form the basis for cross-site comparisons in chapters 11 to 14. Here we focus on networks of sites collecting information about ecosystem dynamics in response to these environmental and human drivers.

Carbon dioxide and water vapor fluxes. Two existing networks of sites are collecting data on carbon, water, and energy fluxes. The two networks use different technology to address similar questions.

The Rangeland Carbon Dioxide Flux Project is examining the effect of management practices on the global carbon balance for eight U.S. sites (including one ARS-LTER site: JRN) (Svejcar et al. 1997). The Bowen ratio-energy balance system is being used to measure energy, water vapor, and carbon dioxide fluxes. An analysis of net ecosystem exchange of carbon during 1996-2001 showed that five sites are sinks for atmospheric CO_2 (figure 10-6) (Svejcar et al. 2008). The three sites that are sources of atmospheric CO_2 are in the Great Plains and Southwestern deserts of the United States.

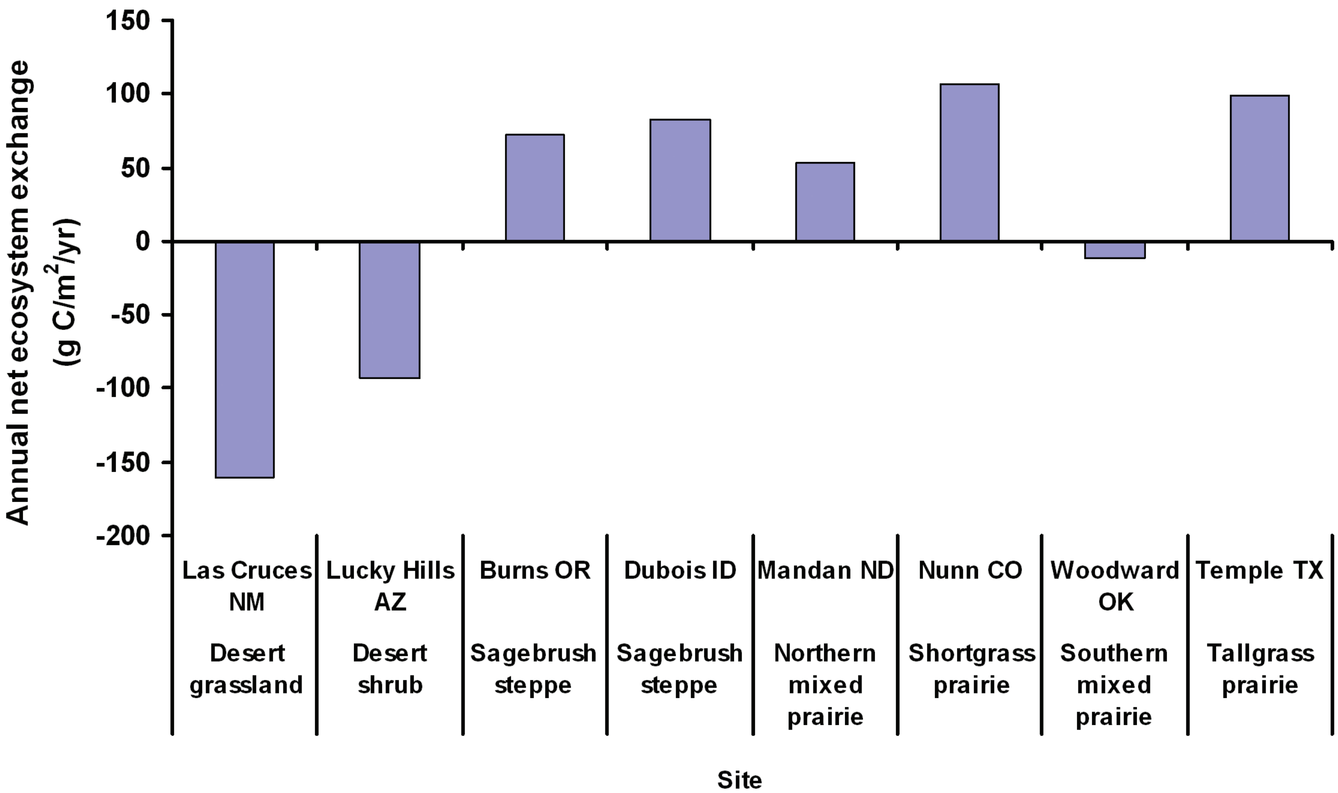

Figure 10-6. Average annual net ecosystem exchange of carbon (g/m/yr) at eight sites from the rangeland carbon dioxide flux project. Sites with positive values are carbon sinks because carbon accumulates in vegetation and soil. Sites with negative values are sources of atmospheric carbon dioxide because carbon is released into the atmosphere. Two ARS-LTER sites are included: desert grassland (JRN) and shortgrass prairie (SGS). Data from Svejcar et al. (2008).

FLUXNET is a network of regional networks monitoring carbon dioxide and water vapor fluxes in terrestrial ecosystems using eddy covariance towers, an alternative approach to Bowen ratio systems (http://www.fluxnet.ornl.gov/fluxnet/). The goals are to characterize spatial and temporal variation in CO_2 and water vapor fluxes and to understand the drivers causing this variation. Started in the 1990s, currently more than 500 sites in Africa, Asia, Australia, Europe, and North and South America participate. Variables related to vegetation, soil, hydrology, and meteorology are collected. The first global standardized dataset was established in 2007 (http://www.fluxdata.org/).

The AmeriFlux network, started in 1996, is a network within FLUXNET (http://public.ornl.gov/ameriflux/). Its research questions are—

- What are the magnitudes of carbon storage and the exchanges of energy, CO_2, and water vapor in terrestrial systems? What are the spatial and temporal variability?
- How is this variability influenced by vegetation type, phenology, land use change, management, and disturbance history, and what is the relative effect of these factors?
- What is the causal link between climate and the exchanges of energy, CO_2, and water vapor for major vegetation types? How do seasonal and interannual climate variability and anomalies influence fluxes?
- What is the spatial and temporal variation of boundary layer CO_2 concentrations, and how does this vary with topography, climatic zone, and vegetation?

Currently the AmeriFlux network consists of 133 sites in 5 countries in North and South America.

New or Developing Monitoring Networks

A number of observational networks have emerged over the past decade to collect similar ecological data from a number of sites (Peters et al. 2008). Existing or emerging networks funded at least in part by the National Science Foundation to collect ecologically relevant data from U.S. sites include the Ocean Observatories Initiative (OOI; http://www.oceanleadership.org/programs-and-partnerships/ocean-observing/ooi/), WATERS Network (http://www.watersnet.org), the Arctic Observing Network (AON; http://www.arcus.org/search/aon.html), the Global Lakes Ecological Observatory Network (GLEON; http://www.gleon.org/), and the National Phenology Network (http://www.usanpn.org/). Here we describe in more detail two networks that include a number of LTER sites, NEON and the Microbial Inventory Research Across Diverse Aquatic (MIRADA) LTERs.

NEON is being designed to study the effects of land use, climate change, and invasive species on structure and functioning of ecosystems in the United States (http://www.neoninc.org/). Observational data will be collected from sites selected to represent one of 20 eco-climatic domains based on vegetation, landform, and climate. All sites will follow the same sampling protocols and collect the same core data, expected to include biological, hydrological, and atmospheric variables (Keller et al. 2008). NEON sites will also use eddy covariance towers to study carbon, water, and energy fluxes, similar to the AmeriFlux network.

The MIRADA LTERs started in 2007 with the goal of building an inventory of microbial operational taxonomic units in marine and freshwater ecosystems (http://amarallab.mbl.edu/mirada/). Both diversity and relative abundance of microbes will be documented, and the physical and chemical drivers behind the observed patterns of microbial diversity will be studied. The project includes 13 LTER sites that study aquatic ecosystems. All sites use a standardized gene sequencing protocol.

Summary

This chapter has presented examples of cross-site experimental manipulations and observations that have yielded unique and extraordinary results. Insights resulting from these cross-site experiments could not have been obtained with another approach. Cross-site experiments allow scientists to address large-scale questions and to isolate cause-and-effect relationships, which are more difficult in observational studies. The importance of large-scale studies across sites has grown in the last decade as society has recognized the need to understand the phenomenon of global change and to predict its impacts on ecosystems and society (MEA 2005). Global change is a large-scale phenomenon that demands studies at this scale (IPCC 2007). However, not all studies can be done at a large scale. For example, elevated carbon dioxide studies can be done only in small plots. Replication across sites provides the means to address differential responses that occur at large scales.

Cross-site experimentation is an ideal tool to address novel and urgent questions, yet this approach faces some difficulties. Costs are usually higher than standard experiments and require major investments in coordination. In addition, funding opportunities for cross-site experimentation are scarce compared with standard grants. Funding agencies and the academic community may need to modify their approaches to allow for this new type of research tool to flourish and yield the results that society demands.

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