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Long-Term Trends in Ecological Systems: A Basis for Understanding Responses to Global Change



Contents

Contributors	VIII
Technical Consultants	X

Introduction to Cross-Site Comparisons and History and Organization of the EcoTrends Project

Chapter 1: Long-Term Trends in Ecological Systems: An Introduction to Cross-Site Comparisons and Relevance to Global Change Studies	1
Chapter 2: History and Organization of the EcoTrends Project	21

Cross-Site Comparisons of Ecological Responses to Global Change Drivers

Chapter 3: Cross-Site Comparisons of Ecological Responses to Climate and Climate-Related Drivers	28
Chapter 4: Cross-Site Comparisons of State-Change Dynamics	36
Chapter 5: Patterns of Net Primary Production Across Sites	42
Chapter 6: Cross-Site Comparisons of Precipitation and Surface Water Chemistry	46
Chapter 7: Cross-Site Comparisons of Ecological Responses to Long-Term Nitrogen Fertilization	51
Chapter 8: Long-Term Trends in Human Population Growth and Economy Across Sites	54
Chapter 9: Disturbance Regimes and Ecological Responses Across Sites	58
Chapter 10: Cross-Site Studies “By Design”: Experiments and Observations That Provide New Insights	72

Long-Term Trends in Global Change Drivers and Responses at Site and Continental Scales

Chapter 11: Long-Term Trends in Climate and Climate-Related Drivers	81
Chapter 12: Long-Term Trends in Precipitation and Surface Water Chemistry	115
Chapter 13: Long-Term Trends in Human Demography and Economy Across Sites	162
Chapter 14: Long-Term Trends in Production, Abundance, and Richness of Plants and Animals	191
Chapter 15: Management and Policy Implications of Cross- and Within-Site Long-Term Studies	206
Chapter 16: Recommendations for Data Accessibility	216
Chapter 17: Long-Term Research Across Sites, Ecosystems, and Disciplines: Synthesis and Research Needs	226

Appendices

Appendix 1: Site Descriptions	234
Appendix 2: Average (Standard Error) Maximum, Mean, and Minimum Air Temperature and Annual Precipitation at Each Site	312

Appendix 3: Average (Standard Error) Ice Duration, Sea Level, Streamflow, Water Clarity, and Water Temperature for Sites With Data	314
Appendix 4: Regression Coefficients and R ² Values for Nine Climatic Variables for Which Linear Regression Against Time Is Significant (p < 0.05)	316
Appendix 5: Annual Average (Standard Error) Nitrogen (as Nitrate) From Various Sources at Sites With Data	319
Appendix 6: Regression Coefficients and R ² Values for Nitrogen (as Nitrate) From Various Sources for Which Linear Regression Against Time Is Significant (p < 0.05)	321
Appendix 7: Annual Average (Standard Error) Nitrogen (as Ammonium) From Various Sources at Sites With Data	323
Appendix 8: Regression Coefficients and R ² Values for Nitrogen (as Ammonium) From Various Sources for Which Linear Regression Against Time Is Significant (p < 0.05)	325
Appendix 9: Annual Average (Standard Error) Sulfur (as Sulfate) From Various Sources at Sites With Data	326
Appendix 10: Regression Coefficients and R ² Values for Sulfur (Sulfate) From Various Sources for Which Linear Regression Against Time Is Significant (p < 0.05)	328
Appendix 11: Annual Average (Standard Error) Chloride From Various Sources at Sites With Data ..	330
Appendix 12: Regression Coefficients and R ² Values for Chloride From Various Sources for Which Linear Regression Against Time Is Significant (p < 0.05)	332
Appendix 13: Annual Average (Standard Error) Calcium From Various Sources at Sites With Data ...	334
Appendix 14: Regression Coefficients and R ² Values for Calcium From Various Sources for Which Linear Regression Against Time Is Significant (p < 0.05)	336
Appendix 15: Human Population and Economy Variables in 2000 for the Focal County of Each Site, as Grouped by Ecosystem Type	338
Appendix 16: Annual Average (Standard Error) Aboveground Net Primary Production (ANPP) at Sites With Data	341
Appendix 17: Other Measures of Average (Standard Error) Terrestrial Production at Sites With Data..	343
Appendix 18: Average (Standard Error) Aquatic Production at Sites With Data	344
Appendix 19: Average (Standard Error) Biomass of Primary Producers (Plants, Algae) for Sites With Data	345
Appendix 20: Average (Standard Error) Plant Species Richness for Sites With Data	347
Appendix 21: Average (Standard Error) Animal Abundance for Sites With Data	349
Appendix 22: Average (Standard Error) Animal Species Richness for Sites With Data	352
Appendix 23: Regression Coefficients and R ² Values for Plant and Animal Variables for Which Linear Regression of Each Variable Against Time Is Significant (p < 0.05) and the Trend Appears Linear	353
Appendix 24: Lead Principal Investigator(s) (PI), Information Managers (IM), and Administrative Program of the LTER Programs	355
Appendix 25: Researchers Involved in the EcoTrends Project at Non-LTER Sites	359

Appendix 26: List of Stations and Length of Record for Each Climate Variable by Site 362

Appendix 27: List of Stations and Length of Record for Each Precipitation or Surface Water
Chemistry Variable by Site 367

Appendix 28: List of Stations and Length of Record for Each Plant and Animal Variable by Site, as
Grouped by Ecosystem Type 371

Index i

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.

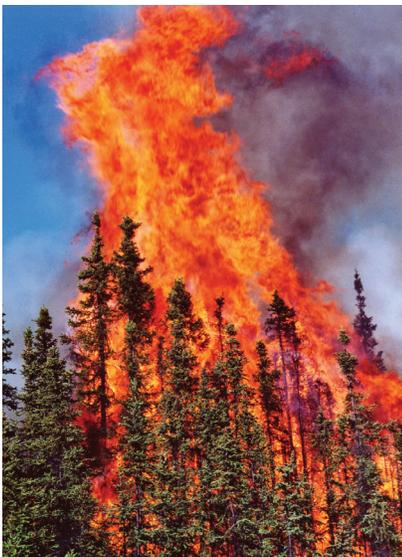
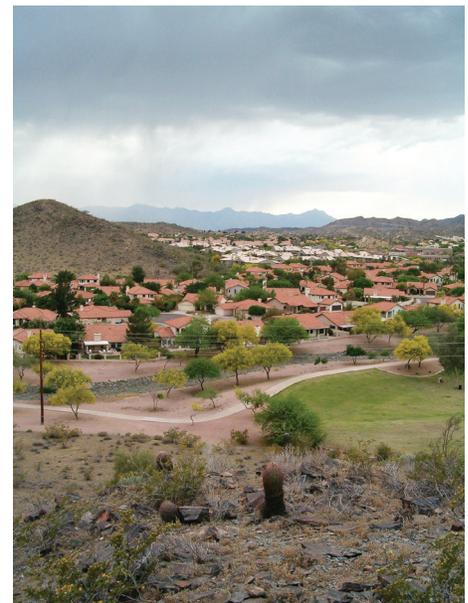


Figure 9-1. Examples of four classes of disturbance based on the type of driver. Top left: Physical—wildfire in Alaska, Bonanza Creek Experimental Forest (BNZ), photo by F. Chapin. Top right: Climatic—hurricane in Puerto Rico, Luquillo Experimental Forest (LUQ), photo by N. Brokaw. Bottom left: Biotic—salt 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).

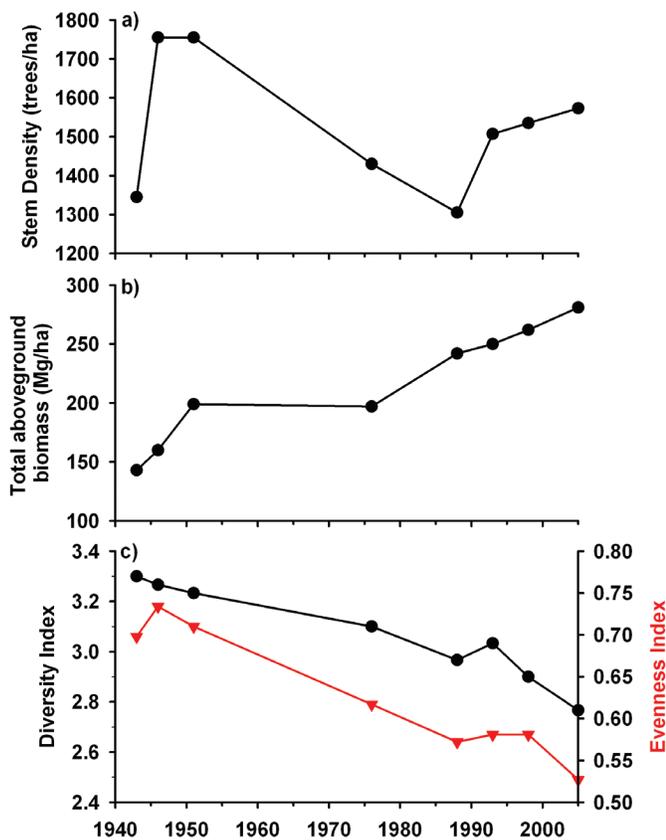


Figure 9-2. (a) Tree stem density; (b) total aboveground biomass (leaves and wood); and (c) Shannon-Weiner plant species diversity (black line) and overall evenness index (Pielou's J) (red line) of trees through time in Puerto Rico, following a hurricane in 1930, Luquillo Experimental Forest (LUQ). Two 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.

Long-Term Trends in Ecological Systems:

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.

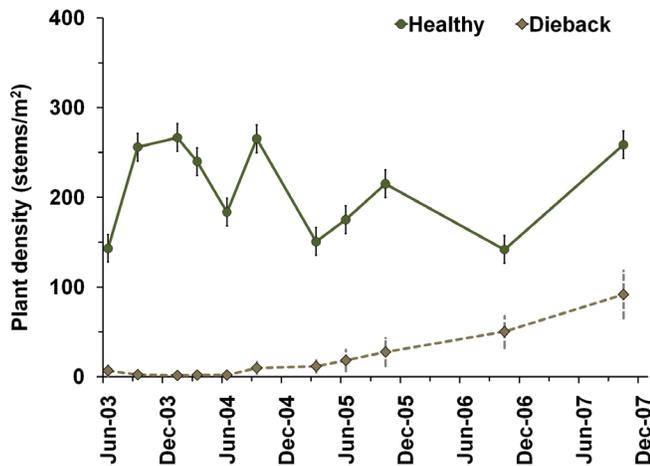


Figure 9-3. Regrowth of *Spartina alterniflora* at a marsh dieback site in coastal Georgia (GCE). Samples collected at dieback (dashed line) and nearby healthy (solid line) areas (Alber et al. 2008). Reprinted with permission from Elsevier.

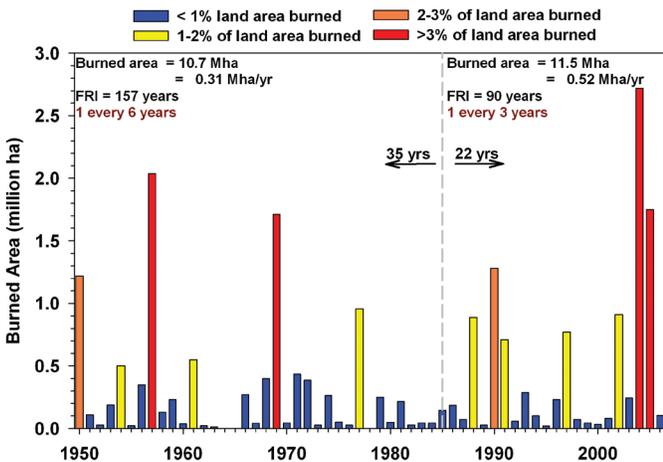
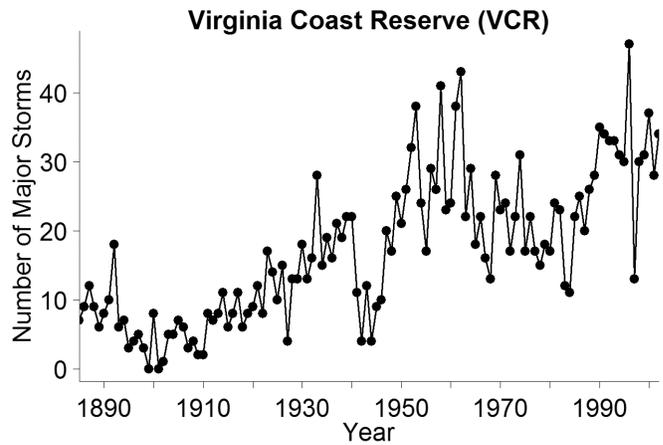


Figure 9-4. Area burned in North America's northern forest, which spans Alaska and Canada, tripled from the 1960s (Fire Return Interval [FRI] 1 every 6 years) to the 1990s (FRI 1 every 3 years). Two of the three most extensive wildfire seasons in Alaska's 56-year record, based on area burned, occurred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



Shoreline Change on Hog Island, VA 1852-2001

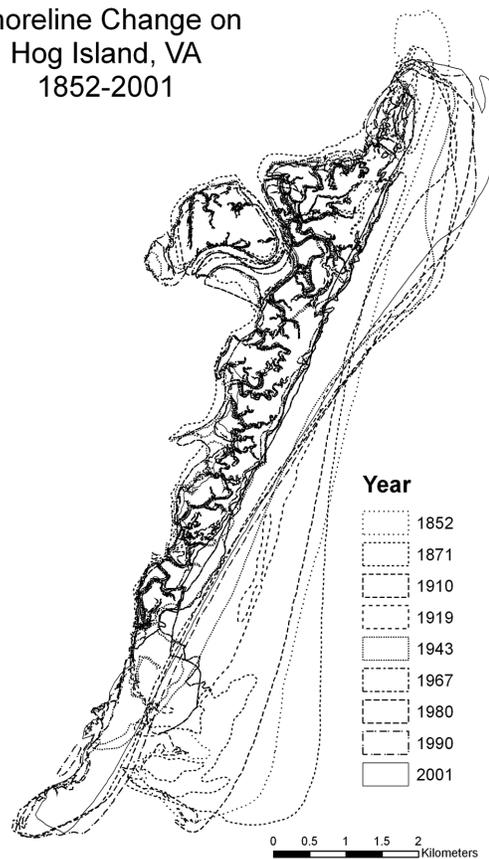


Figure 9-5. Number of major storms along the coast of Virginia, Virginia Coast Reserve (VCR), has increased since 1950 (top: modified from Hayden and Hayden 2003; data from <http://amazon.evsc.virginia.edu>) with associated changes in the shoreline of Hog Island, VA (bottom: modified from Harris 1992, 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).

A Basis for Understanding Responses to Global Change

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).

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.

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).

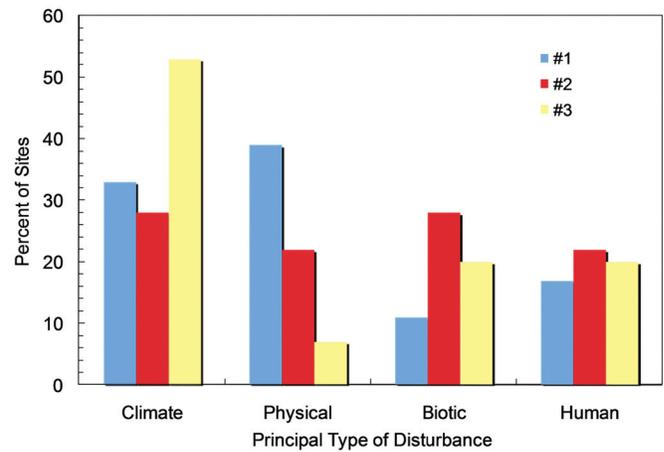


Figure 9-6. In a survey of lead scientists from the 26 LTER sites, physical and climatic disturbances were identified as the most important classes at their site (ranked #1). All four disturbance classes were equally important as the second most important type (ranked #2) (Peters et al. 2011).

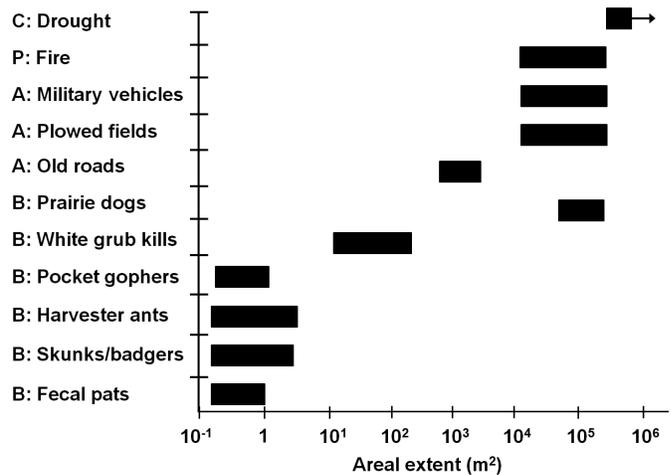


Figure 9-7. The disturbance regime in the Shortgrass Steppe (SGS) consists of all four types of disturbances that vary in spatial extent: C, climatic; P, physical; A, anthropogenic; and B, biotic. Modified from Peters et al. 2008.

Long-Term Trends in Ecological Systems:

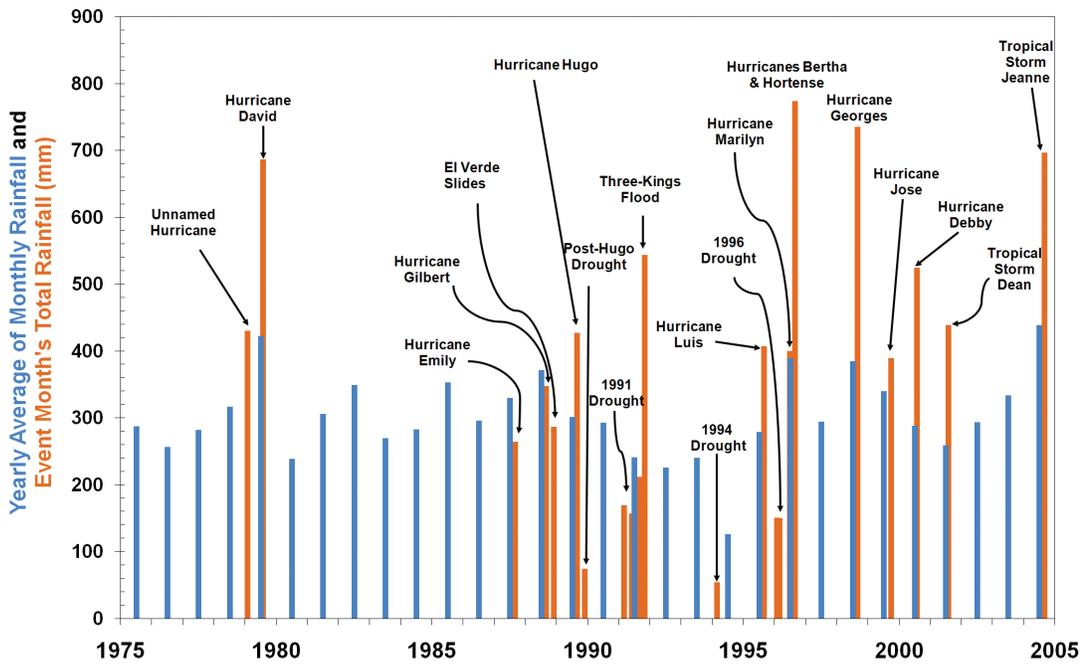


Figure 9-8. Multiple disturbance types often occur at one site as parts of the disturbance regime, for example, at Luquillo Experimental Forest (LUQ). However, physical disturbances (hurricanes) are the most prevalent at LUQ. Data from W. McDowell, D. Schaefer, A. Estrada-Pinto, A. Ramírez, and National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

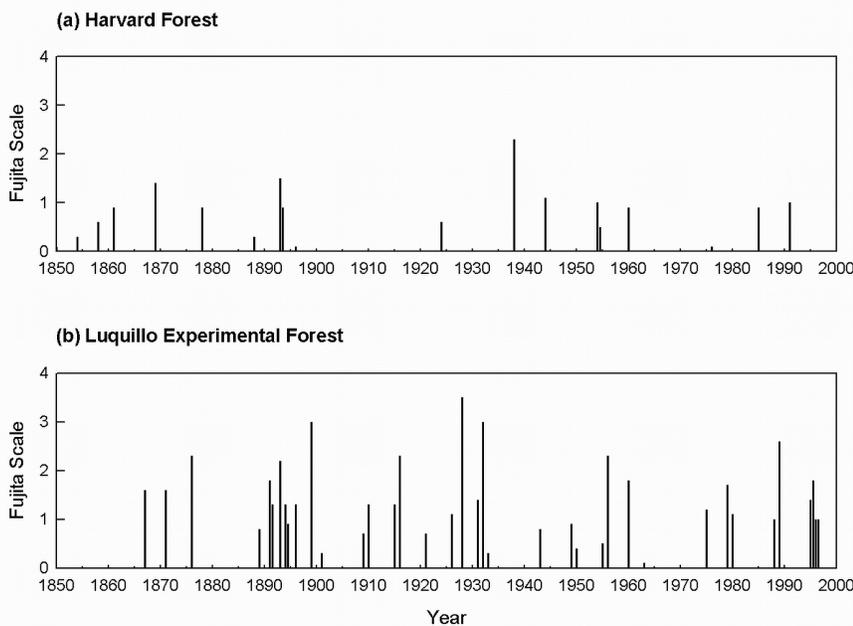


Figure 9-9. Years in which hurricanes occurred at two sites and their intensity based on the Fujita scale in which larger numbers are more intense events: (a) Harvard Forest (HFR) in the northeastern United States and (b) Luquillo Experimental Forest (LUQ) in Puerto Rico (Boose 2003). Reprinted with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

A Basis for Understanding Responses to Global Change

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 m²)

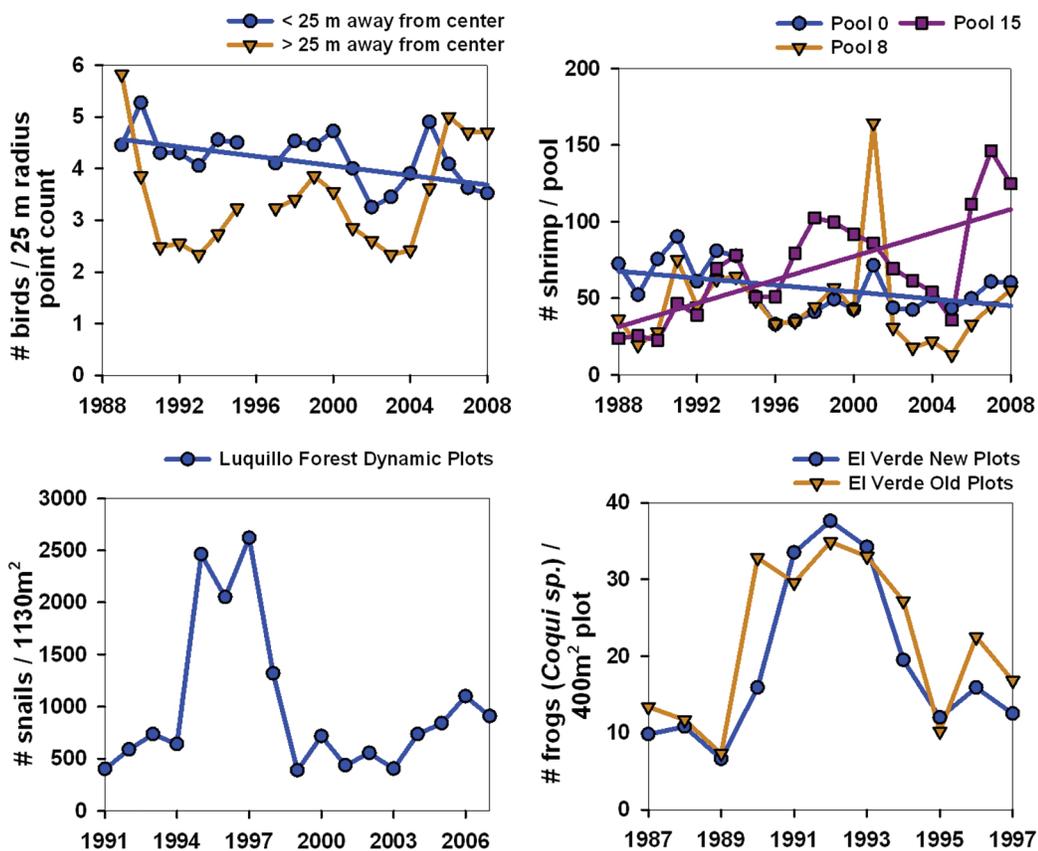


Figure 9-10. Response of different groups of organisms following multiple disturbance types in a forest in Puerto Rico. Data from R. Waide for birds, T. Crowl for shrimp, C. Bloch for snails, and L. Woolbright for frogs.

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).

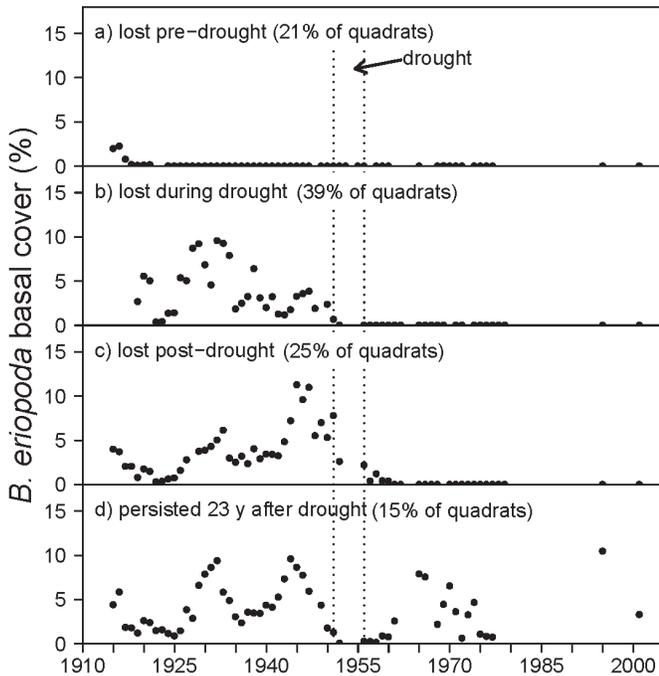


Figure 9-11. Black grama (*Bouteloua eriopoda*), the dominant perennial grass of upland grasslands in the Chihuahuan Desert, went locally extinct on most (64 percent) research quadrats ($1/m^2$) either during (b) or shortly after (c) the 1950s drought. However, this species went locally extinct on 21 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

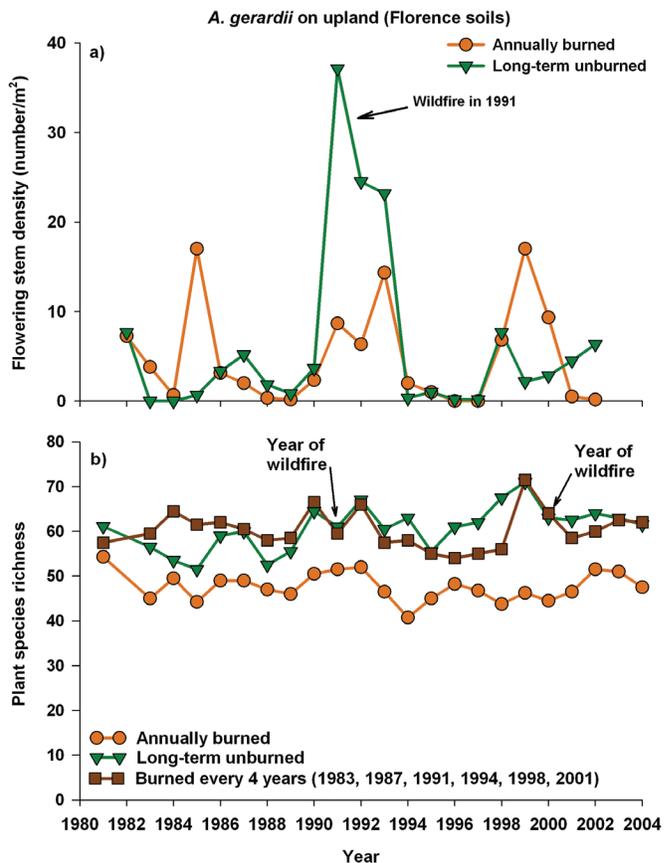


Figure 9-12. Wildfire in tallgrass prairie results in (a) a pulse in flowering stem density of *Andropogon gerardii*, an important perennial grass (data source: KNZ-PRE022; <http://www.konza.ksu.edu>; updated from Hartnett and Fay 1998), and (b) a decrease in plant species richness when it is burned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

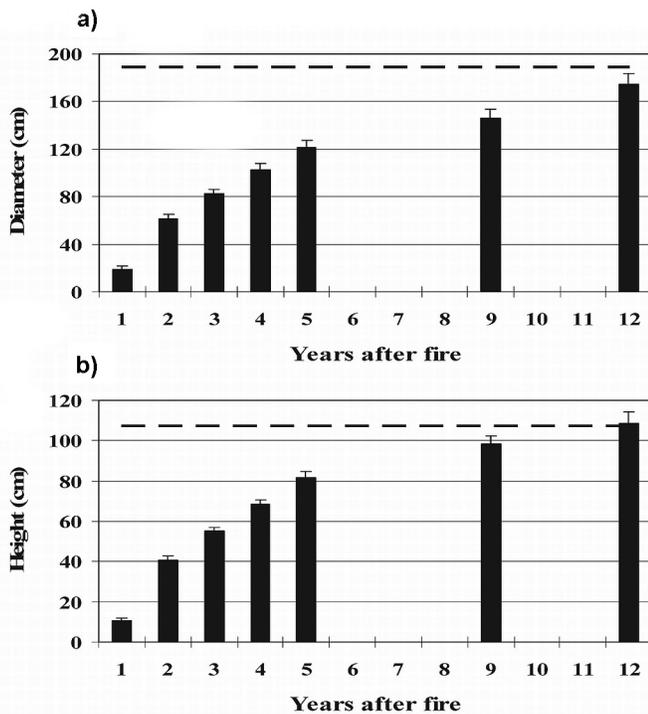


Figure 9-13. Diameter and height of *Larrea tridentata* (creosotebush), a common shrub in the Chihuahuan Desert, following fire at the Sevilleta (SEV) (Parmenter 2008). Twelve years' recovery was required before plants reached prefire height. Reprinted with permission from Allen Press Publishing Services.

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 (Rassweiler et al. 2008).

Long-Term Trends in Ecological Systems:

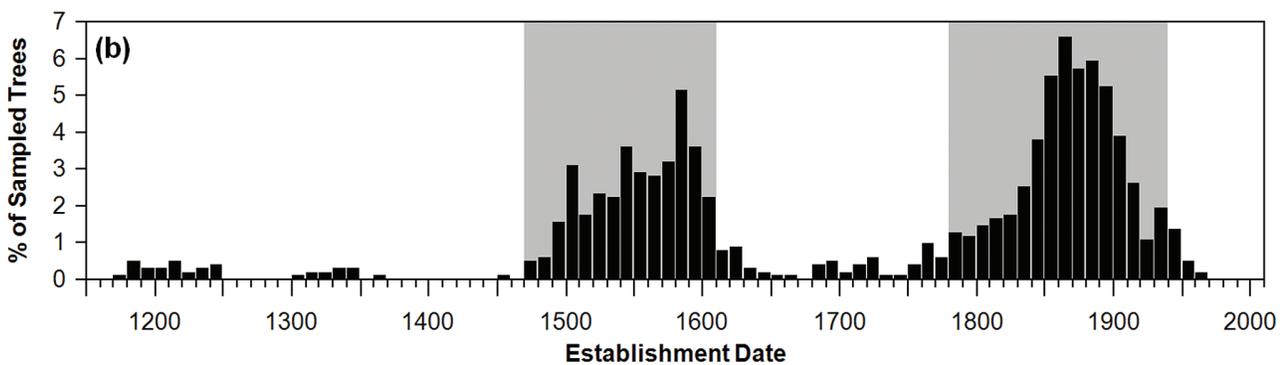
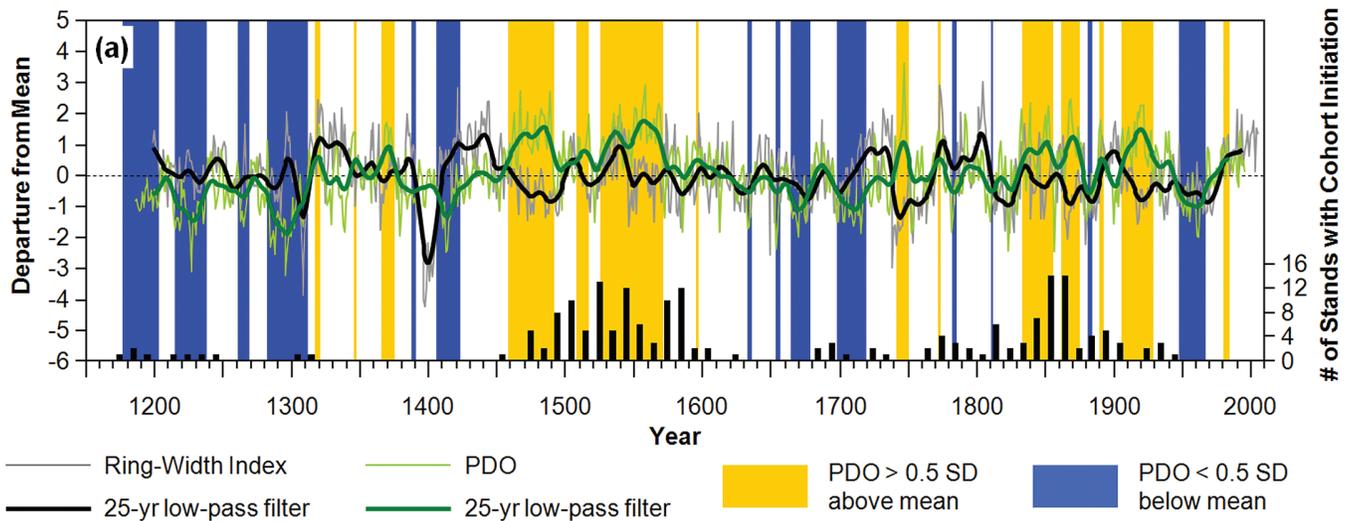


Figure 9-14. Comparison of (a) a tree-ring width chronology for some of the oldest Douglas-fir trees sampled in the central western Cascades of Oregon and a reconstruction of the Pacific Decadal Oscillation (PDO) (Tepley 2010). Yellow and blue shadings indicate extended warm and cold phases of the PDO, 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).

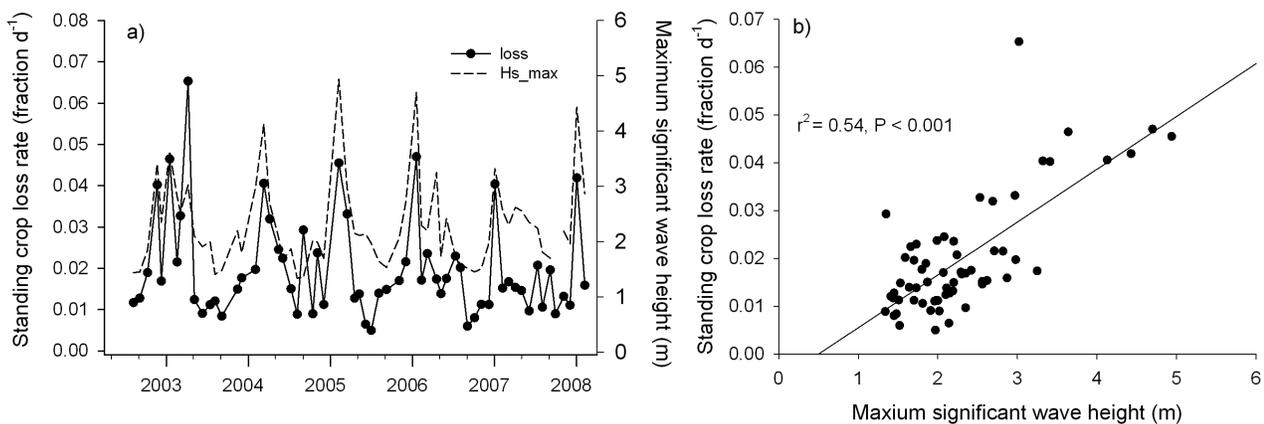


Figure 9-15. Wave disturbance and loss of kelp biomass off the coast of California, Santa Barbara Coastal (SBC). (a) The fraction of the standing crop of giant kelp lost per day each month at Mohawk Reef and the maximum significant wave height ($H_{s_{max}}$) during the monthly sampling interval. (b) 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).

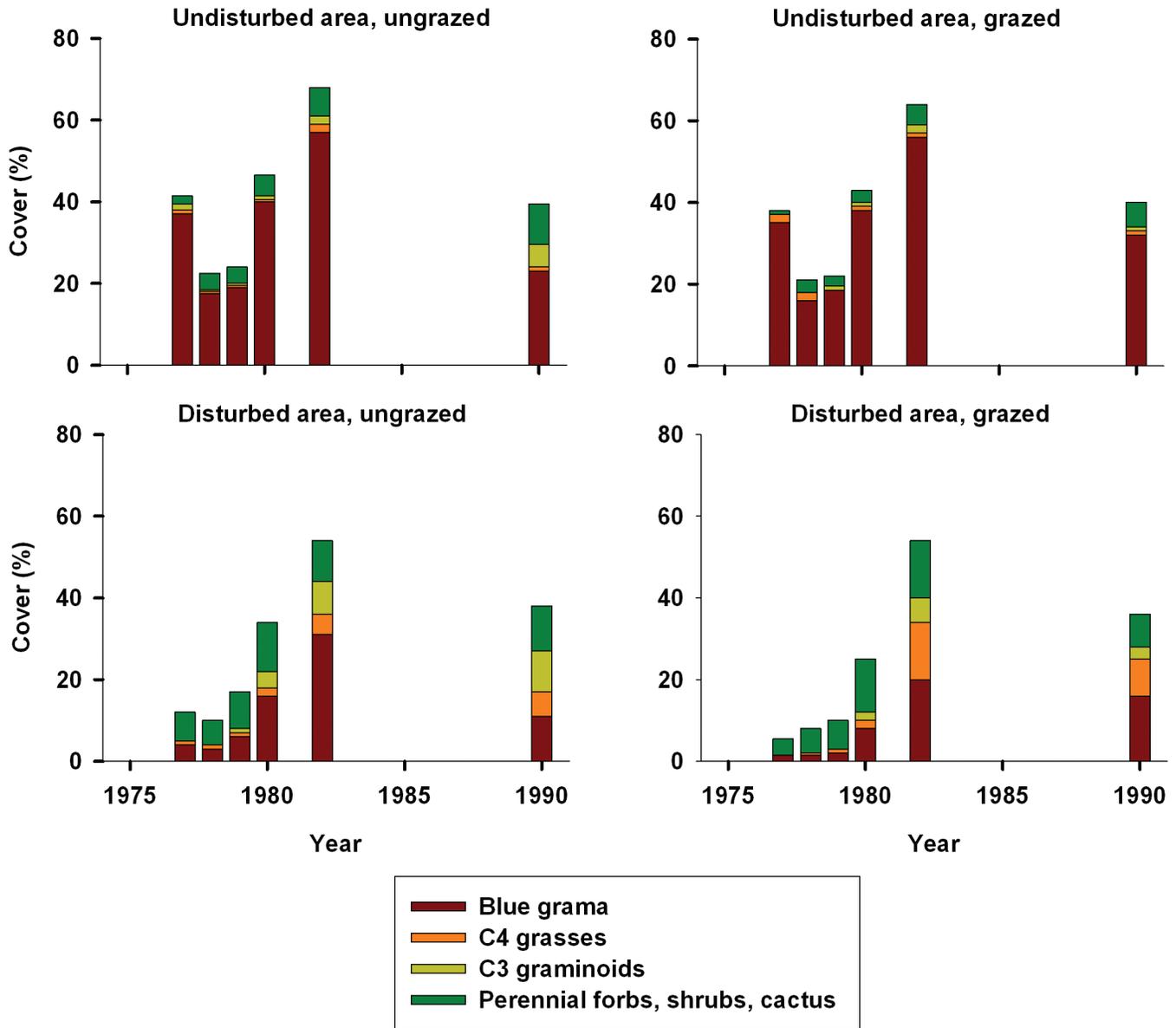


Figure 9-16. Recovery of vegetation at a shortgrass site (SGS) following plant mortality by the larvae of june beetles, a biotic disturbance, in 1977. Disturbed areas had greater percentage cover of perennial forbs and nondominant grasses compared with undisturbed areas that were primarily dominated 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.

Long-Term Trends in Ecological Systems:

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.

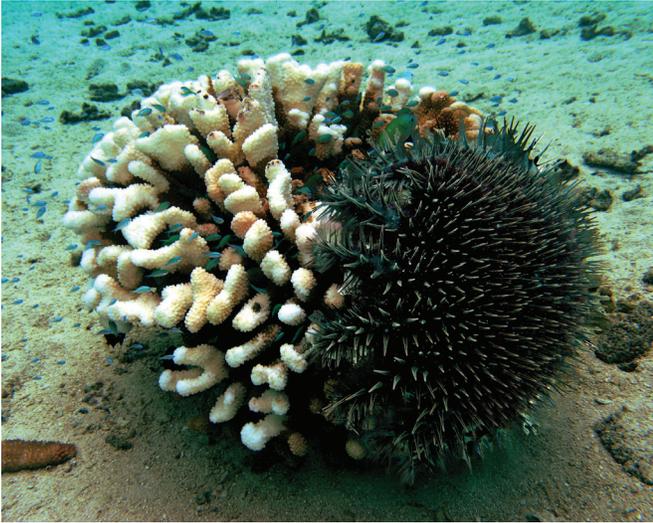


Figure 9-17. Crown-of-thorns sea star feeding on a live coral. Coral reefs of French Polynesia, Moorea Coral Reef (MCR), are experiencing a large crown-of-thorns sea star outbreak, which has decreased the cover of live coral on the reef from about 60 percent to less than 10 percent (P. Edmunds, unpublished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

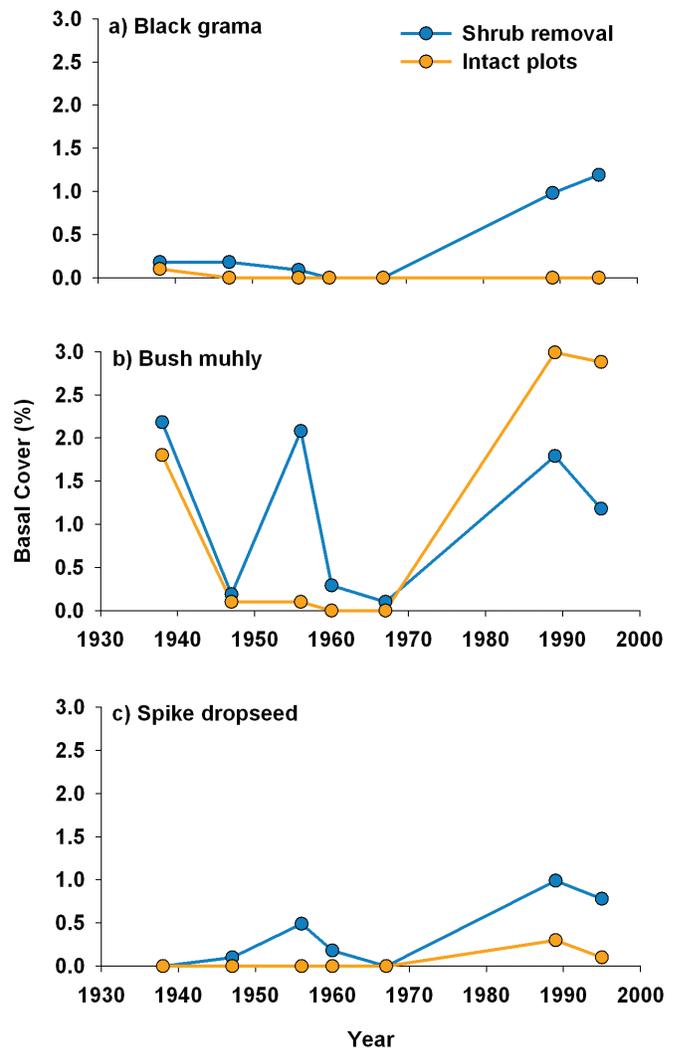


Figure 9-18. Basal cover of (a) black grama, (b) bush muhly, and (c) spike dropseed following shrub removal (blue) and on intact plots (orange) at a site in the northern Chihuahuan Desert, Jornada (JRN) (Havstad et al. 1999). Reprinted with permission from Elsevier.

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-Yáñez 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).

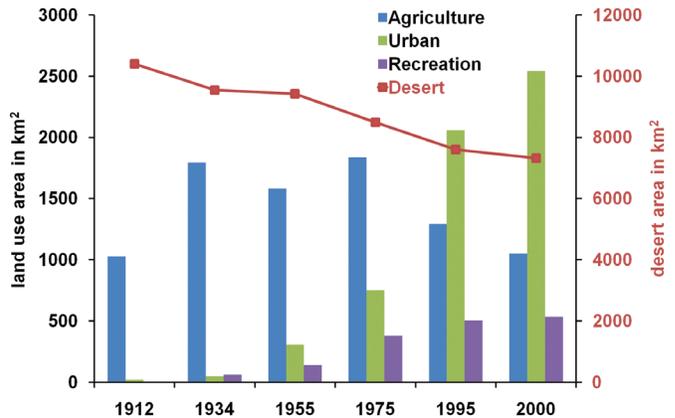


Figure 9-19. Over the past century, land in the Phoenix area, Central Arizona-Phoenix (CAP), has been converted from desert to agriculture, and ultimately to urban use. Data from Knowles-Yáñez et al. (1999).

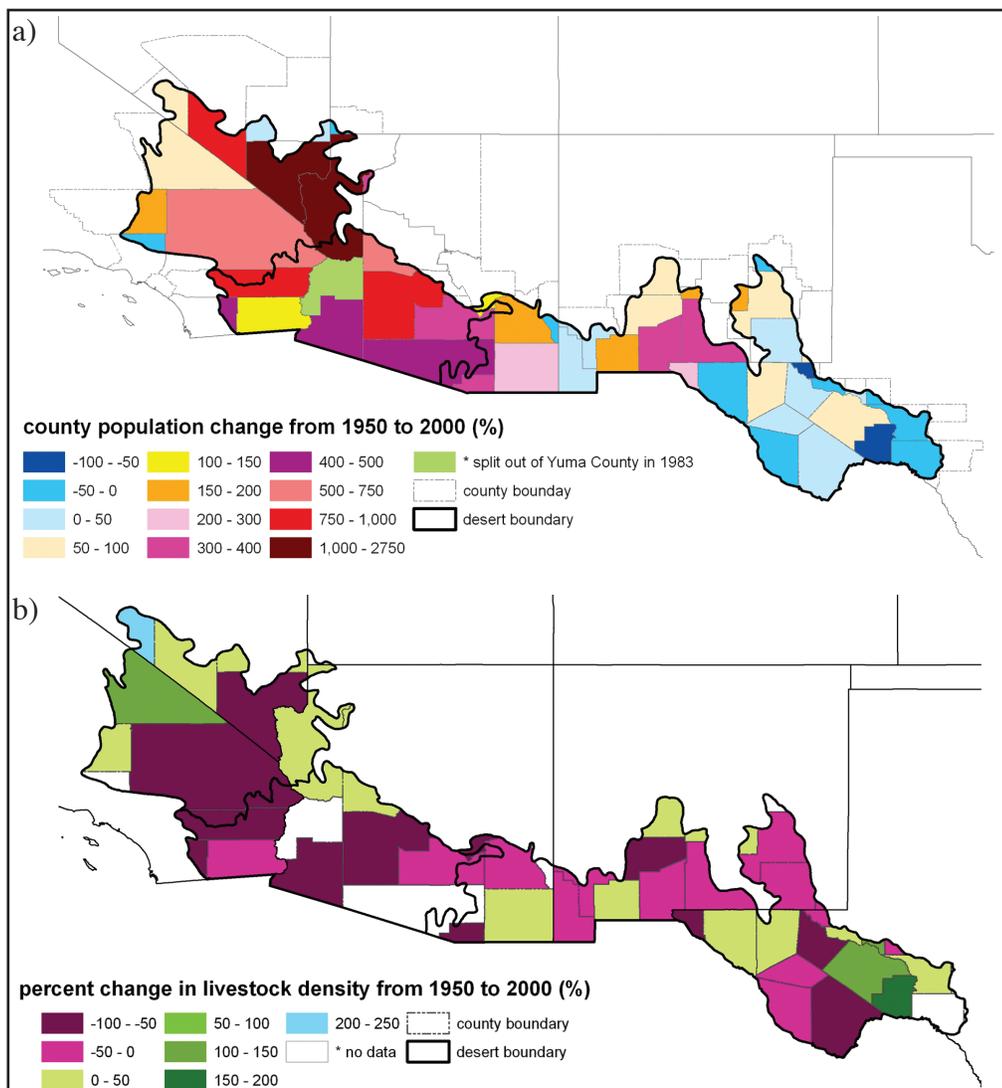


Figure 9-20. (a) Change in population as a percentage of the total from 1950 to 2000. (b) Change in livestock numbers by county for U.S. Bureau of Land Management allotments or districts between 1950 and 2000 for the United States Southwest (Havstad et al. 2009). Reprinted with permission from ASA-SSSA-CSSA.

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 other 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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