

## Chapter 3

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

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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.

## A Basis for Understanding Responses to Global Change

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.

### 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

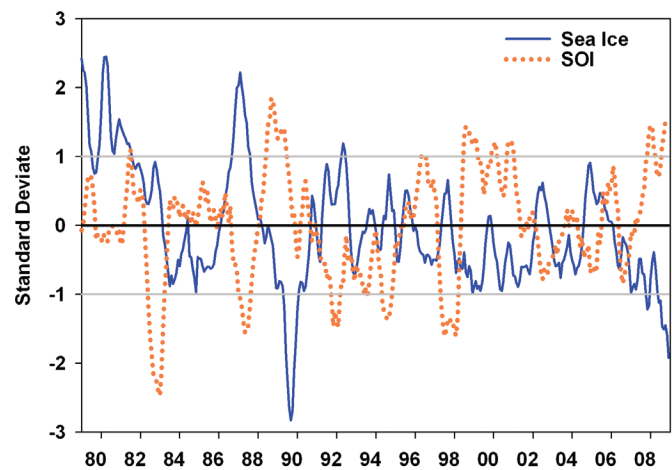


Figure 3-1. Normalized anomalies of a Sea Ice Index from the PAL LTER site (solid line) and the Southern Oscillation Index (SOI) (dashed line). (Adapted from Stammerjohn et al. 2008.)

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

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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 measurable 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).

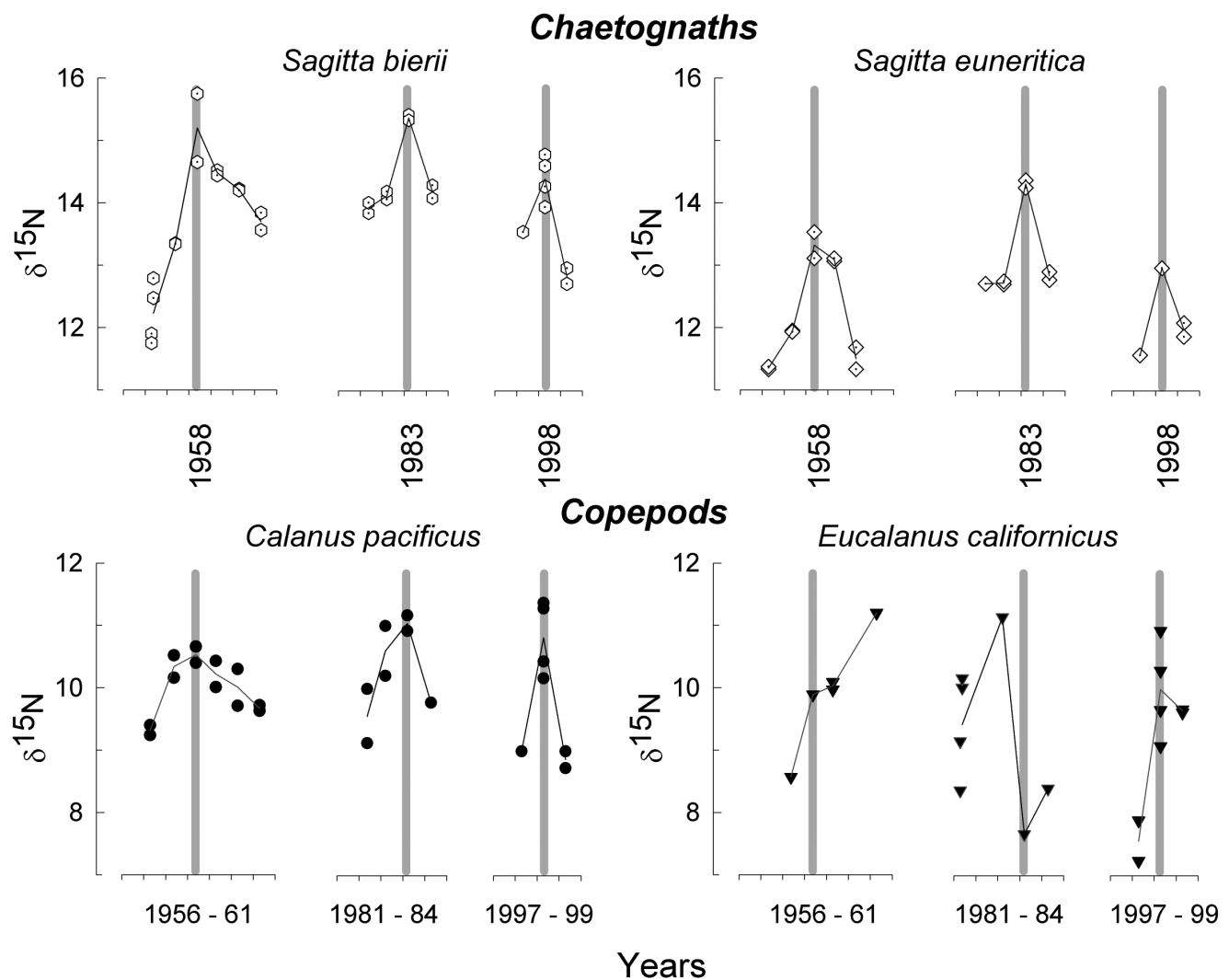


Figure 3-2. Springtime stable nitrogen (N) isotope content of four species of zooplankton from the CCE LTER region. Grey bars indicate major El Niño years (1958, 1983, 1998) (Rau et al. 2003). Reprinted with permission from Elsevier.

**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.

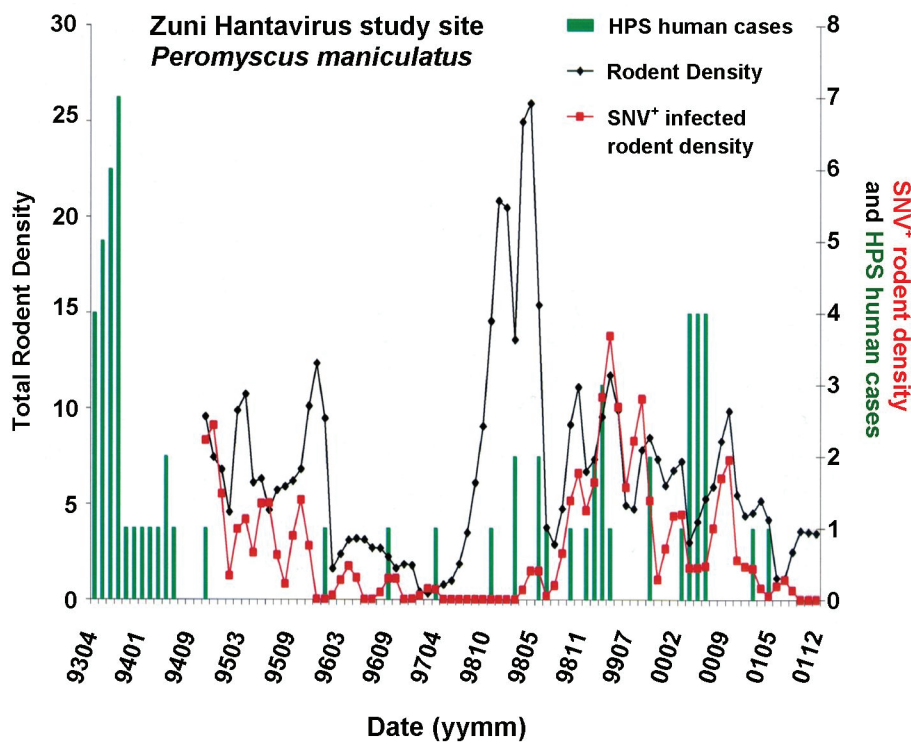


Figure 3-3. Densities of deer mice near Zuni, NM (black line), and densities of deer mice infected with Sin Nombre virus (SNV) at the same localities (red line). Human Hantavirus pulmonary syndrome (HPS) cases (green histograms) from the five counties surrounding Zuni and near the SEV LTER (Yates et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

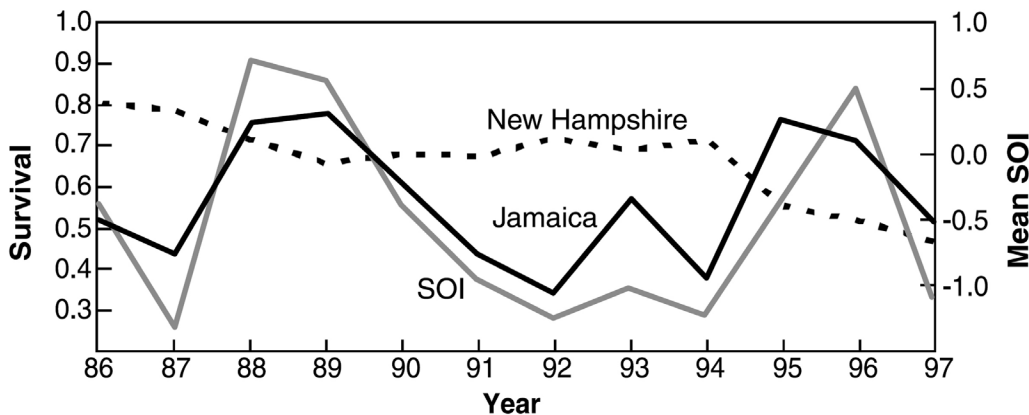


Figure 3-4. Black-throated blue warbler survival in winter in Jamaica (black solid line) is correlated with ENSO variations, as reflected in the Southern Oscillation Index (SOI, gray solid line) (Silllett et al. 2000). These songbirds breed in northeastern United States, including at the HBR in New Hampshire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

**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.

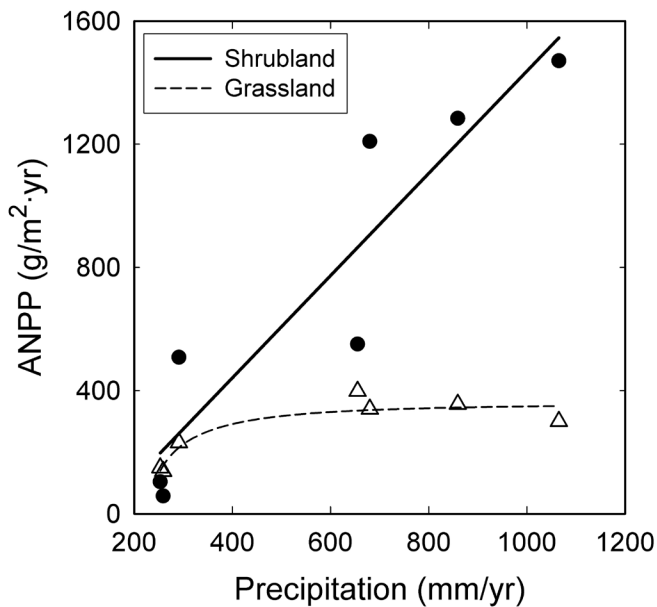


Figure 3-5. Relationship between aboveground annual net primary production (ANPP) and mean annual precipitation for shrublands is linear (solid line) across eight North American sites, including the Arctic (ARC), Jornada (JRN), Konza Prairie Biological Station (KNZ), Sevilleta (SEV), and Virginia Coast 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.)

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

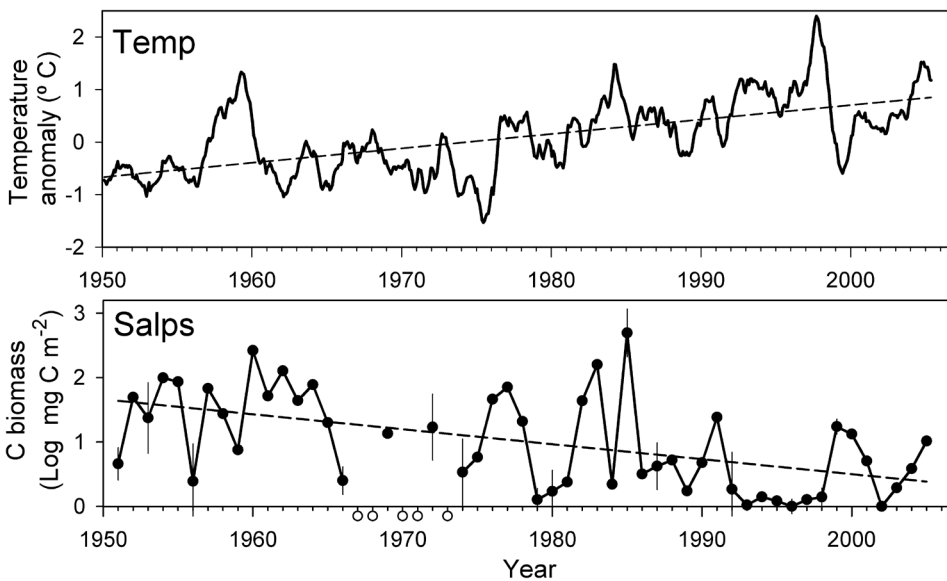


Figure 3-6. Top: Ocean temperature measured at the Scripps pier, California Current Ecosystem (CCE), over the past 5 1/2 decades (anomalies from the seasonal mean). (Data from <http://cce.lternet.edu/data/>.) Bottom: Decline in carbon (C) biomass of a group of pelagic tunicates known as salps, a zooplankton 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).

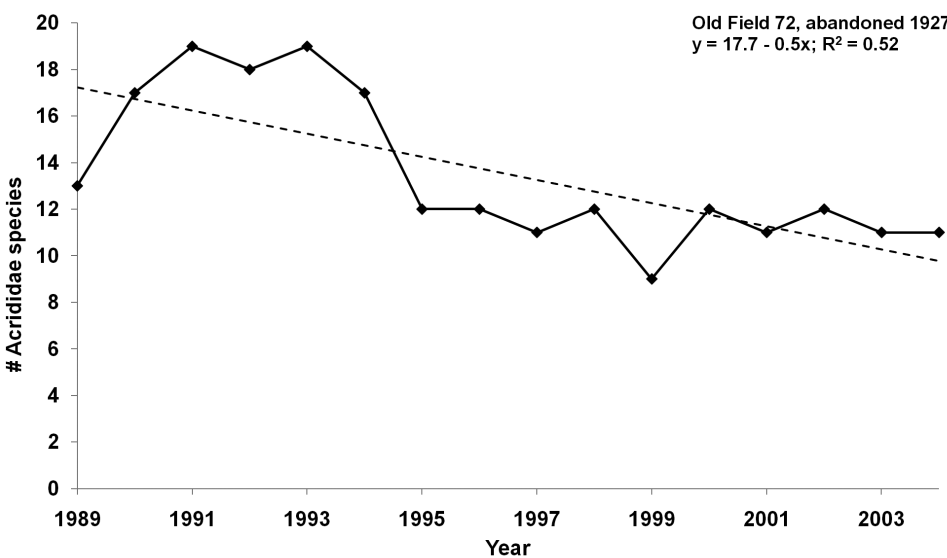


Figure 3-7. Decline of species richness of grasshoppers in the family Acrididae from old field 72 at the Cedar Creek site (CDR) over 15 years (M. Ritchie et al., personal communication). This decline parallels a longer-term increase in precipitation in the region. (Original data from <http://www.cedarcreek.umn.edu/>.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

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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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