CHAPTER 1

A Brief Overview of Recent Climate Change and Its Ecological Context

This chapter summarizes the most prominent abiotic components of recent climate change to establish the environmental context from which the discussion in the rest of the book proceeds. As will become clear in subsequent chapters, the rapid pace and broad geographic extent of abiotic changes reviewed here cannot be viewed in isolation for, as important as they are as drivers of ecological dynamics, in many if not most cases the ecological responses resulting from them owe to an alteration of biotic interactions. As an example we may consider the recent mass abandonment of retreating ice floes by Pacific walrus along the coast of Alaska in 2007 and 2010, which coincided with the lowest and third-lowest arctic sea ice extent recorded to date (Post and Brodie 2012). Walrus are benthic feeders: they consume mussels on the seafloor in shallow water during dives from the ice edge, which they also rest on between foraging bouts (Oliver et al. 1985; Ray et al. 2006). As the ice melts and the edge moves farther away from shore and the shallow-water environments that harbor the mussels walrus eat, it becomes energetically unprofitable for these large marine mammals to try to remain in proximity to the ice edge, for they would have to travel progressively longer distances to reach the shallow-water seafloors (Ray et al. 2010). The rate of annual sea ice loss over the Arctic has been on the order of 56,000 km² each year since 1979 (figure 1.1). As suggested later in this chapter, loss of sea ice does not represent simply an abiotic response to recent warming; it also represents the loss of critical habitat necessary for the survival and reproduction of many species, and it should probably be considered the high-latitude equivalent, in terms of negative impacts on faunal species, of deforestation in the Tropics (Post and Brodie 2012).

Before I summarize the most prominent abiotic features of recent climate change, two points of clarification are necessary. First, what is meant by recent? In the context of this book, recent refers to climatic changes that were set in motion by the onset of the Industrial Revolution but have become most clearly manifest, in terms of global abiotic changes, since approximately the middle
of the twentieth century (Mann et al. 1998, 1999). Second, what is meant by rapid? It is perhaps more difficult to identify the parameters of this characteristic of recent climate change, but at the same time the notion of rapid change is probably more intuitive to ecologists than is the notion of recent change. For the purposes of this book, and in keeping with most of the examples adduced herein, rapid refers to changes occurring on annual to decadal timescales. It will no doubt be tempting to argue that decadal-scale climatic variation is most certainly not rapid in the ecology of soil microorganisms, whose population and community dynamics are important drivers of nutrient flow rates, primary productivity, and even biosphere-atmosphere exchange of trace gases, but constraints must be established, and these are two of the clearest used throughout this book. Rapid environmental change most certainly presents challenges to some species, in terms of individuals’ ability to survive and reproduce, even as it presents distinct advantages to others, and no apparent benefit or disadvantage to yet others. Hence, the dynamics explored in this book include, in some cases, responses to climate change, and in other cases a lack of such response. But before we begin an accounting of these responses, from individual-level
life history responses through population-level dynamics, to community-scale changes, to ecosystem dynamics, we must take a close look at climate change and the abiotic dynamics it encompasses.

CLIMATE CHANGE VERSUS GLOBAL WARMING

It is tempting to use the term climate change to refer to increases in Earth’s temperatures or, similarly, to conflate the terms climate change and global warming. The term global warming is an oversimplification of the current changes in abiotic conditions on Earth because it implies that only changes in temperature are occurring, and that these temperature changes are unidirectional. Furthermore, the term has been applied most recently to connote solely human-driven temperature increases, which has promoted dismissal of the entire notion of climate change by those unconvinced by the evidence of a role for human beings in recent climate change. To draw an analogy that illustrates the importance of avoiding conflation of the terms climate change and global warming, we may recognize that evolution, like climate change, is a fact, whereas natural selection, like anthropogenic emissions of greenhouse gases, is the accepted theory explaining how this factual process occurs.

From an ecological perspective, climate change is most meaningfully considered as the suite of abiotic changes occurring across Earth coincident with the onset of the Industrial Revolution and progressing over the past 150 years, including rising temperatures, temperature variability, changes in precipitation and snow cover, and diminishing sea and land ice. All these changes can be linked to ecological dynamics, though it is probably fair to state that most research to date on the ecological consequences of climate change has focused on temperature changes.

TEMPERATURE CHANGES

The Earth’s surface has warmed by approximately 0.4°C since 1850 (Brohan et al. 2006; Trenberth et al. 2007), and by approximately 0.2°C per decade over the most recent three decades (Hansen et al. 2006) (figure 1.2), largely as a result of increases in atmospheric CO₂ concentrations driven by the human use of fossil fuels (Hansen, Sato, et al. 2008). This increase hardly seems remarkable, and indeed, it would be difficult for you or me to detect from one day to the next. However, this single estimate, representing an average value calculated over the entire surface area of our planet and encompassing over a century and
a half of data, masks a great deal of detail. The biological importance of this seemingly minute amount of change is evident in the widespread ecological dynamics it has elicited (Walther et al. 2002; Post, Forchhammer, et al. 2009). To understand the biological importance of climate change, we need to examine the abiotic data through the eyes of an ecologist.

From figure 1.2, two aspects of the recent temperature trend should become immediately apparent. First, there is considerable variation about the trend from year to year. The existence of this variation should signal to us as ecologists that not all organisms should be expected to respond similarly, in terms of rate and magnitude of change, to the recent and ongoing temperature trend. Short-lived or univoltine organisms, for example, may display life history and population dynamics that mirror interannual temperature variability as well as the overall temperature trend. Long-lived organisms, on the other hand, may display very gradual and at first almost imperceptible life history and population dynamical responses to the trend in temperature while displaying clearer responses to interannual variability about the trend itself.

The second aspect of the time series in figure 1.2 we may be particularly interested in as ecologists is the difference in the magnitude of temperature change between the Northern and Southern Hemispheres. Whereas global mean surface temperature has risen by 0.4°C over the past 150 years, the change in the Northern Hemisphere alone has been closer to 0.6°C (figure 1.2b), while that in the Southern Hemisphere has been about half that much, or 0.3°C (figure 1.2c). This indicates there has been considerable spatial heterogeneity across the globe in the magnitude and perhaps also rate of warming. When spatial resolution is added to the time series shown in figure 1.2, this variability across Earth’s surface becomes readily apparent (figure 1.3). These data reveal that trends in annual mean surface temperatures over the past century (figure 1.3a), and since the onset of the rapid warming trend beginning in the late 1970s (figure 1.3b), vary considerably across the surface of the Earth (Trenberth et al. 2007). During the twentieth century, warming trends were most pronounced in Low Arctic central Canada, the southwestern United States, southeastern South America, and central and northern Asia (Smith and Reynolds 2005) (figure 1.3a). This pattern was largely reproduced during the last three decades of the twentieth century, although with greater apparent surface warming in northwestern South America, southern Africa, and southern Greenland (figure 1.3b) (Smith and Reynolds 2005). The challenge such spatial variation in the strength of local and regional warming poses to the science of ecology lies in the difficulty of predicting the response of any organism with a cosmopolitan or quasi-cosmopolitan distribution to ongoing and future climate change. This difficulty is compounded many times
over if our interest lies in predicting how entire communities of organisms will respond to climate change over continental to global scales. Detecting a response to climate change in a single population or even, in some cases, multiple populations of a given species may not necessarily indicate how the species as a whole will respond to climate change throughout its distribution, especially if this distribution encompasses locales that have undergone widely different local temperature changes. Similarly, detecting responses to climate
Figure 1.3. Spatial variation across the surface of Earth in the direction and magnitude of surface temperature trends (top) over the entire twentieth century and (bottom) during the period of most rapid warming, since the onset of the Northern Hemisphere warming trend in the late 1970s. Relative shading in both panels indicates the linear trend in annual mean temperature over the period indicated in each panel, and blank cells or gray areas indicate insufficient data for estimating a trend, which required a minimum of 66 and 18 years of data for the top and bottom panels, respectively. Reproduced from Trenberth et al. (2007) and derived from data in Smith and Reynolds (2005).
change in the species constituting a community of interest may indicate nothing at all about how the entire community will respond to future increases in temperature. The challenges inherent in such evaluations are explored in subsequent chapters.

Comparing recent temperature estimates with proxies of global mean surface temperatures derived from tree rings, sediment layers, and ice cores reveals that temperatures during the past few decades have exceeded those over the past two millennia (Mann et al. 1999; Mann and Jones 2003). Examining the recent temperature trend through a time-windowing approach reveals further interesting details that are of ecological significance. When the data on average global temperatures are displayed as decadal time series, it becomes evident that the rate of warming has not been constant over the past 150 years (figure 1.4) (Mann and Jones 2003; Trenberth et al. 2007). In each successively more recent multidecadal period plotted in figure 1.4, the slope of temperature change over time increases. The rate of change over the past twenty-five years is approximately four times greater than the rate of change over the 150-year period as a whole. This would seem to indicate that the rate of warming is increasing. From an ecologist’s perspective, this should make us wonder whether organisms will be able to keep pace with the rate of temperature change if it continues to increase. A more refined perspective on this question would try to identify how responses to increasing rates of environmental change might vary among taxonomic groups with different life history strategies and generation times. For instance, certain species with highly plastic life history strategies or short generation times might be better able to match the pace of temperature change than might organisms with more highly conserved life history strategies or longer generation times.

Finally, it is worth noting as well that changes in interannual variability in temperature may prove just as important to the ecology of some species as the temperature trend itself. Here I refer not simply to heat waves or cold spells and the frequency of their occurrence but also to the magnitude of negative autocorrelation in temperatures between successive years. As we will examine in chapter 4 on population dynamics, abiotic fluctuations, when of sufficient magnitude, may influence the stability of population dynamics. Furthermore, the magnitude of serial (temporal) and spatial autocorrelation in temperatures may change as warming continues. Both of these parameters have the potential to influence ecological processes. For instance, increasing temporal autocorrelation in climatic conditions may lead to increases in population size in some types of systems that inevitably lead to population crashes (Wilmers et al. 2007b). Similarly, increasing spatial autocorrelation in temperatures over
large (i.e., subcontinental to continental) scales may increase the spatial synchrony of populations whose dynamics are environmentally entrained, thereby increasing extinction risk among those populations. For instance, temperatures recorded at weather stations along the west coast of Greenland became more spatially autocorrelated as Northern Hemisphere mean annual temperature increased, as did the population dynamics of caribou in the same area (Post and Forchhammer 2004). If increasing short-term—that is, annual to subannual—variability in abiotic conditions is a likely outcome of future climate change, this may have the potential to alter the stability and thereby persistence of some populations of organisms. Whether and how this might affect the stability properties of entire communities are questions examined in subsequent chapters.

Figure 1.4. Observed annual global mean surface temperatures, based on station data, from 1850 to 2005, shown as solid black circles. The left-side y-axis is scaled to depict the data as annual anomalies from the mean for the period 1961–90, and the right-side y-axis shows the actual temperature values expressed as means calculated across measurements recorded at local stations. Linear trends are estimated for the entire period and for the most recent 100 years, 50 years, and 25 years, with rates for the respective periods shown as the slope of the linear regression for each. Reproduced from Trenberth et al. (2007).
PRECIPITATION CHANGES

Just as important in the ecology of some species as temperature changes, if not more so, have been changes in precipitation and aridification (Schlesinger et al. 1990). Here again, when we examine the abiotic data as ecologists, several features of these changes should capture our attention. Although more difficult to discern than the temperature trends described above, there appears to have been an overall decline across the globe in total annual precipitation over land since approximately 1950 (Mitchell and Jones 2005), although precipitation has begun to increase globally since approximately 1993 (figure 1.5) (Wentz et al. 2007). Moreover, it appears that variability among years in total precipitation over land has increased since approximately 1970. Considerable variation

![Figure 1.5](image-url)

**Figure 1.5.** Global terrestrial annual precipitation anomalies relative to mean annual precipitation for the period 1981–2000. Source abbreviations are Global Historical Climate Network (GHCN), Precipitation Reconstruction over Land (PREC/L), Global Precipitation Climatology Project (GPCP), Global Precipitation Climatology Centre (GPCC), and Climate Research Unit (CRU). Adapted from Mitchell and Jones (2005) and Trenberth et al. (2007).
across the globe in trends in streamflow and surface runoff is expected to develop over the next half century, with increases in runoff projected for northern North America and Eurasia and decreases projected for western North America, southern Europe, southern Africa, and the Middle East (Milly et al. 2005). Both trends and variability in precipitation and water availability have an enormous potential to alter global primary productivity. Over the decade from 2000 to 2009, for instance, global terrestrial net primary productivity declined by approximately 0.55 petagrams of carbon annually, driven primarily by a pronounced Southern Hemisphere drying trend (Zhao and Running 2010).

To derive ecological context from such data requires, however, an indication of just how much of a decrease in annual precipitation over land has the potential to constitute a biological constraint on primary productivity if evaporation over land continues to increase with temperature. The Palmer Drought Severity Index (PDSI) provides this quantification as an indication of water stress (Alley 1984; Cook et al. 1999). The PDSI time series reveals worsening and persistent drought-like or drought-potential conditions since 1980 (figure 1.6) (Dai et al. 2004). Not only does this have the potential to alter primary productivity from global down to local scales, it also has the potential to drive shifts in

![Figure 1.6](image_url)

Figure 1.6. Time series for the Palmer Drought Severity Index (Alley 1984), reconstructed for the period 1901–2002. The index quantifies the amount of moisture taken up by the atmosphere relative to that released as precipitation, averaged annually over the surface of the globe. Increasingly positive values indicate increasing drought or drought-like conditions. The black trend line is the decadal average PDSI value. Figure adapted from Dai et al. (2004).
biome-wide plant community composition, transforming the vegetation types characteristic of the biomes we know today.

Aside from the recent trends in precipitation over land during the past several decades, there has also been considerable spatial heterogeneity across the globe in the magnitude and direction of changes in moisture balance. Whereas some regions, such as north temperate and south temperate zones, have received greater precipitation on average since the start of the twentieth century, other regions, most notably the Tropics, have become drier (Trenberth et al. 2007). Changes in moisture balance reflect the influence of temperature increases on the return of moisture to the atmosphere, and this may, over some regions, reflect increasing aridity despite increasing total annual precipitation. Spatial variation in the strength of the PDSI reflects this relationship, with increasing drought severity in tropical Africa, Central America, Malaysia, and the Amazon basin (Dai et al. 2004). Migratory species that travel along north-south gradients between breeding and winter ranges must contend with widely divergent precipitation trends and the consequences of these for resource availability at different stages during their annual life history cycles. As well, the spatial variation in the PDSI trend over the twentieth century suggests that primary productivity may respond differently to temperature trends where precipitation has increased, such as in Scandinavia, the U.S. Midwest, western Russia, and southeastern South America, compared to where it has declined along with rising temperatures, such as in equatorial and subequatorial Latin America and Africa.

CHANGES IN SNOW AND ICE COVER

Unlike temperature and rainfall, snow and ice are not simply abiotic parameters; rather, they should be considered in an ecological context as habitat for many species that are either snow or ice dependent or even obligate. Over the past three decades, Arctic sea ice has disappeared at the rate of 56,000 km² per year, precipitating Arctic-wide changes in tundra vegetation (Bhatt et al. 2010), while snow cover in the Northern Hemisphere has declined at a rate of approximately 100,000 km² per year (figure 1.7) (Post, Forchhammer, et al. 2009; Brown et al. 2010). To put the rate of loss of Arctic sea ice into perspective, deforestation in the Brazilian Amazon basin since the late 1970s has resulted in the loss of approximately 18,000 km² of rain forest per year, or one-third the rate of Arctic sea ice loss. There is likely little doubt in the minds of most people that deforestation in the Amazon basin threatens the persistence of animal species endemic to that region, and yet most people likely do not regard
melting sea ice and vanishing snow cover from a similar perspective as to the difficulties such losses present to species that are dependent on ice and snow as habitat (Ray et al. 2008). Snow cover in particular is important to many species as cover during the period of offspring vulnerability, as a thermal refuge for periods of torpor or temporary inactivity during extreme cold, as an avenue of escape from predators, or as protection for delicate tissues in some plant species from wind and ice crystal abrasion during winter. Indirectly, trends toward earlier annual timing of snowmelt may influence the reproductive ecology of many plant species in alpine and arctic environments, where emergence and flowering are sensitive to the persistence of snow cover. As we will see in

**Figure 1.7.** Annual totals for snow cover extent (gray) and sea ice extent (black), and their linear declines, over the Northern Hemisphere since 1966 and 1979, respectively, in millions of square kilometers. Both sea ice and snow provide crucial habitat and refugia for many snow- and ice-obligate and snow- and ice-associated species of animals in the Northern Hemisphere. Modified from Post et al. (2009b).
chapter 3, the decline of some species of alpine forbs in the U.S. state of Colorado may be related to increasingly early snowmelt.

What matters to ice-dependent and ice-associated species is not simply the total area covered by ice each year but also the quality of this ice. To draw another analogy between deforestation and diminishing sea ice as loss of habitat for ice-dependent and ice-associated species, we may compare multi-annual ice to old-growth forest. Not only is the total amount of sea ice declining across the Arctic, there is evidence that the amount of multi-annual ice is also declining (Barber and Hanesiak 2004). This phenomenon is comparable to the loss of old-growth forest. Ice that reforms every year and melts away later in the same year is annual ice; such ice is less stable than multi-annual ice and likely supports less life than old ice, in much the same way that the monospecific stands of second- or third-generation forest do not compare to old-growth forest in the diversity and abundance of species they support. Species that may be at particular risk of suffering declines as a result of decreases in the extent of snow cover and sea ice include wolverines (Schwartz et al. 2009; Brodie and Post 2010) and polar bears (Regehr et al. 2007; Molnár et al. 2008, 2010), respectively, but more subtle changes to the abundance and dynamics of flora and fauna may derive from the indirect effects of advances in the timing of snow and ice melt in northern environments, as chapter 3 explores in greater detail.

EL NIÑO–SOUTHERN OSCILLATION

The El Niño–Southern Oscillation (ENSO) phenomenon is characterized by periodic fluctuations in sea-surface temperatures in the equatorial Pacific Ocean that influence the seasonal, annual, and decadal magnitude and spatial patterns of precipitation and evaporation over land (Rasmussen and Carpenter 1982; Ropelewski and Halpert 1987; Trenberth and Hurrell 1994). During El Niño events, trade winds either stall or blow eastward from the western Pacific Ocean, elevating ocean surface temperatures across the equatorial Pacific and reducing cold-water upwelling along the Pacific coast of South America (Ropelewski and Halpert 1987). On land, El Niño conditions are associated with elevated temperatures and increased aridity in southeastern North America, northeastern South America, and southeastern Africa (Trenberth and Hurrell 1994).

Biological responses to El Niño events are well documented, and their recognition represents some of the earliest documentation of ecological consequences of contemporary climate change (Barber and Chavez 1983). Suppression of cold-water upwelling along the Pacific coast of South America during El Niño events reduces the productivity of near-shore waters because
it drives phyto- and zooplankton populations into deeper, offshore waters as they track thermohaline zones that are favorable for their survival and reproduction (Barber and Chavez 1983). In turn, a suite of ecological consequences cascades throughout marine ecosystems as planktonic productivity declines. These consequences include the collapse of sardine fisheries, reduced recruitment in seabird colonies, die-offs of entire cohorts of sea lion pups as adults are forced to forage farther and farther from shore, and failed reproduction in Galápagos finches (Barber and Chavez 1983; Grant and Grant 2002). During the 1997–98 El Niño event, carbon retention by the equatorial Pacific Ocean increased as oceanic CO₂ efflux declined (Chavez et al. 1999). In Borneo, droughts accompanying El Niño events appear to trigger flowering and fruit production in dipterocarps (Brearley et al. 2007), but forest fires associated with El Niño events have led to 80–95 percent reductions in the densities of some species of fruit trees Malayan sun bears depend on for food (Fredriksson et al. 2007).

Projections of ENSO behavior and the expected frequency of El Niño events as Earth’s climate continues to warm do not provide a clear picture of what to expect. The magnitude of El Niño events appears to be strengthening (figure 1.8). Expressed as the annual deviation from long-term mean sea-surface

![Darwin Southern Oscillation Index](image)

**Figure 1.8.** Time series of annual values of the Darwin Southern Oscillation Index, an index of the El Niño–Southern Oscillation, calculated as the difference between the normalized sea-surface pressure at the Tahiti and Darwin stations between 1866 and 2005. Strongly negative values of the index are indicative of El Niño years. Adapted from Trenberth et al. (2007).
temperature, a time series of annual values of the Darwin Southern Oscillation Index suggests increasingly strong negative anomalies, indicative of El Niño conditions, between 1866 and 2005 (figure 1.8). Reports that the frequency of El Niño events may increase with future warming, and in fact may already be increasing, have been challenged. However, even if their frequency remains constant, increasingly strong El Niño events would certainly have the potential to disrupt ecosystems throughout the Tropics and subtropics.

PALEOCLIMATIC VARIATION

A crucial consideration as we examine the ecological consequences of current and future climate change is how contemporary climate change compares with what has occurred in the past. I refer to this consideration as crucial because I believe there is a great deal to be learned about the consequences of current climate change by looking at what happened to Earth’s biota during previous warming episodes. I also believe there are some critical unknowns to be unveiled by considering the differences between contemporary climate change and paleoclimatic change.

The paleoclimatic record from the Cenozoic through the Pleistocene, which brings us to the present era, the Holocene, readily reveals several features of interest. First, Earth has been much warmer on many occasions in the deep past than it is today (Zachos et al. 2001). Second, climatic changes in the deep past appear to have occurred over much longer time scales than in the recent past (Zachos et al. 2001). This observation may, however, be an artifact—to some extent—of the greater resolution of more recent temperature proxies. Finally, there has been a close association between atmospheric temperatures and CO₂ concentrations over the past 60 million years (Pearson and Palmer 2000), obviously well before the Industrial Revolution, which heralded the most recent increase in atmospheric CO₂ and global temperatures. With respect to the first observation, however, we may be tempted to ask why it matters, in an ecological context, that Earth is warming now, given that it has been much warmer in the past. The most tempting reply may be that widespread extinctions have also occurred in the past, but the rebuttal to this would, of course, be that not all extinctions can be linked to past climatic changes, and, perhaps more important, that many taxonomic groups have persisted despite dramatic climatic changes in the past.

The next chapter is devoted to the most recent period of warming in Earth’s history, the Late Pleistocene, but an introduction is warranted here. The Late Pleistocene may constitute a very apt model of the ecological consequences of
warming that is ongoing today because it may have been comparable in rate to current warming, the Pleistocene-Holocene transitional warming having occurred over the course of decades (Alley et al. 2003). Important distinctions must be drawn, however, between current climate change and paleoclimatic changes, especially the most recent episode. First, the baseline temperature from which warming is proceeding today far exceeds that of the colder, drier Pleistocene. Second, human population size and growth rate, as well as the extent of human modification of the environment, outweigh those of early hominids or even of anatomically modern humans during the Pleistocene. Humans currently exert greater pressure on species in all of Earth’s biomes than they have at any time during their existence, either through habitat destruction or through direct exploitation. Thus, taxonomic groups that persisted through previous climatic changes may not find the strategies that allowed them to do so then similarly viable today simply because of the difference our presence makes this time around. Indeed, understanding and foreseeing the outcomes in terms of species persistence of the nexus of climate change and human exploitation presents a particularly difficult challenge (Post and Brodie in review). This may be especially, and perhaps uniquely, the case in the Tropics, where human pressure on rare and endemic species is highest and where research on the ecological consequences of climate change is made difficult by the complexity of species interactions (Brodie, Post, and Laurance 2012).

STUDYING THE ECOLOGICAL EFFECTS OF CLIMATE CHANGE

Conducting research on the ecological effects of climate change is an inherently multidisciplinary undertaking. It requires an understanding of pattern and process, of abiotic and biological dynamics, and it relies on an appreciation for the nuances of scale characteristic of ecological dynamics (Levin 1992), as well as diverse disciplinary approaches (Schlesinger 2010). That said, approaches to studying ecology in a climate change context fall principally into three categories of research: observational, experimental, and mathematical.

Observational studies generally make use of long-term data to draw relationships between records of abundance or occurrence of species, or springtime events, and climate change. A prototypical example of such studies is the analysis of a two-century record of phenological observations known as the Marsham data (Sparks and Carey 1995). This remarkable record of spring indicators was begun in 1736 by members of the Marsham family on their estate north of Norfolk, England (Marsham 1789; Margary 1926) and continued
through five generations of Marshams until records ceased in 1947 (Sparks and Carey 1995). The data consist of observations indicative of the annual arrival of spring, including first flowering records for several species of plants; “leafing” dates of multiple species of trees, which are the dates on which leaves reached a specified size; and arrival or appearance dates of migratory birds, butterflies, and unspecified anurans (Sparks and Carey 1995). The utility of such a data set for investigating ecological responses to climate change is immediately obvious. First, the record spans two centuries, a healthy length of time by the standards of ecology, though with gaps in the records. Second, it quantifies variation in life history events of multiple species representing several useful categories of organisms for comparative analyses, including plants and animals, vertebrates and invertebrates, migrants and residents, forbs and trees, and homeotherms and ecototherms. Third, it quantifies the timing of events during two important periods, before and after the Industrial Revolution, or before and after humans markedly influenced Earth’s climate. An additional remarkable feature of this data set is the fairly high degree of consistency in the quality and manner of recording of observations throughout the two-century period it covers. For such long-term data sets, this is probably a unique characteristic.

Sparks and Carey (1995) undertook an analysis of the entire Marsham phenological record that is fairly typical of those used with observational data. Their analysis focused on identifying correlations between phenological events in the data set and monthly weather data from a nearby station, and on fitting regression models that included time to account for temporal trends in the data and multiple candidate predictor variables from the list of weather variables displaying correlation with the phenological variables (Sparks and Carey 1995). This approach is useful for identifying trends in the ecological data and potential abiotic drivers of those trends. An obvious limitation of this approach is that other factors that have also changed over this period but are not included in the regression models might have contributed just as much or more to the observed ecological dynamics. Nonetheless, it is difficult to turn away from the opportunities afforded by such unique data sets in the interest of examining relationships between temperature or precipitation trends and ecological dynamics. Another limitation of the use of long-term ecological data sets in studying the effects of climate change is that many such collections of data were begun for purposes other than understanding ecological responses to climate change.

The Marsham record is not immune to this criticism, although it is probably closer in character to meeting this requirement than are many other similar long-term records because it was initiated with an interest in indicators of the arrival of spring. The long-term ecological monitoring project at the High
Arctic research station Zackenberg, in northeastern Greenland, is an example of a comprehensive, standardized program developed specifically to collect multi-annual data for the purpose of studying ecological responses to observed climate change (Forchhammer et al. 2008; Meltofte and Rasch 2008; Meltofte et al. 2008). Long-term observational data may be more readily available in Europe than in the United States, in part because there is a longer tradition of estate record keeping in Europe (Lauscher and Lauscher 1990). Nonetheless, the historical records of natural history observations made by American naturalists such as Aldo Leopold and Henry David Thoreau have come into use recently in analyses comparing the timing of events recorded earlier in the twentieth century with the timing of events at the same locations in the late twentieth century or early twenty-first century (Bradley et al. 1999; Miller-Rushing and Primack 2008).

There is some disagreement between advocates of experimental and observational approaches to the study of the ecological consequences of climate change (Agrawal et al. 2007b; Sagarin 2007; Wolkovich et al. 2012), and it is my personal impression that the experimental approach to this problem may be stronger in North America and the observational approach may be stronger in Europe. Experimental investigation of ecological responses to climate change most typically involves increasing near-surface temperatures on experimental plots. This can be achieved using elevated infrared heaters (Harte et al. 1995), warming coils buried under the soil surface (Bokhorst et al. 2008), or passive warming devices called open-top chambers (OTCs) that elevate near-surface temperatures by hindering the transverse movement of air over the ground within the enclosed chamber (Henry and Molau 1997; Marion et al. 1997; Sullivan and Welker 2005). Each of these approaches has inherent drawbacks. Overhead infrared heaters and warming coils both require a power source, and all three methods can alter the near-surface moisture regime or lead to soil drying. Additionally, OTCs, although designed to minimize unwanted side effects such as interference with evaporation and precipitation, may nonetheless create a rain shadow under the upper edge of the cone. In the Arctic, OTCs have also been employed in combination with snow fences to manipulate snow depth and, thereby, dates of snowmelt, to investigate their influences on plant community dynamics (Wahren et al. 2005) and plant ecophysiology (Welker et al. 2005). The timing of snowmelt is an important driver of the timing of life history events in a wide array of terrestrial species (Høye et al. 2007). In addition to temperature manipulations, some investigations of ecological responses to climate change have employed soil nutrient additions (Chapin and Shaver 1985; Hobbie and Chapin 1998; Shaver and Jonasson 1999; Arens et al. 2008). This approach has enjoyed particular favor in high-latitude studies.
In the Arctic, for instance, plant growth and ecosystem function are limited by the availability and turnover of soil nutrients, especially nitrogen (Shaver and Chapin 1991; Chapin et al. 1992a, 1992b; Shaver and Kummerow 1992; Chapin et al. 1995). The addition of fertilizer to experimental plots is intended, in this approach, to simulate the increased availability of soil nutrients in response to increased soil microbial activity and organic matter decomposition under warmer conditions.

Under the umbrella of mathematical approaches to studying ecological effects of climate change I would include statistical modeling, simulation modeling, and data-driven environmental niche modeling. The first form, statistical modeling, obviously goes hand-in-hand with long-term data collection. This approach has been widely used to quantify relations between recent climate change and population dynamics or life history variation. In fact, the study of ecological response to climate change has engendered the development of statistical modeling approaches specific to this task (Forchhammer, Stenseth, et al. 1998; Sæther et al. 2000, 2003; Post and Forchhammer 2001; Post et al. 2001; Ellis and Post 2004), based on preceding developments in the statistical analysis of time series data (Tong 1990; Bjørnstad et al. 1995; Framstad et al. 1997; Leirs et al. 1997). The main limitations of statistical analysis of time series data in a climate change context have to do with the problem of relating pattern to process, and to the frequent use in such models of harvest data rather than actual counts of individuals (Stenseth et al. 1999).

Simulation modeling and environmental niche modeling are closely related attempts to project the responses of species, communities, and ecosystems to expected future climate change. Ecosystem process models and gap models are forms of simulation modeling that attempt to quantify the carbon uptake potential of an ecosystem or biome in response to elevated atmospheric CO₂ and temperature. Ecosystem process models, such as the Terrestrial Ecosystem Model (TEM), work by—in a very simplistic interpretation—scaling up whole-plant ecophysiology of the dominant species in a biome to the scale of that biome (Melillo et al. 1993). Gap models, such as the Ecosystem Demography model, are demographic models that simulate the birth, reproduction, and death of individual plants of the dominant species in a community and scale up these processes to estimate carbon uptake by the entire biome (Moorcroft et al. 2001). Environmental niche modeling, on the other hand, is used to project the distribution and abundance of species under climate change scenarios (Jeschke and Strayer 2008). In this approach, the abiotic correlates of the presence and abundance of a species throughout its current distribution are used to predict the presence or absence of that species in accordance with changes in those abiotic correlates in time and space (Peterson et al. 2002). The main
criticism leveled at environmental niche modeling is that abiotic environmental variables do not necessarily capture important biological interactions that also limit the distribution and abundance of organisms (Jeschke and Strayer 2008); this criticism is addressed in greater detail in chapter 5.

No single approach to the study of ecological consequences of climate change is adequate on its own, or without its particular set of limitations, some of which have already been acknowledged. Observational studies in the best cases are powered by long-term data, spatial replication of those data, and large-scale coverage, but suffer primarily from an inability to determine causality in the relationships they uncover (Agrawal et al. 2007b). Experiments, when properly designed, have the capacity to assign causality, but often suffer from small scales of study in both space and time. Even long-term, large-scale experiments suffer limitations arising from logistical and practical constraints, such as insufficient replication (Krebs et al. 1995). As well, incorporating biological realism into experiments and determining the magnitude of the treatment applied in them are far from trivial undertakings. For instance, microcosm experiments in the laboratory are useful for controlling unwanted background processes (Petchey et al. 1999) but may not translate readily into an understanding of ecological dynamics in nature. Similarly, detection of a significant response to resource manipulation may be an artifact of the level of resource manipulation applied rather than a biologically meaningful identification of the magnitude of resource limitation in nature. Proponents of time series analysis steadfastly defend the capacity of this approach to identify biological interactions in the structure and behavior of time series data (Turchin 2003), but withering criticisms of this view of the world are regularly leveled by experimentalists (Krebs 1998, 2003) and even, in some cases, by time series analysts themselves (Berteaux et al. 2006).

The argument for the utility of time series analysis in detecting the influence of interactions within and among species relates to what is referred to as the dimensionality of the time series data under inspection (Royama 1992). The dimensionality, or order, of the time series refers to the number of steps \( n \) back in time between which there is a relationship between an observation in year \( t \) and year \( t - n \) (Royama 1992). First-order dynamics are assumed to indicate density dependence, second-order dynamics indicate a role of reproduction or trophic interactions in dynamics, and third-order dynamics indicate both (Framstad et al. 1997; Forchhammer, Stenseth, et al. 1998; Bjørnstad and Grenfell 2001). Similarly, as will be demonstrated in chapter 4, the order or dimensionality of climate terms in statistical models of population dynamics indicates direct or delayed effects of climate, the latter of which are presumed to operate through reproduction or trophic interactions (Forchhammer, Stenseth, et al. 1998; Post
and Stenseth 1999; Post and Forchhammer 2001). Somewhat ironically, the best support to date that I am aware of for the capacity of time series analyses to capture biological interactions in determining the dimensionality of time series data derives from a laboratory experiment (Bjørnstad et al. 2001).

THE STUDY SITE AT KANGERLUSSUAQ, GREENLAND

Throughout this book, I refer occasionally to the results of my own research at my long-term study site in Low Arctic West Greenland, where I began observational fieldwork in 1993 and where I implemented an ongoing, uninterrupted experimental complement to my observational work in 2002. My approach to the study of the ecological consequences of climate change thus employs observation, experimentation, and modeling. I believe this constitutes a powerful combination of approaches, each one of which in isolation suffers from its own limitations but which in concert provide a potent toolkit. I began fieldwork at what would develop into a long-term study site near Kangerlussuaq, Greenland, in 1993. During that initial field season, my research focused on quantifying the timing of the caribou calving season in relation to the timing of the onset and progression of the plant growing season. Over the period for which station data are available, from 1974 to the present, mean annual temperature in Kangerlussuaq has increased at a rate of 0.68°C per decade (figure 1.9a), with the rate of warming since the initiation of my fieldwork there exceeding this figure by a factor of three (figure 1.9b).

The research protocol at my study site has been described elsewhere (Post 1995; Post et al. 2003, 2008a, 2008b; Post and Pedersen 2008) but will be reviewed briefly here. On a daily or near daily basis throughout the plant growing season, permanently marked plots distributed over an approximately 6 km² area within the study site are monitored for plant phenology. These observations include a tabulation of species present and their phenological states on all plots. The number of plots has increased from twelve in 1993–2008 to twenty-seven since 2009. Concurrently with observations of plant phenology, the entire study site, including an adjacent core calving area that has been in use by caribou since approximately 4,000 years years before the present (YBP) (Thing 1984; Meldgaard 1986), is monitored daily for the presence of caribou and muskoxen and their calves. All adults, yearlings, and calves are counted and recorded and their locations noted. These data are used to quantify the timing of the caribou calving season and to monitor both herbivore species’ use of the study site in relation to an ongoing herbivore exclosure and tundra warming experiment. This experiment consists of excluding both species of herbivore
from six 800 m² circular, fenced-in areas adjacent to control sites of the same size. Inside and outside these exclosures we have applied a passive warming treatment using OTCs that elevate surface temperatures by 1.5–3°C (Post et al. 2008a). Chambers are put in place on permanently marked plots in May of each year and removed again in August. Plots that receive this warming treatment are paired with adjacent control plots that remain at ambient temperature. The biomass of all standing vegetation, both live and dead, is quantified in late July or early August of each year using a nondestructive point-frame method.
that relates the numbers of hits by a lowered pin to the biomass on each plot. Data recorded in this manner also allow us to identify and monitor the number of plant species, and changes in these, on each plot. Over the course of this study we have been able to monitor changes in the timing and progression of the plant growing season, plant community dynamics in relation to warming and herbivory, offspring production by caribou and muskoxen, and the population dynamics of both species. Recently we have begun monitoring gas flux on the experimental plots to measure the effects of herbivory and experimental warming on ecosystem CO$_2$ dynamics. Many of the results of this study will be detailed in subsequent chapters where relevant.