

Ecological and Evolutionary Responses to Recent Climate Change

Camille Parmesan

Section of Integrative Biology, University of Texas, Austin, Texas 78712;
email: parmesan@mail.utexas.edu

Annu. Rev. Ecol. Evol. Syst. 2006. 37:637–69

First published online as a Review in Advance
on August 24, 2006

The *Annual Review of Ecology, Evolution, and Systematics* is online at
<http://ecolsys.annualreviews.org>

This article's doi:
10.1146/annurev.ecolsys.37.091305.110100

Copyright © 2006 by Annual Reviews.
All rights reserved

1543-592X/06/1201-0637\$20.00

Key Words

aquatic, global warming, phenology, range shift, terrestrial, trophic asynchrony

Abstract

Ecological changes in the phenology and distribution of plants and animals are occurring in all well-studied marine, freshwater, and terrestrial groups. These observed changes are heavily biased in the directions predicted from global warming and have been linked to local or regional climate change through correlations between climate and biological variation, field and laboratory experiments, and physiological research. Range-restricted species, particularly polar and mountaintop species, show severe range contractions and have been the first groups in which entire species have gone extinct due to recent climate change. Tropical coral reefs and amphibians have been most negatively affected. Predator-prey and plant-insect interactions have been disrupted when interacting species have responded differently to warming. Evolutionary adaptations to warmer conditions have occurred in the interiors of species' ranges, and resource use and dispersal have evolved rapidly at expanding range margins. Observed genetic shifts modulate local effects of climate change, but there is little evidence that they will mitigate negative effects at the species level.

INTRODUCTION

Historical Perspective

Climate change is not a new topic in biology. The study of biological impacts of climate change has a rich history in the scientific literature, since long before there were political ramifications. Grinnell (1917) first elucidated the role of climatic thresholds in constraining the geographic boundaries of many species, followed by major works by Andrewartha & Birch (1954) and MacArthur (1972). Observations of range shifts in parallel with climate change have been particularly rich in northern European countries, where observational records for many birds, butterflies, herbs, and trees date back to the mid-1700s. Since the early part of the twentieth century, researchers have documented the sensitivity of insects to spring and summer temperatures (Bale et al. 2002, Dennis 1993, Uvarov 1931). Ford (1945) described northward range shifts of several butterflies in England, attributing these shifts to a summer warming trend that began around 1915 in Britain. Ford noted that one of these species, *Limenitis camilla*, expanded to occupy an area where attempted introductions prior to the warming had failed. Kaisila (1962) independently documented range shifts of Lepidoptera (primarily moths) in Finland, using historical data on range boundaries dating back to 1760. He showed repeated instances of southward contractions during decades of “harsh” climatic conditions (cold wet summers), followed by northward range expansion during decades with climate “amelioration” (warm summers and lack of extreme cold in winter). Further corroboration came from the strong correlations between summer temperatures and the northern range boundaries for many butterflies (Dennis 1993).

Similar databases exist for northern European birds. A burst of papers documented changed abundances and northerly range shifts of birds in Iceland, Finland, and Britain associated with the 1930s–1940s warming period (Gudmundsson 1951; Harris 1964; Kalela 1949, 1952; Salomonsen 1948). A second wave of papers in the 1970s described the subsequent retreats of many of these temperate bird and butterfly species following the cool, wet period of the 1950s–1960s (Burton 1975, Heath 1974, Severnty 1977, Williamson 1975).

Complementing this rich observational database is more than 100 years of basic research on the processes by which climate and extreme weather events affect plants and animals. As early as the 1890s, Bumpus (1899) noted the differential effects of an extreme winter storm on the introduced house sparrow (*Parus domesticus*), resulting in stabilizing selection for intermediate body size in females and directional selection for large body size in males (Johnston et al. 1972). The first extensive studies of climate variability as a powerful driver of population evolution date back to the 1940s, when Dobzhansky (1943, 1947) discovered repeated cycles of seasonal evolution of temperature-associated chromosomal inversions within *Drosophila pseudoobscura* populations in response to temperature changes from spring through summer.

In summary, the history of biological research is rich in both mechanistic and observational studies of the impacts of extreme weather and climate change on wild species: Research encompasses impacts of single extreme weather events; experimental studies of physiological tolerances; snapshot correlations between

climatic variables and species' distributions; and correlations through time between climatic trends and changes in distributions, phenologies, genetics, and behaviors of wild plants and animals.

Anthropogenic Climate Change

In spite of this wealth of literature on the fundamental importance of climate to wild biota, biologists have been reluctant to believe that modern (greenhouse gas-driven) climate change is a cause of concern for biodiversity. In his introduction to the 1992 *Annual Review of Ecology, Evolution, and Systematics* volume on "Global Environmental Change," Vitousek wrote, "ultimately, climate change probably has the greatest potential to alter the functioning of the Earth system . . . nevertheless, the major effects of climate change are mostly in the future while most of the others are already with us." Individual authors in that volume tended to agree—papers were predominantly concerned with other global change factors: land use change, nitrogen fertilization, and the direct effects of increased atmospheric CO₂ on plant ecophysiology.

Just 14 years later, the direct impacts of anthropogenic climate change have been documented on every continent, in every ocean, and in most major taxonomic groups (reviewed in Badeck et al. 2004; Hoegh-Guldberg 1999, 2005b; Hughes 2000; IPCC 2001a; Parmesan 2005b; Parmesan & Galbraith 2004; Parmesan & Yohe 2003; Peñuelas & Filella 2001; Pounds et al. 2005; Root & Hughes 2005; Root et al. 2003; Sparks & Menzel 2002; Thomas 2005; Walther et al. 2002, 2005). The issue of whether observed biological changes can be conclusively linked to anthropogenic climate change has been analyzed and discussed at length in a plethora of syntheses, including those listed above. Similarly, complexity surrounding methodological issues of detection (correctly detecting a real trend) and attribution (assigning causation) has been explored in depth (Ahmad et al. 2001; Dose & Menzel 2004; Parmesan 2002, 2005a,b; Parmesan & Yohe 2003; Parmesan et al. 2000; Root et al. 2003, Root & Hughes 2005, Schwartz 1998, 1999; Shoo et al. 2006). The consensus is that, with proper attention to sampling and other statistical issues and through the use of scientific inference, studies of observed biological changes can provide rigorous tests of climate-change hypotheses. In particular, independent syntheses of studies worldwide have provided a clear, globally coherent conclusion: Twentieth-century anthropogenic global warming has already affected Earth's biota.

Scope of This Review

This review concentrates on studies of particularly long time series and/or particularly good mechanistic understanding of causes of observed changes. It deals exclusively with observed responses of wild biological species and systems to recent, anthropogenic climate change. In particular, agricultural impacts, human health, and ecosystem-level responses (e.g., carbon cycling) are not discussed. Because they have been extensively dealt with in previous publications, this review does not repeat discussions of detection and attribution, nor of the conservation implications of climate

Detection: ability to discern long-term trends above yearly variability and real changes from apparent changes brought about by changes in sampling methodology and/or sampling intensity

Attribution: teasing out climate change as the causal driver of an observed biological change amid a backdrop of potential confounding factors

Globally coherent: a common term in economics, a process or event is globally coherent when it has similar effect across multiple systems spread across different locations throughout the world

change. Rather, some of the best-understood cases are presented to illustrate the complex ways in which various facets of climatic change impact wild biota. The choice of studies for illustration attempts to draw attention to the taxonomic and geographic breadth of climate-change impacts and to the most-recent literature not already represented in prior reviews.

Researchers have frequently associated biological processes with indices of ocean-atmosphere dynamics, such as the El Niño Southern Oscillation and the North Atlantic Oscillation (Blenckner & Hillebrand 2002, Holmgren et al. 2001, Ottersen et al. 2001). However, the nature of the relationship between atmospheric dynamics, ocean circulation, and temperature is changing (Alley et al. 2003, IPCC 2001b, Karl & Trenberth 2003, Meehl et al. 2000). Therefore, there is large uncertainty as to how past relationships between biological systems and ocean indices reflect responses to ongoing anthropogenic climate change. Although I use individual examples where appropriate, this complex topic is not fully reviewed here.

OVERVIEW OF IMPACTS LITERATURE

An extensive, but not exhaustive, literature search revealed 866 peer-reviewed papers that documented changes through time in species or systems that could, in whole or in part, be attributed to climate change. Some interesting broad patterns are revealed. Notably, the publication rate of climate-change responses increases sharply each year. The number of publications between 1899 and January 2003 (the date of two major syntheses) was 528. Therefore, approximately 40% of the 866 papers compiled for this review were published in the past three years (January 2003 to January 2006).

The studies are spread broadly across taxonomic groups. Whereas distributional studies concentrated on animals rather than plants, the reverse is true of phenological time series. This may simply be because historical data on species range boundaries have higher resolution for animals than for plants. Conversely, local records of spring events are much more numerous for plants (e.g., flowering and leaf out) than for animals (e.g., nesting).

Although there is still a terrestrial bias, studies in marine and freshwater environments are increasing in proportional representation. The largest gaps are geographic rather than taxonomic. In absolute numbers, most biological impact studies are from North America, northern Europe and Russia. Few biological studies have come from South America, and there are large holes in Africa and Asia, with most of the studies from these two continents coming from just two countries: South Africa and Japan. In past decades, Australia's impact studies have stemmed predominantly from the coral reef community, but in recent years scientists have dug deep to find historical data, and terrestrial impact studies are now emerging. Similarly, the Mediterranean/North African region (Spain, France, Italy, and Israel) has recently spawned a spate of studies. Antarctica stands out as a region where impacts (or lack of impacts) on most species and systems have been documented, even though data often have large geographic or temporal gaps.

Few studies have been conducted at a scale that encompasses an entire species' range (i.e., a continental scale), with only a moderate number at the regional scale (e.g., the United Kingdom or Germany). Most have been conducted at local scales, typically at a research station or preserve. Continental-scale studies usually cover most or all of a species' range in terrestrial systems (Both et al. 2004, Burton 1998a,b, Dunn & Winkler 1999, Menzel & Fabian 1999, Parmesan 1996, Parmesan et al. 1999). However, even a continental scale cannot encompass the entire ranges of many oceanic species (Ainley & Divoky 1998, Ainley et al. 2003, Beaugrand et al. 2002, Croxall et al. 2002, Hoegh-Gulberg 1999, McGowan et al. 1998, Reid et al. 1998, Spear & Ainley 1999). Terrestrial endemics, in contrast, can have such small ranges that regional, or even local, studies may represent impacts on entire species (Pounds et al. 1999, 2006).

Meta-analysis: set of statistical techniques designed to synthesize quantitative results from similar and independent experiments

Meta-Analyses and Syntheses: Globally Coherent Signals of Climate-Change Impacts

A handful of studies have conducted statistical meta-analyses of species' responses or have synthesized independent studies to reveal emergent patterns. The clear conclusion across global syntheses is that twentieth-century anthropogenic global warming has already affected the Earth's biota (IPCC 2001a; Parmesan 2005a,b; Parmesan & Galbraith 2004; Parmesan & Yohe 2003; Peñuelas & Filella 2001; Pounds et al. 2005; Root & Hughes 2005; Root et al. 2003; Thomas 2005; Walther et al. 2002, 2005).

One study estimated that more than half (59%) of 1598 species exhibited measurable changes in their phenologies and/or distributions over the past 20 to 140 years (Parmesan & Yohe 2003). Analyses restricted to species that exhibited change documented that these changes were not random: They were systematically and predominantly in the direction expected from regional changes in the climate (Parmesan & Yohe 2003, Root et al. 2003). Responding species are spread across diverse ecosystems (from temperate grasslands to marine intertidal zones and tropical cloud forests) and come from a wide variety of taxonomic and functional groups, including birds, butterflies, alpine flowers, and coral reefs.

A meta-analysis of range boundary changes in the Northern Hemisphere estimated that northern and upper elevational boundaries had moved, on average, 6.1 km per decade northward or 6.1 m per decade upward ($P < 0.02$) (Parmesan & Yohe 2003). Quantitative analyses of phenological responses gave estimates of advancement of 2.3 days per decade across all species (Parmesan & Yohe 2003) and 5.1 days per decade for the subset of species showing substantive change (>1 day per decade) (Root et al. 2003).

A surprising result is the high proportion of species responding to recent, relatively mild climate change (global average warming of 0.6°C). The proportion of wild species impacted by climate change was estimated at 41% of all species (655 of 1598) (Parmesan & Yohe 2003). This estimate was derived by focusing on multispecies studies that reported stable as well as responding species. Because responders and

stable species were often sympatric, variation of response is not merely a consequence of differential magnitudes of climate change experienced.

PHENOLOGICAL CHANGES

By far, most observations of climate-change responses have involved alterations of species' phenologies. This is partly a result of the tight links between the seasons and agriculture: Planting and harvest dates (and associated climatic events such as day of last frost) have been well recorded, dating back hundreds of years for some crops. But the plethora of records also stems from the strong sociological significance of the change of the seasons, particularly in high-latitude countries. Peoples of Great Britain, the Netherlands, Sweden, and Finland have been keen on (some might say even obsessed with) recording the first signs of spring—the first leaf on an oak, the first peacock butterfly seen flying, the first crocus in bloom—as a mark that the long, dark winter is finally over. Fall has not captured as much enthusiasm as spring, but some good records exist, for example, for the turning of leaf color for trees.

The longest records of direct phenological observations are for flowering of cherry trees *Prunus jamasakura* and for grape harvests. Menzel & Dose (2005) show that timing of cherry blossom in Japan was highly variable among years, but no clear trends were discerned from 1400 to 1900. A statistically significant change point is first seen in the early 1900s, with steady advancement since 1952. Recent advancement exceeds observed variation of the previous 600 years. Menzel (2005) analyzed grape-harvest dates across Europe, for which April–August temperatures explain 84% of the variation. She found that the 2003 European heat wave stands out as an extreme early harvest (i.e., the warmest summer) going back 500 years. Although such lengthy observational records are extremely rare, these two unrelated plants on opposite sides of the world add an important historical perspective to results from shorter time series.

Several lines of evidence indicate a lengthening of vegetative growing season in the Northern Hemisphere, particularly at higher latitudes where temperature rise has been greatest. Summer photosynthetic activity (normalized difference vegetation index estimates from satellite data) increased from 1981–1991 (Myneni et al. 1997), concurrent with an advance and increase in amplitude of the annual CO₂ cycle (Keeling et al. 1996). White et al. (1999) modeled meteorological and satellite data to estimate actual growing season length each year from 1900–1987 in the United States. Growing season was unusually long during the warm period of the 1940s at all 12 sites. However, patterns have recently diverged. Since 1966, growing season length has increased only in four of the coldest, most-northerly zones (42°–45° latitude), not in the three warmest zones (32°–37° latitude). Across the European Phenological Gardens (experimental clones of 16 species of shrubs and trees at sites across Europe), a lengthening of the growing season by 10.8 days occurred from 1959–1993 (Menzel 2000, Menzel & Fabian 1999). Analysis of climatological variables (e.g., last frost date of spring and first frost date of fall) mirrors this finding, with an estimated lengthening of the growing season of 1.1–4.9 days per decade since 1951 (Menzel et al. 2003).

Bradley et al. (1999) built on Aldo Leopold's observations from the 1930s and 1940s on the timing of spring events on a Wisconsin farm. Of 55 species resurveyed in the 1980s and 1990s, 18 (35%) showed advancement of spring events, whereas the rest showed no change in timing (with the exception of cowbirds arriving later). On average, spring events occurred 7.3 days earlier by the 1990s compared with 61 years before, coinciding with March temperatures being 2.8°C warmer.

Another long-term (100-year) study by Gibbs & Breisch (2001) compared recent records (1990–1999) of the calling phenology of six frog species in Ithaca, New York, with a turn-of-the-century study (1900–1912). They showed a 10–13-day advance associated with a 1.0–2.3°C rise in temperature during critical months. Amphibian breeding has also advanced in England, by 1–3 weeks per decade (Beebee 1995). Ecophysiological studies in frogs have shown that reproduction is closely linked to both nighttime and daytime temperatures (Beebee 1995).

In the United Kingdom, Crick et al. (1997), analyzing more than 74,000 nest records from 65 bird species between 1971 and 1995, found that the mean laying dates of first clutches for 20 species had advanced by an average 8.8 days. Brown et al. (1999) found a similar result for the Mexican jay (*Apelocoma ultramarina*) in the mountains of southern Arizona. In the North Sea, migrant birds have advanced their passage dates by 0.5–2.8 days per decade since 1960, with no significant difference between short- and long-distance migrants (Hüppop & Hüppop 2003). In contrast, Gordo et al. (2005) found that three of six long-distance migrant birds had significantly delayed arrival to breeding grounds in Spain, with arrival date highly correlated with climatic conditions in their overwintering grounds in the southern Sahara.

Butterflies frequently show a high correlation between dates of first appearance and spring temperatures, so it is not surprising that their first appearance has advanced for 26 of 35 species in the United Kingdom (Roy & Sparks 2000) and for all 17 species analyzed in Spain (Stefanescu et al. 2003). Seventy percent of 23 species of butterfly in central California have advanced their first flight date over 31 years, by an average of 24 days (Forister & Shapiro 2003). Climate variables explained 85% of variation in flight date in the California study, with warmer, drier winters driving early flight.

There are only two continental-scale studies of bird phenology. Dunn & Winkler (1999) analyzed changes in breeding for tree swallows (*Tachycineta bicolor*) from 1959 to 1991 over the entire breeding range in the contiguous United States and Canada. Laying date was significantly correlated with mean May temperature and had advanced by an average of nine days over the 32-year period. In a complementary study, Both et al. (2004) analyzed the pied flycatcher (*Ficedula hypoleuca*) at 23 sites across Europe and found a significant advance in laying date for nine of the populations, which also tended to be those with the strongest warming trends. Continental-scale studies of both lilac (*Syringa vulgaris*) and honeysuckle (*Lonicera tatarica* and *L. korolkowii*) in the western United States have shown an advance in mean flowering dates of 2 and 3.8 days per decade, respectively (Cayan et al. 2001).

Aquatic systems exhibit similar trends to those of terrestrial systems. In a lake in the northwestern United States, phytoplankton bloom has advanced by 19 days from

1962 to 2002, whereas zooplankton peak is more varied, with some species showing advance and others remaining stable (Winder & Schindler 2004). The Arctic seabird Brunnich's guillemot, *Uria lomvia*, has advanced its egg-laying date at its southern boundary (Hudson Bay) with no change at its northern boundary (Prince Leopold Island); both trends are closely correlated with changes in sea-ice cover (Gaston et al. 2005).

Roetzer et al. (2000) explicitly quantified the additional impacts of urban warming by comparing phenological trends between urban and rural sites from 1951 to 1995. Urban sites showed significantly stronger shifts toward earlier spring timing than nearby rural sites, by 2–4 days. An analysis of greening across the United States via satellite imagery also concluded that urban areas have experienced an earlier onset of spring compared with rural areas (White et al. 2002).

Researchers generally report phenological changes as a separate category from changes in species' distributions, but these two phenomena interplay with each other and with other factors, such as photoperiod, to ultimately determine how climate change affects each species (Bale et al. 2002, Chuine & Beaubien 2001).

INTERACTIONS ACROSS TROPHIC LEVELS: MATCHES AND MISMATCHES

Species differ in their physiological tolerances, life-history strategies, probabilities of population extinctions and colonizations, and dispersal abilities. These individualistic traits likely underlie the high variability in strength of climate response across wild species, even among those subjected to similar climatic trends (Parmesan & Yohe 2003). For many species, the primary impact of climate change may be mediated through effects on synchrony with that species' food and habitat resources. More crucial than any absolute change in timing of a single species is the potential disruption of coordination in timing between the life cycles of predators and their prey, herbivorous insects and their host plants, parasitoids and their host insects, and insect pollinators with flowering plants (Harrington et al. 1999, Visser & Both 2005). In Britain, the butterfly *Anthocharis cardamines* has accurately tracked phenological shifts of its host plant, even when bud formation came two to three weeks early (Sparks & Yates 1997). However, this may be the exception rather than the rule.

Visser & Both (2005) reviewed the literature and found only 11 species' interactions in which sufficient information existed to address the question of altered synchrony. Nine of these were predator-prey interactions, and two were insect-host plant interactions. In spite of small sample size, an important trend emerged from this review: In the majority of cases (7 of 11), interacting species responded differently enough to climate warming that they are more out of synchrony now than at the start of the studies. In many cases, evidence for negative fitness consequences of the increasing asynchrony has been either observed directly or predicted from associated studies (Visser & Both 2005).

In one example, Inouye et al. (2000) reported results of monitoring between 1975 and 1999 at Rocky Mountain Biological Laboratory in Colorado, where there has been a 1.4°C rise in local temperature. The annual date of snowmelt and plant flowering did

not change during the study period, but yellow-bellied marmots (*Marmota flaviventris*) advanced their emergence from hibernation by 23 days, changing the relative phenology of marmots and their food plants. In a similar vein, Winder & Schindler (2004) documented a growing asynchrony between peak phytoplankton bloom and peak zooplankton abundances in a freshwater lake.

More complex phenomena resulting from trophic mismatches have also been documented. For example, phenological asynchrony has been linked to a range shift in the butterfly *Euphydryas editha*. Warm and/or dry years alter insect emergence time relative to both the senescence times of annual hosts and the time of blooming of nectar sources (Singer 1972, Singer & Ehrlich 1979, Singer & Thomas 1996, Thomas et al. 1996, Weiss et al. 1988). Field studies have documented that butterfly-host asynchrony has resulted directly in population crashes and extinctions. Long-term censuses revealed that population extinctions occurred during extreme droughts and low snowpack years (Ehrlich et al. 1980, Singer & Ehrlich 1979, Singer & Thomas 1996, Thomas et al. 1996), and these extinctions have been highly skewed with respect to both latitude and elevation, shifting mean location of extant populations northward and upward (Parmesan 1996, 2003, 2005a).

Van Nouhuys & Lei (2004) showed that host-parasitoid synchrony was influenced significantly by early spring temperatures. Warmer springs favored the parasitoid wasp *Cotesia melitaearum* by bringing it more in synchrony with its host, the butterfly *Melitaea cinxia*. Furthermore, they argue that because most butterfly populations are protandrous (i.e., males pupating earlier than females), temperature-driven shifts in synchrony with parasitoids may affect butterfly sex ratios.

OBSERVED RANGE SHIFTS AND TRENDS IN LOCAL ABUNDANCE

Expected distributional shifts in warming regions are poleward and upward range shifts. Studies on these shifts fall mainly into two types: (a) those that infer large-scale range shifts from small-scale observations across sections of a range boundary (with the total study area often determined by a political boundary such as state, province, or country lines) and (b) those that infer range shifts from changes in species' composition (abundances) in a local community. Studies encompassing the entire range of a species, or at least the northern and southern (or lower and upper) extremes, are few and have been concentrated on amphibians (Pounds et al. 1999, 2006), a mammal (Beever et al. 2003), and butterflies (Parmesan 1996, Parmesan et al. 1999). The paucity of whole-range studies likely stems from the difficulties of gathering data on the scale of a species' range—often covering much of a continent.

Shifts at Polar Latitudes

Broad impacts of climate change in polar regions—from range shifts to community restructuring and ecosystem functioning—have been reviewed by the Intergovernmental Panel on Climate Change (Anisimov et al. 2001), the Arctic Climate Impact Assessment (2004) and the Millenium Ecosystem Assessment (Chapin et al. 2006).

Intergovernmental Panel on Climate Change: a scientific panel formed under the auspices of the United Nations and the World Meteorological Organization for the purpose of synthesizing literature and forming scientific consensus on climate change and its impacts

Antarctic. Plant, bird, and marine life of Antarctica have exhibited pronounced responses to anthropogenic climate change. These responses have been largely attributed to extensive changes (mostly declines) in sea-ice extent, which in turn appears to have stimulated a trophic cascade effect in biological systems. Declines in sea-ice extent and duration since 1976 have apparently reduced abundances of ice algae, in turn leading to declines in krill (from 38%–75% per decade) in a large region where they have been historically concentrated, the southwest Atlantic (Atkinson et al. 2004). Krill (*Euphausia superba*) is a primary food resource for many fish, seabirds, and marine mammals. Interestingly, McMurdo Dry Valleys, which actually cooled between 1990 and 2000, also showed declines in lake phytoplankton abundances and in soil invertebrate abundances (Doran et al. 2002).

Penguins and other seabirds in Antarctica have shown dramatic responses to changes in sea-ice extent over the past century (Ainley et al. 2003, Croxall et al. 2002, Smith et al. 1999). The sea-ice dependent Adélie and emperor penguins (*Pygoscelis adeliae* and *Aptenodytes forsteri*, respectively) have nearly disappeared from their northernmost sites around Antarctica since 1970. Emperors have declined from 300 breeding pairs down to just 9 in the western Antarctic Peninsula (Gross 2005), with less severe declines at Terre Adélie (66° S), where they are now at 50% of pre-1970s abundances (Barbraud & Weimerskirch 2001). Adélies have declined by 70% on Anvers Island (64°–65° S along the Antarctic peninsula (Emslie et al. 1998, Fraser et al. 1992), whereas they are thriving at the more-southerly Ross Island at 77° S (Wilson et al. 2001)—effectively shifting this species poleward. In the long-term, sea-ice-dependent birds will suffer a general reduction of habitat as ice shelves contract [e.g., as has already occurred in the Ross Sea (IPCC 2001b)] or collapse [e.g., as did the Larsen Ice Shelves along the Antarctic Peninsula in 2002 (Alley et al. 2005)].

In contrast, open-ocean feeding penguins—the chinstrap and gentoo—invaded southward along the Antarctic Peninsula between 20 and 50 years ago, with paleo-logical evidence that gentoo had been absent from the Palmer region for 800 years previously (Emslie et al. 1998, Fraser et al. 1992). Plants have also benefited from warming conditions. Two Antarctic vascular plants (a grass, *Deschampsia antarctica*, and a cushion plant, *Colobanthus quitensis*) have increased in abundance and begun to colonize novel areas over a 27-year period (Smith 1994).

Arctic. Nearly every Arctic ecosystem shows marked shifts. Diatom and invertebrate assemblages in Arctic lakes have shown huge species' turnover, shifting away from benthic species toward more planktonic and warm-water-associated communities (Smol et al. 2005). Across northern Alaska, Canada, and parts of Russia, shrubs have been expanding into the tundra (Sturm et al. 2005). Field studies, experimentation, and modeling link this major community shift to warming air temperatures, increased snow cover, and increased soil microbial activity (Chapin et al. 1995; Sturm et al. 2001, 2005). Populations of a pole-pole migrant, the sooty shearwater (*Puffinus griseus*), have shifted their migration routes by hundreds of kilometers in concert with altered sea surface temperature (SST) in the Pacific (Spear & Ainley 1999).

Sea-ice decline in the Arctic has been more evenly distributed than in the Antarctic. Because of differing geology, with an ocean at the pole rather than land, Arctic species

that are sea-ice dependent are effectively losing habitat at all range boundaries. Polar bears have suffered significant population declines at opposite geographic boundaries. At their southern range boundary (Hudson Bay), polar bears are declining both in numbers and in mean body weight (Stirling et al. 1999). Climate change has caused a lengthening of ice-free periods on Hudson Bay, periods during which the bears starve and live on their reserves because an ice shelf is necessary for feeding. Furthermore, researchers have also linked warming trends to reductions of the bears' main food, the ringed seal (Derocher et al. 2004, Ferguson et al. 2005). At the bears' northern range boundaries off Norway and Alaska, sea ice has also been reduced, but poorer records make it less clear whether observed declines in body size and the number of cubs per female are linked to climate trends or to more basic density-dependent processes (Derocher 2005, Stirling 2002).

Shifts in Northern-Hemisphere Temperate Species

On a regional scale, a study of the 59 breeding bird species in Great Britain showed both expansions and contractions of northern range boundaries, but the average boundary change for 12 species that had not experienced overall changes in density was a mean northward shift of 18.9 km over a 20-year period (Thomas & Lennon 1999). For a few well-documented bird species, their northern U.K. boundaries have tracked winter temperatures for over 130 years (Williamson 1975). Physiological studies indicate that the northern boundaries of North American songbirds may generally be limited by winter nighttime temperatures (Burger 1998, Root 1988).

Analogous studies exist for Lepidoptera (butterflies and moths), which have undergone an expansion of northern boundaries situated in Finland (Marttila et al. 1990, Mikkola 1997), Great Britain (Hill et al. 2002, Pollard 1979, Pollard & Eversham 1995, Warren 1992), and across Europe (Parmesan et al. 1999). Depending on the study, some 30% to 75% of northern boundary sections had expanded north; a smaller portion (<20%) had contracted southward; and the remainder were classified as stable. In a study of 57 nonmigratory European butterflies, data were obtained from both northern and southern range boundaries for 35 species (Parmesan et al. 1999). Nearly two thirds (63%) had shifted their ranges to the north by 35–240 km, and only two species had shifted to the south (Parmesan et al. 1999). In the most-extreme cases, the southern edge contracted concurrent with northern edge expansion. For example, the sooty copper (*Heodes tityrus*) was common in the Montseny region of central Catalonia in the 1920s, but modern sightings are only from the Pyrenees, 50 km to the north. Symmetrically, *H. tityrus* entered Estonia for the first time in 1998, by 1999 had established several successful breeding populations, and by 2006 had reached the Baltic Sea (Parmesan et al. 1999; T. Tammara, personal communication).

Another charismatic insect group with good historical records is Odonata (dragonflies and damselflies). In a study of all 37 species of resident odonates in the United Kingdom, Hickling et al. (2005) documented that 23 of the 24 temperate species had expanded their northern range limit between 1960–1995, with mean northward shift of 88 km.

Nondiapausing (i.e., active year-round) butterfly species are also moving northward with warmer winters. The northern boundary of the sagemaster butterfly has expanded from California to Washington State (420 miles) in just 35 years (Crozier 2003, 2004). During a single year—the warmest on record (1998)—it moved 75 miles northward. Laboratory and field manipulations showed that individuals are killed by a single, short exposure to extreme low temperatures (-10°C) or repeated exposures to -4°C , indicating winter cold extremes dictate the northern range limit (Crozier 2003, 2004). The desert orange tip (*Colotis evagore*), which historically was confined to northern Africa, has established resident populations in Spain while maintaining the same ecological niche. Detailed ecological and physiological studies confirm that *C. evagore* has remained a specialist of hot microclimates, needing more than 164 days at greater than 12°C to mature. It has not undergone a host switch in its new habitat, and it has not evolved a diapause stage (Jordano et al. 1991).

In the Netherlands between 1979 and 2001, 77 new epiphytic lichens colonized from the south, nearly doubling the total number of species for that community (van Herk et al. 2002). Combined numbers of terrestrial and epiphytic lichen species increased from an average of 7.5 per site to 18.9 per site. An alternate approach to documenting colonizations is to document extinction patterns. Comparing recent censuses across North America (1993–1996) with historical records (1860–1986), Parmesan (1996) documented that high proportions of population extinctions along the southern range boundary of Edith's checkerspot butterfly (*E. editha*) had shifted the mean location of living populations 92 km farther north (Parmesan 1996, 2003, 2005a).

Shifts of Tropical Species Ranges

Warming trends at lower latitudes are associated with movements of tropical species into more-temperate areas. The rufous hummingbird has undergone a dramatic shift in its winter range (Hill et al. 1998). Thirty years ago it wintered mainly in Mexico, and between 1900 and 1990, there were never more than 30 winter sightings per year along the Gulf Coast of the United States. In the early 1990s, sightings increased to more than 100 per year in the southern United States. The number of sightings has increased steadily since then—up to 1,643 by 1996, with evidence that, by 1998, resident populations had colonized 400 km inland (Howell 2002). Over this same period, winter temperatures rose by approximately 1°C (IPCC 2001b). In Florida, five new species of tropical dragonfly established themselves in 2000, an apparently natural invasion from Cuba and the Bahamas (Paulson 2001).

Similarly, North African species are moving into Spain and France, and Mediterranean species are moving up into the continental interior. The African plain tiger butterfly (*Danaus chrysippus*) established its first population in southern Spain in 1980 and by the 1990s had established multiple, large metapopulations (Haeger 1999).

Elevational Shifts

Montane studies have generally been scarcer and less well documented (lower sampling resolution), but a few good data sets show a general movement of species upward

in elevation. By comparing species compositions in fixed plots along an elevational gradient in Monteverde National Park, Costa Rica, Pounds et al. (1999, 2005) documented that lowland birds have begun breeding in montane cloud-forest habitat over the past 20 years. A similar study across 26 mountains in Switzerland documented that alpine flora have expanded toward the summits since the plots were first censused in the 1940s (Grabherr et al. 1994, Pauli et al. 1996). Upward movement of treelines has been observed in Siberia (Moiseev & Shiyatov 2003) and in the Canadian Rocky Mountains, where temperatures have risen by 1.5°C (Luckman & Kavanagh 2000).

The few studies of lower elevational limits show concurrent contractions upward of these warm range boundaries. Because warm boundaries generally have data gaps through time, these studies have conducted recensuses of historically recorded (sedentary) populations and looked for nonrandom patterns of long-term population extinctions.

A 1993–1996 recensus of Edith's checkerspot butterfly (*E. editha*) populations recorded 1860–1986 throughout its range (Mexico to Canada) documented that more than 40% of populations from 0–2400 m were extinct (in spite of having suitable habitat), whereas less than 15% were extinct at the highest elevations (2400–3500 m) (Parmesan 1996). Over the past 50–100 years, snowpack below 2400 m has become lighter by 14% and melts 7 days earlier, whereas higher elevations (2400–3500 m) have 8% heavier snowpack and no change in melt date (Johnson et al. 1999). In concert with altered snow dynamics, the mean location of *E. editha* populations has shifted upward by 105 m (Parmesan 1996, 2003, 2005a).

In southern France, metapopulations of the cool-adapted Apollo butterfly (*Parnassius apollo*) have gone extinct over the past 40 years on plateaus less than 850 m high but have remained healthy where plateaus were greater than 900 m high (Descimon et al. 2006). The data suggest that dispersal limitation was important, and this strong flyer can persist when nearby higher elevation habitats exist to colonize. In Spain, the lower elevational limits of 16 species of butterfly have risen an average of 212 m in 30 years, concurrent with a 1.3°C rise in mean annual temperatures (Wilson et al. 2005).

In the Great Basin of the western United States, 7 out of 25 recensused populations of the pika (*Ochotona princeps*, Lagomorpha) were extinct since being recorded in the 1930s (Beever et al. 2003). Human disturbance is minimal because pika habitat is high-elevation talus (scree) slopes, which are not suitable for ranching or recreational activities. Extinct populations were at significantly lower elevations than those still present (Parmesan & Galbraith 2004). Field observations by Smith (1974) documented that adult pika stopped foraging in the midday heat in August at low elevation sites. Subsequent experiments showed that adults were killed within a half hour at more than 31°C (Smith 1974).

Marine Community Shifts

Decades of ecological and physiological research document that climatic variables are primary drivers of distributions and dynamics of marine plankton and fish (Hays et al. 2005, Roessig et al. 2004). Globally distributed planktonic records show strong shifts of phytoplankton and zooplankton communities in concert with regional oceanic

climate regime shifts, as well as expected poleward range shifts and changes in timing of peak biomass (Beaugrand et al. 2002, deYoung et al. 2004, Hays et al. 2005, Richardson & Schoeman 2004). Some copepod communities have shifted as much as 1000 km northward (Beaugrand et al. 2002). Shifts in marine fish and invertebrate communities have been particularly well documented off the coasts of western North America and the United Kingdom. These two systems make an interesting contrast (see below) because the west coast of North America has experienced a 60-year period of significant warming in nearshore sea temperatures, whereas much of the U.K. coast experienced substantial cooling in the 1950s and 1960s, with warming only beginning in the 1970s (Holbrook et al. 1997, Sagarin et al. 1999, Southward et al. 2005).

Sagarin et al. (1999) related a 2°C rise of SST in Monterey Bay, California, between 1931 and 1996 to a significant increase in southern-ranged species and decrease of northern-ranged species. Holbrook et al. (1997) found similar shifts over the past 25 years in fish communities in kelp habitat off California.

Much of the data from the North Atlantic, North Sea, and coastal United Kingdom have exceptionally high resolution and long time series, so they provide detailed information on annual variability, as well as long-term trends. Over 90 years, the timing of animal migration (e.g., veined squid, *Loligo forbesi*, and flounder *Platichthys flesus*) followed decadal trends in ocean temperature, being later in cool decades and up to 1–2 months earlier in warm years (Southward et al. 2005).

In the English Channel, cold-adapted fish (e.g., herring *Clupea harengus*) declined during both warming periods (1924 to the 1940s, and post-1979), whereas warm-adapted fish did the opposite (Southward et al. 1995, 2005). For example, pilchard *Sardina pilchardus* increased egg abundances by two to three orders of magnitude during recent warming. In the North Sea, warm-adapted species (e.g., anchovy *Engraulis encrasicolus* and pilchard) have increased in abundances since 1925 (Beare et al. 2004), and seven out of eight have shifted their ranges northward (e.g., bib, *Trisopterus luscus*) by as much as 100 km per decade (Perry et al. 2005). Records dating back to 1934 for intertidal invertebrates show equivalent shifts between warm- and cold-adapted species (e.g., the barnacles *Semibalanus balanoides* and *Cbthamalus* spp., respectively), mirroring decadal shifts in coastal temperatures (Southward et al. 1995, 2005).

Pest and Disease Shifts

Pest species are also moving poleward and upward. Over the past 32 years, the pine processionary moth (*Thaumetopoea pityocampa*) has expanded 87 km at its northern range boundary in France and 110–230 m at its upper altitudinal boundary in Italy (Battisti et al. 2005). Laboratory and field experiments have linked the feeding behavior and survival of this moth to minimum nighttime temperatures, and its expansion has been associated with warmer winters. In the Rocky Mountain range of the United States, mountain pine beetle (*Dendroctonus ponderosae*) has responded to warmer temperatures by altering its life cycle. It now only takes one year per generation rather than its previous two years, allowing large increases in population abundances, which, in turn, have increased incidences of a fungus they transmit (pine blister rust,

Cronartium ribicola) (Logan et al. 2003). Increased abundance of a nematode parasite has also occurred as its life cycle shortened in response to warming trends. This has had associated negative impacts on its wild musk oxen host, causing decreased survival and fecundity (Kutz et al. 2005).

In a single year (1991), the oyster parasite *Perkinsus marinus* extended its range northward from Chesapeake Bay to Maine—a 500 km shift. Censuses from 1949 to 1990 showed a stable distribution of the parasite from the Gulf of Mexico to its northern boundary at Chesapeake Bay. The rapid expansion in 1991 has been linked to above-average winter temperatures rather than human-driven introduction or genetic change (Ford 1996). A kidney disease has been implicated in low-elevation trout declines in Switzerland. High mortality from infection occurs above 15°–16°C, and water temperatures have risen in recent decades. High infection rates (27% of fish at 73% of sites) at sites below 400 m have been associated with a 67% decline in catch; mid-elevation sites had lower disease incidence and only moderate declines in catch; and the highest sites (800–3029 m) had no disease present and relatively stable catch rates (Hari et al. 2006).

Changes in the wild also affect human disease incidence and transmission through alterations in disease ecology and in distributions of their wild vectors (Parmesan & Martens 2006). For example, in Sweden, researchers have documented marked increases in abundances of the disease-transmitting tick *Ixodes ricinus* along its northernmost range limit (Lindgren & Gustafson 2001). Between the early 1980s and 1994, numbers of ticks found on domestic cats and dogs increased by 22%–44% along the tick's northern range boundary across central Sweden. In the same time period, this region had a marked decrease in the number of extremely cold days (<−12°C) in winter and a marked increase in warm days (>10°C) during the spring, summer, and fall. Previous studies on temperature developmental and activity thresholds indicated the observed warmer temperatures cause decreased tick mortality and longer growing seasons (Lindgren & Gustafson 2001).

Trees and Treelines: Complex Responses

A complex of interacting factors determines treeline, often causing difficulties in interpretation of twentieth-century trends. Some species are “well behaved” in that they show similar patterns of increased growth at treeline during the early warming in the 1930s and 1940s as during the recent warming of the past 20 years. In recent decades, treelines have shifted northward in Sweden (Kullman 2001) and eastern Canada (Lescop-Sinclair & Payette 1995), and upward in Russia (Meshinev et al. 2000, Moiseev & Shiyatov 2003) and New Zealand (Wardle & Coleman 1992).

However, in other studies, researchers saw a strong response to warming in the late 1930s and 1940s but a weaker (or absent) response in recent warm decades (Innes 1991, Jacoby & D'Arrigo 1995, Lescop-Sinclair & Payette 1995, Briffa et al. 1998a,b), possibly resulting from differences in rainfall between the two warm periods. In Alaska, recent decades have been relatively dry, which may have prevented trees from responding to current warming as they did before (Barber et al. 2000, Briffa et al. 1998b). In contrast, treelines in the arid southwest United States, which has

had increased rainfall, have shown unprecedented increased tree-ring growth at high elevations (Swetnam & Betancourt 1998).

An impressive study across all of northern Russia from 1953–2002 showed a shift in tree allometries. In areas where summer temperatures and precipitation have both increased, a general increase in biomass (up 9%) is primarily a result of increased greenery (33% more carbon in leaves and needles), rather than woody parts (roots and stem). In areas that have experienced warming and drying trends, greenery has decreased, and both roots and stems have increased (Lapenis et al. 2005).

EXTINCTIONS

Amphibians

Documented rapid loss of habitable climate space makes it no surprise that the first extinctions of entire species attributed to global warming are mountain-restricted species. Many cloud-forest-dependent amphibians have declined or gone extinct on a mountain in Costa Rica (Pounds et al. 1999, 2005). Among harlequin frogs in Central and South American tropics, an astounding 67% have disappeared over the past 20–30 years. Pounds et al. (2006) hypothesised that recent trends toward warmer nights and increased daytime cloud cover have shifted mid-elevation sites (1000–2400 m), where the preponderance of extinctions have occurred, into thermally optimum conditions for the chytrid fungus, *Batrachochytrium dendrobatidis*.

Tropical Coral Reefs

Elevated sea temperatures as small as 1°C above long-term summer averages lead to bleaching (loss of coral algal symbiont), and global SST has risen an average of 0.1°–0.2°C since 1976 (Hoegh-Guldberg 1999, IPCC 2001b). A more acute problem for coral reefs is the increase in extreme temperature events. El Niño events have been increasing in frequency and severity since records began in the early 1900s, and researchers expect this trend to continue over coming decades (Easterling et al. 2000, IPCC 2001b, Meehl et al. 2000). A particularly strong El Niño in 1997–1998 caused bleaching in every ocean (up to 95% of corals bleached in the Indian Ocean), ultimately resulting in 16% of corals rendered extinct globally (Hoegh-Guldberg 1999, 2005b; Wilkinson 2000).

Recent evidence for genetic variation among the obligate algal symbiont in temperature thresholds suggests that some evolutionary response to higher water temperatures may be possible (Baker 2001, Rowan 2004). Changes in genotype frequencies toward increased frequency of high-temperature-tolerant symbiont appear to have occurred within some coral populations between the mass bleaching events of 1997–1998 and 2000–2001 (Baker et al. 2004). However, other studies indicate that many entire reefs are already at their thermal tolerance limits (Hoegh-Guldberg 1999). Coupled with poor dispersal of symbiont between reefs, this has led several researchers to conclude that local evolutionary responses are unlikely to mitigate the negative impacts of future temperature rises (Donner et al. 2005, Hoegh-Guldberg et al. 2002).

One optimistic result suggests that corals, to some extent, may be able to mirror terrestrial range shifts. Two particularly cold-sensitive species (staghorn coral, *Acropora cervicornis*, and elkhorn coral, *Acropora palmata*) have recently expanded their ranges into the northern Gulf of Mexico (first observation in 1998), concurrent with rising SST (Precht & Aronson 2004). Although continued poleward shift will be limited by light availability at some point (Hoegh-Guldberg 1999), small range shifts may aid in developing new refugia against extreme SST events in future.

Although impacts have not yet been observed, the fate of coral reefs may be as, or more, affected in coming decades by the direct effects of CO₂ rather than temperature rise. Increased atmospheric CO₂ since industrialization has significantly lowered ocean pH by 0.1. The more dire projections (a doubling to tripling of current CO₂ levels) suggest that, by 2050, oceans may be too acidic for corals to calcify (Caldeira & Wickett 2003, Hoegh-Guldberg 2005a, Orr et al. 2005).

Population Extinctions Leading to Range Contractions

Many species have suffered reduced habitable area due to recent climate change. For those species that have already been driven extinct at their equatorial or lower range boundaries, some have either failed to expand poleward or are unable to expand due to geographic barriers. Such species have suffered absolute reductions in range size, putting them at greater risk of extinction in the near future.

This is particularly evident in polar species, as these are already pushed against a geographical limit. Researchers have seen large reductions in population abundances and general health along the extreme southern populations of Arctic polar bears (Derocher 2005, Derocher et al. 2004, Stirling et al. 1999) and the extreme northern populations of Antarctic Adélie and emperor penguins (Ainley et al. 2003, Croxall et al. 2002, Emslie et al. 1998, Fraser et al. 1992, Smith et al. 1999, Taylor & Wilson 1990, Wilson et al. 2001). In the United Kingdom, four boreal odonates have contracted northward by an average of 44 km over 40 years (Hickling et al. 2005).

Similarly, high numbers of population extinctions have occurred along the lower elevational boundaries of mountaintop species, such as pikas in the western United States (Beever et al. 2003) and the Apollo butterfly in France (Descimon et al. 2006). For 16 mountain-restricted butterflies in Spain, warming has already reduced their habitat by one third in just 30 years (Wilson et al. 2005). Warming and drying trends on Mt. Kilimanjaro have increased fire impacts, which have caused a 400-m downward contraction of closed (cloud) forest, now replaced by an open, dry alpine system (Hemp 2005). Temperate low-elevation species are not immune: Twenty-five percent of temperate butterflies in Europe contracted northward by 35–50 km over a 30–70-year period. For one of these, its northern range boundary had not expanded, so it suffered an overall contraction of range size (Parmesan et al. 1999).

EVOLUTION AND PLASTICITY

Species ranges are dynamic. Historically, ecologists have viewed species' niches as static and range shifts over time as passive responses to major environmental changes (global climate shifts or geological changes in corridors and barriers).

There is no doubt that climate plays a major role in limiting terrestrial species' ranges (Andrewartha & Birch 1954; Bale et al. 2002; Parmesan et al. 2000, 2005; Precht et al. 1973; Webb & Bartlein 1992; Weiser 1973; Woodward 1987). Recent physiological and biogeographic studies in marine systems also implicate temperature as a primary driver of species' ranges (Hoegh-Guldberg 1999, 2005b; Hoegh-Guldberg & Pearse 1995).

However, evolutionary processes clearly can substantially influence the patterns and rates of response to climate change. Theoretically, evolution can also drive range shifts in the absence of environmental change (Holt 2003). A prime example of this is the hybridization of two species of Australian fruit fly that led to novel adaptations, allowing range expansion with no concomitant environmental change (Lewontin & Birch 1966).

The problem of estimating the relative roles of evolution and plasticity is tractable with extensive, long-term ecological and genetic data. For example, genetic analysis of a population of red squirrels in the Arctic indicated that 62% of the change in breeding dates occurring over a 10-year period was a result of phenotypic plasticity, and 13% was a result of genetic change in the population (Bertheaux et al. 2004, Réale et al. 2003).

Geneticists in the 1940s noticed that certain chromosomal inversions in fruit flies (*Drosophila*) were associated with heat tolerance (Dobzhansky 1943, 1947). These "hot" genotypes were more frequent in southern than in northern populations and increased within a population during each season, as temperatures rose from early spring through late summer. Increases in the frequencies of warm-adapted genotypes have occurred in wild populations of *Drosophila* *ssp* in Spain between 1976 and 1991 (Rodríguez-Trelles & Rodríguez 1998, Rodríguez-Trelles et al. 1996, 1998), as well as in the United States between 1946 and 2002 (Levitan 2003). The change in the United States was so great that populations in New York in 2002 were converging on genotype frequencies found in Missouri in 1946.

In contrast, red deer in Norway show completely plastic responses. Their body size responds rapidly to yearly variability of winter temperatures. Warmer winters cause developing males to become larger while females become smaller (Post et al. 1999). In consequence, the end result of a gradual winter warming trend has been an increase in sexual dimorphism.

A surprising twist is that species whose phenology is under photoperiodic control have also responded to temperature-driven selection for spring advancement or fall delay. Bradshaw & Holzapfel (2001) showed that the pitcher plant mosquito, *Wyeomyia smithii*, has evolved a shorter critical photoperiod in association with a longer growing season. Northern populations of this mosquito now use a shorter day-length cue to enter winter diapause, doing so later in the fall than they did 24 years ago.

The Role of Evolution in Shaping Species' Impacts

Increasing numbers of researchers use analyses of current intraspecific genetic variation for climate tolerance to argue for a substantive role of evolution in mitigating

negative impacts of future climate change (Baker 2001, Baker et al. 2004, Davis & Shaw 2001, Rowan 2004). However, in spite of a plethora of data indicating local adaptation to climate change at specific sites, the fossil record shows little evidence for the evolution of novel phenotypes across a species as a whole. Pleistocene glaciations represent shifts 5–10 times the magnitude of twentieth-century global warming. These did not result in major evolution at the species level (i.e., appearance of new forms outside the bounds of known variation for that species), nor in major extinction or speciation events. Existing species appeared to shift their geographical distributions as though tracking the changing climate, rather than remaining stationary and evolving new forms (Coope 1994, Davis & Zabiniski 1992, Huntley 1991).

Most of the empirical evidence for rapid adaptation to climate change comes from examples of evolution in the interiors of species' ranges toward higher frequencies of already existing heat-tolerant genotypes. In studies that focus on dynamics at the edge of a species' range or across an entire range, a different picture emerges. Several studies suggest that the effects of both genetic constraints and asymmetrical gene flow are intensified close to species' borders (Antonovics 1976, Garcia-Ramos & Kirkpatrick 1997, Hoffmann & Blows 1994). It is expected that a warming climate strengthens climate stress at equatorial range boundaries and reduces it at poleward boundaries. Equatorial boundary populations are often under natural selection for increased tolerance to extreme climate in the absence of climate change, but may be unable to respond due to lack of necessary genetic variance. Furthermore, gene flow from interior populations may stifle response to selection at the range limits, even when sufficient genetic variation exists (Kirkpatrick & Barton 1997).

Because of strong trade-offs between climate tolerance and resource/habitat preferences, a relaxation of selection on climate tolerance at northern boundaries may cause rapid evolution of these correlated traits. This process has been investigated in the European butterfly *Aricia agestis*, in which populations near the northern range boundary had previously adapted to cool conditions by specializing on the host genus, *Helianthemum*, which grows in hot microclimates and hence supports fast larval growth. Climate warming did not initially cause range expansion because *Helianthemum* was absent to the immediate north of the range limit. However, warming did permit rapid evolution of a broader diet at the range limit, to a host used in more southern populations, *Geranium*, which grows in cooler microclimates. Once this local diet evolution occurred, the boundary expanded northward across the band from which *Helianthemum* was absent but *Geranium* was present (Thomas et al. 2001).

This example shows how a complex interplay may occur between evolutionary processes and ecological responses to extreme climates and climate change. However, these evolutionary events did not constitute alternatives to ecological responses to climate change; they modulated those changes. Adaptive evolution of host preference occurred at the northern range boundary in response to temperature rise, but genetic variation for host use already existed within the *A. agestis* butterfly. In this case, evolutionary processes are not an alternative to range movement, but instead modulate the magnitude and dynamics of the range shift. This is not likely to be an isolated example because populations of other species near poleward boundaries

are known to specialize on resources that mitigate the effects of cool climate. Such resources either support rapid growth or occur in the hottest available microclimates (Nylin 1988, Scriber & Lederhouse 1992, Thomas et al. 2001).

In addition to resource choice, dispersal tendency evolves at range margins in response to climate change. In nonmigratory species, the simplest explanation of northward range expansions is that individuals have always crossed the species' boundary, and with climate warming, some of these emigrants are successful at founding new populations outside the former range. When dispersal tendency is heritable, these new populations contain dispersive individuals and higher rates of dispersal will soon evolve at the expanding boundary.

Evolution toward greater dispersal has indeed been documented in several species of insect. Two species of wing-dimorphic bush crickets in the United Kingdom have evolved longer wings at their northern range boundary, as mostly long-winged forms participated in the range expansion and short-winged forms were left behind (Thomas et al. 2001). Adults of newly colonized populations of the speckled wood butterfly (*Pararge aegeria*) in the United Kingdom have larger thoraces and greater flight capability than historical populations just to the south (Hill et al. 1999). Variation in dispersal abilities can be cryptic. Newly founded populations of the butterfly *M. cinxia* contained females that were genetically superior dispersers due to increased production of ATP (Hanski et al. 2004).

Overall, empirical evidence suggests that evolution can complement, rather than supplant, projected ecological changes. However, there is little theoretical or experimental support to suggest that climate warming will cause absolute climatic tolerances of a species to evolve sufficiently to allow it to conserve its geographic distribution in the face of climate change and thereby inhabit previously unsuitable climatic regimes (Donner et al. 2005; Hoegh-Guldberg 1999, 2005b; Hoegh-Guldberg et al. 2002; Jump & Peñuelas 2005).

CONCLUDING THOUGHTS ON EVOLUTION AND CLIMATE CHANGE

For species-level evolution to occur, either appropriate novel mutations or novel genetic architecture (new gene complexes) would have to emerge to allow a response to selection. Lynch & Lande (1993) used a genetic model to infer rates of environmental change that would allow populations to respond adaptively. However, Travis & Futuyma (1993)—discussing the same question from broad paleontological, population, genetic, and ecological perspectives—highlighted the complexity of predicting future responses from currently known processes. Fifteen years later, answers still lie very much in empirical observations. These observations indicate that, although local evolutionary responses to climate change have occurred with high frequency, there is no evidence for change in the absolute climate tolerances of a species. This view is supported by the disproportionate number of population extinctions documented along southern and low-elevation range edges in response to recent climate warming, resulting in contraction of species' ranges at these warm boundaries, as well as by extinctions of many species.

SUMMARY POINTS

1. The advance of spring events (bud burst, flowering, breaking hibernation, migrating, breeding) has been documented on all but one continent and in all major oceans for all well-studied marine, freshwater, and terrestrial groups.
2. Variation in phenological response between interacting species has already resulted in increasing asynchrony in predator-prey and insect-plant systems, with mostly negative consequences.
3. Poleward range shifts have been documented for individual species, as have expansions of warm-adapted communities, on all continents and in most of the major oceans for all well-studied plant and animal groups.
4. These observed changes have been mechanistically linked to local or regional climate change through long-term correlations between climate and biological variation, experimental manipulations in the field and laboratory, and basic physiological research.
5. Shifts in abundances and ranges of parasites and their vectors are beginning to influence human disease dynamics.
6. Range-restricted species, particularly polar and mountaintop species, show more-severe range contractions than other groups and have been the first groups in which whole species have gone extinct due to recent climate change. Tropical coral reefs and amphibians are the taxonomic groups most negatively impacted.
7. Although evolutionary responses have been documented (mainly in insects), there is little evidence that observed genetic shifts are of the type or magnitude to prevent predicted species extinctions.

FUTURE ISSUES

1. Ocean-atmosphere processes are dynamically changing in response to anthropogenic forcings. Indices such as the El Niño Southern Oscillation and the North Atlantic Oscillation may be a poor basis for projecting future biological impacts.
2. Projections of impacts will be aided by a better mechanistic understanding of ecological, behavioral, and evolutionary responses to complex patterns of climate change, and in particular to impacts of extreme weather and climate events.

ACKNOWLEDGMENTS

I would like to give many thanks to C. Britt, M. Butcher, J. Mathews, C. Metz, and P. van der Meer for help with the literature search and to D. Simberloff and D. Futuyma for helpful comments on earlier versions. I also want to give special appreciation to M.C. Singer for his critique and editorial assistance.

LITERATURE CITED

- Ahmad QK, Warrick RA, Downing TE, Nishioka S, Parikh KS, et al. 2001. Methods and tools. See IPCC 2001a, pp. 105–43
- Ainley DG, Ballard G, Emslie SD, Fraser WR, Wilson PR, Woehler EJ. 2003. Adelie penguins and environmental change. *Science* 300:429–30
- Ainley DG, Divoky GJ. 1998. Climate change and seabirds: a review of trends in the eastern portion of the Pacific Basin. *Pac. Seab.* 25:20
- Alley RB, Clark PU, Huybrechts P, Joughin I. 2005. Ice-sheet and sea-level changes. *Science* 310:456–60
- Alley RB, Marotzke J, Nordhaus WD, Overpeck JT, Peteet DM, et al. 2003. Abrupt climate change. *Science* 299:2005–10
- Andrewartha HG, Birch LC. 1954. *The Distribution and Abundance of Animals*. Chicago, IL: Univ. Chicago Press
- Anisimov O, Fitzharris B, Hagen JO, Jefferies R, Marchant H, et al. 2001. Polar regions (Arctic and Antarctic). See IPCC 2001a, pp. 801–47
- Antonovics J. 1976. The nature of limits to natural selection. *Ann. Mo. Bot. Gard.* 63:224–47
- Arctic Climate Impact Assessment. 2004. *Impacts of a Warming Arctic*. Cambridge, UK: Cambridge Univ. Press
- Atkinson A, Siegel V, Pakhomov E, Rothery P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–3
- Badeck FW, Bondeau A, Böttcher K, Doktor D, Lucht W, et al. 2004. Responses of spring phenology to climate change. *New Phytol.* 162:295–309
- Baker AC. 2001. Reef corals bleach to survive change. *Nature* 411:765–66
- Baker AC, Starger CJ, McClanahan TR, Glynn PW. 2004. Coral reefs: corals' adaptive response to climate change. *Nature* 430:741
- Bale JS, Masters GJ, Hodgkinson ID, Awmack C, Bezemer TM, et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Change Biol.* 8:1–16
- Barber VA, Juday GP, Finney BP. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* 405:668–73
- Barbraud C, Weimerskirch H. 2001. Emperor penguins and climate change. *Nature* 411:183–86
- Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, et al. 2005. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecol. Appl.* 15:2084–96

- Beare DJ, Burns F, Greig A, Jones EG, Peach K, et al. 2004. Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. *Mar. Ecol. Prog. Ser.* 284:269–78
- Beaugrand G, Reid PC, Ibanez F, Lindley JA, Edwards M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296:1692–94
- Beebee TJC. 1995. Amphibian breeding and climate. *Nature* 374:219–20
- Beever EA, Brussard PF, Berger J. 2003. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. *J. Mammal.* 84:37–54
- Berteaux D, Reale D, McAdam AG, Boutin S. 2004. Keeping pace with fast climate change: Can Arctic life count on evolution? *Integr. Comp. Biol.* 44:140–51
- Blenckner T, Hillebrand H. 2002. North Atlantic Oscillation signatures in aquatic and terrestrial ecosystems: a meta-analysis. *Glob. Change Biol.* 8:203–12
- Both C, Artemyev AV, Blaauw B, Cowie RJ, Dekhuijzen AJ, et al. 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proc. R. Soc. London Ser. B* 271:1657–62
- Bradley NL, Leopold AC, Ross J, Wellington H. 1999. Phenological changes reflect climate change in Wisconsin. *Proc. Natl. Acad. Sci. USA* 96:9701–4
- Bradshaw WE, Holzapfel CM. 2001. Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl. Acad. Sci. USA* 98:14509–11
- Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Harris IC, et al. 1998a. Trees tell of past climates, but are they speaking less clearly today? *Philos. Trans. R. Soc. London Ser. B* 353:65–73
- Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Shiyatov SG, Vaganov EA. 1998b. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature* 391:678–82
- Brown JL, Li SH, Bhagabati N. 1999. Long-term trend toward earlier breeding in an American bird: a response to global warming? *Proc. Natl. Acad. Sci. USA* 96:5565–69
- Bumpus HC. 1899. The elimination of the unfit as illustrated by the introduced sparrow, *Passer domesticus*. In *Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Holl*, 1896–97, pp. 209–26. Boston: Ginn & Co
- Burger M. 1998. *Physiological mechanisms limiting the northern boundary of the winter range of the northern cardinal* (*Cardinalis cardinalis*). PhD diss. Univ. Mich., Ann Arbor
- Burton J. 1975. The effects of recent climatic change on British insects. *Bird Study* 22:203–4
- Burton JF. 1998a. The apparent effects of climatic changes since 1850 on European lepidoptera. *Mém. Soc. R. Belge Entomol.* 38:125–44
- Burton JF. 1998b. The apparent responses of European lepidoptera to the climate changes of the past hundred years. *Atropos* 5:24–30
- Caldeira K, Wickett ME. 2003. Anthropogenic carbon and ocean pH. *Nature* 425:365
- Cayan DR, Kammerdiener SA, Dettinger MD, Caprio JM, Peterson DH. 2001. Changes in the onset of spring in the western United States. *Bull. Am. Meteorol. Soc.* 82:399–415

- Chapin FS III, Berman M, Callaghan TV, Convey P, Crepin AS, et al. 2006. Polar systems. In *Millennium Ecosystem Assessment, Ecosystems and Human Well-Being, Volume 1: Current State and Trends*, ed. R Hassan, R Scholes, N Ash, pp. 717–43. Washington, DC: Island Press
- Chapin FS III, Shaver GR, Giblin AE, Nadelhoffer KG, Laundre JA. 1995. Response of Arctic tundra to experimental and observed changes in climate. *Ecology* 76:694–711
- Chuine I, Beaubien E. 2001. Phenology is a major determinant of tree species range. *Ecol. Lett.* 4:500–10
- Coope GR. 1994. The response of insect faunas to glacial-interglacial climatic fluctuations. *Philos. Trans. R. Soc. London Ser. B.* 344:19–26
- Crick HQ, Dudley C, Glue DE. 1997. UK birds are laying eggs earlier. *Nature* 388:526
- Croxall JP, Trathan PN, Murphy EJ. 2002. Environmental change and Antarctic seabird populations. *Science* 297:1510–14
- Crozier L. 2003. Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris*. *Oecologia* 135:648–56
- Crozier L. 2004. Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology* 85:231–41
- Davis MB, Shaw RG. 2001. Range shifts and adaptive responses to quaternary climate change. *Science* 292:673–79
- Davis MB, Zabinski C. 1992. Changes in geographical range resulting from greenhouse warming: effects on biodiversity in forests. In *Global Warming and Biological Diversity*, ed. TEL Peters, R Lovejoy, pp. 297–308. New Haven, CT: Yale Univ. Press
- Dennis RLH. 1993. *Butterflies and Climate Change*. Manchester, UK: Manchester Univ. Press
- Derocher AE. 2005. Population ecology of polar bears at Svalbard, Norway. *Popul. Ecol.* 47:267–75
- Derocher AE, Lunn NJ, Stirling I. 2004. Polar bears in a warming climate. *Integr. Comp. Biol.* 44:163–76
- Descimon H, Bachelard P, Boitier E, Pierrat V. 2006. Decline and extinction of *Parnassius apollo* populations in France—continued. In *Studies on the Ecology and Conservation of Butterflies in Europe (EBIE)*, ed. E Kühn, R Feldmann, J Settele. Bulgaria: PENSOFT. In press
- deYoung B, Harris R, Alheit J, Beaugrand G, Mantua N, Shannon L. 2004. Detecting regime shifts in the ocean: data considerations. *Prog. Oceanogr.* 60:143–64
- Dobzhansky TH. 1943. Genetics of natural populations. IX. Temporal changes in the composition of populations of *Drosophila pseudoobscura*. *Genetics* 28:162–86
- Dobzhansky TH. 1947. A response of certain gene arrangements in the third chromosome of *Drosophila pseudoobscura* to natural selection. *Genetics* 32:142–60
- Donner SD, Skirving WJ, Little CM, Oppenheimer M, Hoegh-Guldberg O. 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. *Glob. Change Biol.* 11:2251–65
- Doran PT, Prisco JC, Lyons WB, Walsh JE, Fountain AG, et al. 2002. Antarctic climate cooling and terrestrial ecosystem response. *Nature* 415:517–22

- Dose V, Menzel A. 2004. Bayesian analysis of climate change impacts in phenology. *Glob. Change Biol.* 10:259–72
- Dunn PO, Winkler DW. 1999. Climate change has affected the breeding date of tree swallows throughout North America. *Proc. R. Soc. London Ser. B* 266:2487–90
- Easterling DR, Meehl J, Parmesan C, Chagnon S, Karl TR, Mearns LO. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289:2068–74
- Ehrlich PR, Murphy DD, Singer MC, Sherwood CB, White RR, Brown IL. 1980. Extinction, reduction, stability and increase: the responses of checkerspot butterfly populations to the California drought. *Oecologia* 46:101–5
- Emslie SD, Fraser W, Smith RC, Walker W. 1998. Abandoned penguin colonies and environmental change in the Palmer Station area, Anvers Island, Antarctic Peninsula. *Antarct. Sci.* 10:257–68
- Ferguson SH, Stirling I, McLoughlin P. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. *Mar. Mamm. Sci.* 21:121–35
- Ford EB. 1945. *Butterflies*. London: Collins
- Ford SE. 1996. Range extension by the oyster parasite *Perkinsus marinus* into the northeastern United States: response to climate change? *J. Shellfish Res.* 15:45–56
- Forister ML, Shapiro AM. 2003. Climatic trends and advancing spring flight of butterflies in lowland California. *Glob. Change Biol.* 9:1130–35
- Fraser WR, Trivelpiece WZ, Ainley DC, Trivelpiece SG. 1992. Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biol.* 11:525–31
- Garcia-Ramos G, Kirkpatrick M. 1997. Genetic models of adaptation and gene flow in peripheral populations. *Evolution* 51:21–28
- Gaston AJ, Gilchrist HG, Hipfner M. 2005. Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich's guillemot (*Uria lomvia* L.). *J. Anim. Ecol.* 74:832–41
- Gibbs JP, Breisch AR. 2001. Climate warming and calling phenology of frogs near Ithaca, New York, 1900–1999. *Conserv. Biol.* 15:1175–78
- Gordo O, Brotons L, Rerrer X, Comass P. 2005. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Glob. Change Biol.* 11:12–21
- Grabherr G, Gottfried M, Pauli H. 1994. Climate effects on mountain plants. *Nature* 369:448
- Grinnell J. 1917. Field tests of theories concerning distributional control. *Am. Nat.* 51:115–28
- Gross L. 2005. As the Antarctic ice pack recedes, a fragile ecosystem hangs in the balance. *PLoS Biol.* 3(4):e127
- Gudmundsson F. 1951. The effects of the recent climatic changes on the bird life of Iceland. *Proc. 10th Int. Ornithol. Congr., Uppsala, June 1950*, pp. 502–14
- Gurevitch J, Hedges LV. 1999. Statistical issues in ecological meta-analyses. *Ecology* 80:1142–49
- Haeger JF. 1999. *Danaus chrysippus* (Linnaeus 1758) en la Península Ibérica: migraciones o dinámica de metapoblaciones? *Shilap* 27:423–30

- Hanski I, Erälahti C, Kankare M, Ovaskainen O, Sirén H. 2004. Variation in migration propensity among individuals maintained by landscape structure. *Ecol. Lett.* 7:958–66
- Hari RE, Livingstone DM, Siber R, Burkhardt-Holm P, Güttinger H. 2006. Consequences of climatic change for water temperature and brown trout population in Alpine rivers and streams. *Glob. Change Biol.* 12:10–26
- Harrington R, Woiwod I, Sparks T. 1999. Climate change and trophic interactions. *Trends Ecol. Evol.* 14:146–50
- Harris G. 1964. Climatic changes since 1860 affecting European birds. *Weather* 19:70–79
- Hays GC, Richardson AJ, Robinson C. 2005. Climate change and marine plankton. *Trends Ecol. Evol.* 20:337–44
- Heath J. 1974. A century of changes in the lepidoptera. In *The Changing Flora and Fauna of Britain*, ed. DL Hawkesworth, 6:275–92. London: Syst. Assoc.
- Hemp A. 2005. Climate change-driven forest fires marginalize the impact of ice cap wasting on Kilimanjaro. *Glob. Change Biol.* 11:1013–23
- Hickling R, Roy DB, Hill JK, Thomas CD. 2005. A northward shift of range margins in British Odonata. *Glob. Change Biol.* 11:502–6
- Hill GE, Sargent RR, Sargent MB. 1998. Recent change in the winter distribution of Rufous Hummingbirds. *Auk* 115:240–45
- Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, et al. 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proc. R. Soc. London Ser. B* 269:2163–71
- Hill JK, Thomas CD, Lewis OT. 1999. Flight morphology in fragmented populations of a rare British butterfly, *Hesperia comma*. *Biol. Conserv.* 87:277–84
- Hoegh-Guldberg O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshw. Res.* 50:839–66
- Hoegh-Guldberg O. 2005a. Low coral cover in a high-CO₂ world. *J. Geophys. Res.* 110:C09S06
- Hoegh-Guldberg O. 2005b. Marine ecosystems and climate change. See Lovejoy & Hannah 2005, pp. 256–71
- Hoegh-Guldberg O, Jones RJ, Ward S, Loh WK. 2002. Is coral bleaching really adaptive? *Nature* 415:601–2
- Hoegh-Guldberg O, Pearse JS. 1995. Temperature, food availability, and the development of marine invertebrate larvae. *Am. Zool.* 35:415–25
- Hoffmann AA, Blows MW. 1994. Species borders: ecological and evolutionary perspectives. *Trends Ecol. Evol.* 9:223–27
- Holbrook SJ, Schmitt RJ, Stephens JS Jr. 1997. Changes in an assemblage of temperate reef fishes associated with a climatic shift. *Ecol. Appl.* 7:1299–310
- Holmgren M, Scheffer M, Ezcurra E, Gutierrez JR, Mohren GMJ. 2001. El Niño effects on the dynamics of terrestrial ecosystems. *Trends Ecol. Evol.* 16:89–94
- Holt RD. 2003. On the evolution ecology of species' ranges. *Evol. Ecol. Res.* 5:159–78
- Howell SNG. 2002. *Hummingbirds of North America*. San Diego, CA: Academic
- Hughes L. 2000. Biological consequences of global warming: Is the signal already apparent? *Trends Ecol. Evol.* 15:56–61

- Huntley B. 1991. How plants respond to climate change: migration rates, individualism and the consequences for the plant communities. *J. Bot.* 67:15–22
- Hüppop O, Hüppop K. 2003. North Atlantic Oscillation and timing of spring migration in birds. *Proc. R. Soc. London Ser. B* 270:233–40
- Innes JL. 1991. High-altitude and high-latitude tree growth in relation to past, present, and future global climate change. *Holocene* 1:168–73
- Inouye DW, Barr B, Armitage KB, Inouye BD. 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proc. Natl. Acad. Sci. USA* 97:1630–33
- IPCC (Intergovernmental Panel Climate Change). 2001a. *Climate Change 2001: Impacts, Adaptation, and Vulnerability, Contribution of Working Group II to the Intergovernmental Panel on Climate Change Third Assessment Report*, ed. JJ McCarthy, OF Canziani, NA Leary, DJ Dokken, KS White. Cambridge, UK: Cambridge Univ. Press
- IPCC (Intergovernmental Panel Climate Change). 2001b. *Climate Change 2001: The Science of Climate Change, Contribution of Working Group I to the Intergovernmental Panel on Climate Change Third Assessment Report*, ed. JT Houghton, Y Ding, DJ Griggs, M Noguer, PJ van der Linden, X Dai, K Maskell, CA Johnson. Cambridge, UK: Cambridge Univ. Press
- Jacoby GC, D'Arrigo RD. 1995. Tree ring width and density evidence of climatic and potential forest change in Alaska. *Glob. Biogeochem. Cycles* 9:227–34
- Johnson T, Dozier J, Michaelsen J. 1999. Climate change and Sierra Nevada snowpack. *LAHS Publ.* 256:63–70
- Johnston RF, Niles DM, Rohwer SA. 1972. Hermon Bumpus and natural selection in the house sparrow *Passer domesticus*. *Evolution* 26:20–31
- Jordano D, Retamosa EC, Fernandez H. 1991. Factors facilitating the continued presence of *Colotis evagore* (Klug 1829) in southern Spain. *J. Biogeogr.* 18:637–46
- Jump AS, Peñuelas J. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol. Lett.* 8:1010–20
- Kaisila J. 1962. Immigration und Expansion der Lepidopteren in Finnland in den Jahren 1869–1960. *Acta Entomol. Fenn.* 18:1–452
- Kalela O. 1949. Changes in geographic ranges in the avifauna of northern and central Europe in response to recent changes in climate. *Bird-Band.* 20:77–103
- Kalela O. 1952. Changes in the geographic distribution of Finnish birds and mammals in relation to recent changes in climate. In *The Recent Climatic Fluctuation in Finland and its Consequences: A Symposium*, ed. I Hustichi, pp. 38–51. Helsinki: Fennia
- Karieva PM, Kingsolver JG, Huey RB, eds. 1993. *Biotic Interactions and Global Change*. Sunderland, MA: Sinauer
- Karl TR, Trenberth KE. 2003. Modern global climate change. *Science* 302:1719–23
- Keeling CD, Chin JFS, Whorf TP. 1996. Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature* 382:146–49
- Kirkpatrick M, Barton NH. 1997. Evolution of a species' range. *Am. Nat.* 150:1–23
- Kullman L. 2001. 20th century climate warming and tree-limit rise in the southern Scandes of Sweden. *Ambio* 30:72–80

- Kutz SJ, Hoberg EP, Polley L, Jenkins EJ. 2005. Global warming is changing the dynamics of Arctic host-parasite systems. *Proc. R. Soc. London Ser. B* 272:2571–76
- Lapenis A, Shvidenko A, Shepaschenko D, Nilsson S, Aiyyer A. 2005. Acclimation of Russian forests to recent changes in climate. *Glob. Change Biol.* 11:2090–102
- Lescop-Sinclair K, Payette S. 1995. Recent advance of the Arctic treeline along the eastern coast of Hudson Bay. *J. Ecol.* 83:929–36
- Levitan M. 2003. Climatic factors and increased frequencies of ‘southern’ chromosome forms in natural populations of *Drosophila robusta*. *Evol. Ecol. Res.* 5:597–604
- Lewontin RC, Birch LC. 1966. Hybridization as a source of variation for adaptation to new environments. *Evolution* 20:315–36
- Lindgren E, Gustafson R. 2001. Tick-borne encephalitis in Sweden and climate change. *Lancet* 358:16–18
- Logan JA, Regniere J, Powell JA. 2003. Assessing the impacts of global warming on forest pest dynamics. *Front. Ecol. Environ.* 1:130–37
- Lovejoy T, Hannah L, eds. 2005. In *Climate Change and Biodiversity*. New Haven, CT: Yale Univ. Press
- Luckman B, Kavanagh T. 2000. Impact of climate fluctuations on mountain environments in the Canadian Rockies. *Ambio* 29:371–80
- Lynch M, Lande R. 1993. Evolution and extinction in response to environmental change. See Karieva et al. 1993, pp. 234–50
- MacArthur RM. 1972. *Geographical Ecology*. New York: Harper & Row
- Marttila O, Hahtela T, Aarnio H, Ojalainen P. 1990. *Suomen Päiväperhoset*. Helsinki: Kirjayhtymä
- McGowan JA, Cayan DR, Dorman LM. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* 281:210–17
- Meehl GA, Zwiers F, Evans J, Knutson T, Mearns LO, Whetton P. 2000. Trends in extreme weather and climate events: issues related to modeling extremes in projections of future climate change. *Bull. Am. Meteorol. Soc.* 81:427–36
- Menzel A. 2000. Trends in phenological phases in Europe between 1951 and 1996. *Int. J. Biometeorol.* 44:76–81
- Menzel A. 2005. A 500 year pheno-climatological view on the 2003 heatwave in Europe assessed by grape harvest dates. *Meteorol. Z.* 14:75–77
- Menzel A, Dose V. 2005. Analysis of long-term time-series of beginning of flowering by Bayesian function estimation. *Meteorol. Z.* 14:429–34
- Menzel A, Fabian P. 1999. Growing season extended in Europe. *Nature* 397:659
- Menzel A, Jakobi G, Ahas R, Scheifinger H, Estrella N. 2003. Variations of the climatological growing season (1951–2000) in Germany compared with other countries. *Int. J. Climatol.* 23:793–812
- Meshinev T, Apostolova I, Koleva E. 2000. Influence of warming on timberline rising: a case study on *Pinus peuce* Griseb. in Bulgaria. *Phytocoenologia* 30:431–38
- Mikkola K. 1997. Population trends of Finnish Lepidoptera during 1961–1996. *Entomol. Fenn.* 3:121–43
- Moiseev PA, Shiyatov SG. 2003. The use of old landscape photographs for studying vegetation dynamics at the treeline ecotone in the Ural Highlands, Russia. In *Alpine Biodiversity in Europe*, ed. L Nagy, G Grabherr, C Körner, DBA Thompson, pp. 423–36. Berlin: Springer-Verlag

- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386:698–702
- Nylin S. 1988. Host plant specialization and seasonality in a phytophagous butterfly, *Polygonia c-album* (Nymphalidae). *Oikos* 53:381–86
- Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, et al. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681–86
- Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC. 2001. Ecological effects of the North Atlantic Oscillation. *Oecologia* 128:1–14
- Parmesan C. 1996. Climate and species' range. *Nature* 382:765–66
- Parmesan C. 2002. Detection of range shifts: general methodological issues and case studies using butterflies. In *Fingerprints of Climate Change: Adapted Behaviour and Shifting Species' Ranges*, ed. G-R Walther, CA Burga, PJ Edwards, pp. 57–76. Dordrecht, Netherlands: Kluwer Acad./Plenum
- Parmesan C. 2003. Butterflies as bio-indicators of climate change impacts. In *Evolution and Ecology Taking Flight: Butterflies as Model Systems*, ed. CL Boggs, WB Watt, PR Ehrlich, pp. 541–60. Chicago: Univ. Chicago Press
- Parmesan C. 2005a. Detection at multiple levels: *Euphydryas editha* and climate change. Case study. See Lovejoy & Hannah 2005, pp. 56–60
- Parmesan C. 2005b. Range and abundance changes. See Lovejoy & Hannah 2005, pp. 41–55
- Parmesan C, Gaines S, Gonzalez L, Kaufman DM, Kingsolver J, et al. 2005. Empirical perspectives on species' borders: environmental change as challenge and opportunity. *Oikos* 108:58–75
- Parmesan C, Galbraith H. 2004. *Observed Ecological Impacts of Climate Change in North America*. Arlington, VA: Pew Cent. Glob. Clim. Change
- Parmesan C, Martens P. 2006. Climate change. In *Biodiversity, Health and the Environment: SCOPE/Diversitas Rapid Assessment Project*, ed. O Sala, L Meyerson, C Parmesan. Washington, DC: Island Press. In press
- Parmesan C, Root TL, Willig MR. 2000. Impacts of extreme weather and climate on terrestrial biota. *Bull. Am. Meteorol. Soc.* 81:443–50
- Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–83
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42
- Pauli H, Gottfried M, Grabherr G. 1996. Effects of climate change on mountain ecosystems: upward shifting of mountain plants. *World Res. Rev.* 8:382–90
- Paulson DR. 2001. Recent odonata records from southern Florida: effects of global warming? *Int. J. Odonatol.* 4:57–69
- Peñuelas J, Filella I. 2001. Responses to a warming world. *Science* 294:793–94
- Perry AL, Low PJ, Ellis JR, Reynolds JD. 2005. Climate change and distribution shifts in marine fishes. *Science* 308:1912–15
- Pollard E. 1979. Population ecology and change in range of the white admiral butterfly *Ladoga camilla* L. in England. *Ecol. Entomol.* 4:61–74

- Pollard E, Eversham BC. 1995. Butterfly monitoring 2: interpreting the changes. In *Ecology and Conservation of Butterflies*, ed. AS Pullin, pp. 23–36. London: Chapman & Hall
- Post E, Langvatn R, Forchhammer MC, Stenseth NC. 1999. Environmental variation shapes sexual dimorphism in red deer. *Proc. Natl. Acad. Sci. USA* 96:4467–71
- Pounds JA, Bustamente MR, Coloma LA, Consuegra JA, Fogden MPL, et al. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439:161–67
- Pounds JA, Fogden MPL, Campbell JH. 1999. Biological response to climate change on a tropical mountain. *Nature* 398:611–15
- Pounds JA, Fogden MPL, Masters KL. 2005. Responses of natural communities to climate change in a highland tropical forest. Case study. See Lovejoy & Hannah 2005, pp. 70–74
- Precht H, Christophersen J, Hensel H, Larcher W. 1973. *Temperature and Life*. New York: Springer-Verlag
- Precht WF, Aronson RB. 2004. Climate flickers and range shifts of reef corals. *Front. Ecol. Environ.* 2:307–14
- Réale D, McAdam A, Outin G, Berteaux S. 2003. Genetic and plastic response of a northern mammal to climate change. *Proc. R. Soc. London Ser. B* 270:591–96
- Reid PC, Edwards M, Hunt HG, Warner AJ. 1998. Phytoplankton change in the North Atlantic. *Nature* 391:546
- Richardson AJ, Schoeman DS. 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305:1609–12
- Rodríguez-Trelles F, Álvarez G, Zapata C. 1996. Time-series analysis of seasonal changes of the O inversion polymorphism of *Drosophila subobscura*. *Genetics* 142:179–87
- Rodríguez-Trelles F, Rodríguez MA. 1998. Rapid micro-evolution and loss of chromosomal diversity in *Drosophila* in response to climate warming. *Evol. Ecol.* 12:829–38
- Rodríguez-Trelles F, Rodríguez MA, Scheiner SM. 1998. Tracking the genetic effects of global warming: *Drosophila* and other model systems. *Conserv. Ecol.* 2:2
- Roessig JM, Woodley CM, Cech JJ, Hansen LJ. 2004. Effects of global climate change on marine and estuarine fishes. *Rev. Fish Biol. Fish.* 14:215–75
- Roetzer T, Wittenzeller M, Haeckel H, Nekovar J. 2000. Phenology in central Europe: difference and trends of spring phenophases in urban and rural areas. *Int. J. Biometeorol.* 44:60–66
- Root TL. 1988. Energy constraints on avian distributions and abundances. *Ecology* 69:330–39
- Root TL, Hughes L. 2005. Present and future phenological changes in wild plants and animals. See Lovejoy & Hannah 2005, pp. 61–69
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60
- Rowan R. 2004. Thermal adaptation in reef coral symbionts. *Nature* 430:742
- Roy DB, Sparks TH. 2000. Phenology of British butterflies and climate change. *Glob. Change Biol.* 6:407–16

- Sagarin RD, Barry JP, Gilman SE, Baxter CH. 1999. Climate-related change in an intertidal community over short and long time scales. *Ecol. Monogr.* 69:465–90
- Salomonsen F. 1948. The distribution of birds and the recent climatic change in the North Atlantic area. *Dansk. Orn. Foren. Tidsskr.* 42:85–99
- Schwartz MD. 1998. Green-wave phenology. *Nature* 394:839–40
- Schwartz MD. 1999. Advancing to full bloom: planning phenological research for the 21st century. *Int. J. Biometeorol.* 42:113–18
- Scriber JM, Lederhouse RC. 1992. The thermal environment as a resource dictating geographic patterns of feeding specialization of insect herbivores. In *Effects of Resource Distribution on Plant-Animal Interactions*, ed. MR Hunter, T Ohgushi, PW Price, pp 429–66. New York: Academic
- Severnty DL. 1977. The use of data on the distribution of birds to monitor climatic changes. *Emu* 77:162–66
- Shoo LP, Williams SE, Hero JM. 2006. Detecting climate change induces range shifts: Where and how should we be looking? *Aust. Ecol.* 31:22–29
- Singer MC. 1972. Complex components of habitat suitability within a butterfly colony. *Science* 176:75–77
- Singer MC, Ehrlich PR. 1979. Population dynamics of the checkerspot butterfly *Euphydryas editha*. *Fortschr. Zool.* 25:53–60
- Singer MC, Thomas CD. 1996. Evolutionary responses of a butterfly metapopulation to human and climate-caused environmental variation. *Am. Nat.* 148:S9–39
- Smith AT. 1974. The distribution and dispersal of pikas: influences of behavior and climate. *Ecology* 55:1368–76
- Smith RC, Ainley D, Kaber K, Domack E, Emslie S, et al. 1999. Marine ecosystem sensitivity to historical climate change in the Antarctic Peninsula. *BioScience* 49:393–404
- Smith RIL. 1994. Vascular plants as bioindicators of regional warming in Antarctica. *Oecologia* 99:322–28
- Smol JP, Wolfe AP, Birks HJB, Douglas MSV, Jones VJ, et al. 2005. Climate-driven regime shifts in the biological communities of Arctic lakes. *Proc. Natl. Acad. Sci. USA* 102:4397–402
- Southward AJ, Hawkins SJ, Burrows MT. 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *J. Therm. Biol.* 20:127–55
- Southward AJ, Langmead O, Hardman-Mountford NJ, Aiken J, Boalch GT, et al. 2005. Long-term oceanographic and ecological research in the western English Channel. *Adv. Mar. Biol.* 47:1–105
- Sparks TH, Menzel A. 2002. Observed changes in seasons, an overview. *Int. J. Climatol.* 22:1715–26
- Sparks TH, Yates TJ. 1997. The effect of spring temperature on the appearance dates of British butterflies 1883–1993. *Ecography* 20:368–74
- Spear LB, Ainley DG. 1999. Migration routes of sooty shearwaters in the Pacific Ocean. *Condor* 101:205–18
- Stefanescu C, Peñuelas J, Filella I. 2003. Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Glob. Change Biol.* 9:1494

- Stirling I. 2002. Polar bears and seals in the eastern Beaufort Sea and Amundsen Gulf: a synthesis of population trends and ecological relationships over three decades. *Arctic* 55:59–76
- Stirling I, Lunn NJ, Iacozza J. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52:294–306
- Sturm M, Racine C, Tape K. 2001. Increasing shrub abundance in the Arctic. *Nature* 411:546–47
- Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, et al. 2005. Winter biological processes could help convert Arctic tundra to shrubland. *BioScience* 55:17–26
- Swetnam TW, Betancourt JL. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *J. Clim.* 11:3128–47
- Taylor RH, Wilson PR. 1990. Recent increase and southern expansion of Adelie penguin populations in the Ross Sea, Antarctica, related to climatic warming. *N.Z. J. Ecol.* 14:25–29
- Thomas C. 2005. Recent evolutionary effects of climate change. See Lovejoy & Hannah 2005, pp. 75–90
- Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, et al. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* 411:577–81
- Thomas CD, Lennon JJ. 1999. Birds extend their ranges northwards. *Nature* 399:213
- Thomas CD, Singer MC, Boughton D. 1996. Catastrophic extinction of population sources in a butterfly metapopulation. *Am. Nat.* 148:957–75
- Travis J, Futuyma DJ. 1993. Global change: lessons from and for evolutionary biology. See Karieva et al. 1993, pp. 234–50
- Uvarov BP. 1931. Insects and climate. *R. Entomol. Soc. London* 79:174–86
- van Herk CM, Aptroot A, van Dobben HF. 2002. Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *Lichenologist* 34:141–54
- Van Nouhuys S, Lei G. 2004. Parasitoid-host metapopulation dynamics: the causes and consequences of phenological asynchrony. *J. Anim. Ecol.* 73:526–35
- Visser ME, Both C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. B* 272:2561–69
- Walther GR, Hughes L, Vitousek P, Stenseth NC. 2005. Consensus on climate change. *Trends Ecol. Evol.* 20:648–49
- Walther GR, Post E, Convery P, Menzel A, Parmesan C, et al. 2002. Ecological responses to recent climate change. *Nature* 416:389–95
- Wardle P, Coleman MC. 1992. Evidence for rising upper limits of four native New Zealand forest trees. *N.Z. J. Bot.* 30:303–14
- Warren MS. 1992. The conservation of British butterflies. In *The Ecology of Butterflies in Britain*, ed. RLH Dennis, pp. 246–74. Oxford, UK: Oxford Univ. Press
- Webb T III, Bartlein PJ. 1992. Global changes during the last 3 million years: climatic controls and biotic responses. *Annu. Rev. Ecol. Syst.* 23:141–73
- Weiser W, ed. 1973. *Effects of Temperature on Ectothermic Organisms*. New York: Springer-Verlag

- Weiss SB, Murphy DD, White RR. 1988. Sun, slope and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. *Ecology* 69:1486–96
- White MA, Nemani RR, Thornton PE, Running SW. 2002. Satellite evidence of phenological differences between urbanized and rural areas of the eastern United States deciduous broadleaf forest. *Ecosystems* 5:260–73
- White MA, Running SW, Thornton PE. 1999. The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *Int. J. Biometeorol.* 42:139–45
- Wilkinson CR, ed. 2000. *Global Coral Reef Monitoring Network: Status of Coral Reefs of the World in 2000*. Townsville, Qld: Aust. Inst. Mar. Sci.
- Williamson K. 1975. Birds and climatic change. *Bird Study* 22:143–64
- Wilson JW, Gutiérrez D, Martínez D, Agudo R, Monserrat VJ. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. *Ecol. Lett.* 8:1138–46
- Wilson PR, Ainley DG, Nur N, Jacobs SS, Barton KJ, et al. 2001. Adélie penguin population change in the pacific sector of Antarctica: relation to sea-ice extent and the Antarctic Circumpolar Current. *Mar. Ecol. Prog. Ser.* 213:301–9
- Winder M, Schindler DE. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* 85:2100–6
- Woodward FI. 1987. *Climate and Plant Distribution*. Cambridge, UK: Cambridge Univ. Press

RELATED RESOURCES

- Alford, RA, Richards SJ. 1999. Global amphibian declines: a problem in applied ecology. *Annu. Rev. Ecol. Syst.* 30:133–65
- Glynn PW. 1988. El Niño–Southern Oscillation 1982–1983: nearshore population, community, and ecosystem responses. *Annu. Rev. Ecol. Syst.* 19:309–45
- Ludwig D, Marc M, Haddad B. 2001. Ecology, conservation, and public policy. *Annu. Rev. Ecol. Syst.* 32:481–517
- Smith SV, Buddemeier RW. 1992. Global change and coral reef ecosystems. *Annu. Rev. Ecol. Syst.* 23:89–118
- Stevens GC, Fox JF. 1991. The causes of treeline. *Annu. Rev. Ecol. Syst.* 22:177–91



Contents

Birth-Death Models in Macroevolution <i>Sean Nee</i>	1
The Posterior and the Prior in Bayesian Phylogenetics <i>Michael E. Alfaro and Mark T. Holder</i>	19
Unifying and Testing Models of Sexual Selection <i>Hanna Kokko, Michael D. Jennions, and Robert Brooks</i>	43
Genetic Polymorphism in Heterogeneous Environments: The Age of Genomics <i>Philip W. Hedrick</i>	67
Ecological Effects of Invasive Arthropod Generalist Predators <i>William E. Snyder and Edward W. Evans</i>	95
The Evolution of Genetic Architecture <i>Thomas F. Hansen</i>	123
The Major Histocompatibility Complex, Sexual Selection, and Mate Choice <i>Manfred Milinski</i>	159
Some Evolutionary Consequences of Being a Tree <i>Rémy J. Petit and Arndt Hampe</i>	187
Late Quaternary Extinctions: State of the Debate <i>Paul L. Koch and Anthony D. Barnosky</i>	215
Innate Immunity, Environmental Drivers, and Disease Ecology of Marine and Freshwater Invertebrates <i>Laura D. Mydlarz, Laura E. Jones, and C. Drew Harvell</i>	251
Experimental Methods for Measuring Gene Interactions <i>Jeffery P. Demuth and Michael J. Wade</i>	289
Corridors for Conservation: Integrating Pattern and Process <i>Cheryl-Lesley B. Chetkiewicz, Colleen Cassady St. Clair, and Mark S. Boyce</i>	317

The Population Biology of Large Brown Seaweeds: Ecological Consequences of Multiphase Life Histories in Dynamic Coastal Environments <i>David R. Schiel and Michael S. Foster</i>	343
Living on the Edge of Two Changing Worlds: Forecasting the Responses of Rocky Intertidal Ecosystems to Climate Change <i>Brian Helmuth, Nova Mieszkowska, Pippa Moore, and Stephen J. Hawkins</i>	373
Has Vicariance or Dispersal Been the Predominant Biogeographic Force in Madagascar? Only Time Will Tell <i>Anne D. Yoder and Michael D. Nowak</i>	405
Limits to the Adaptive Potential of Small Populations <i>Yvonne Willi, Josh Van Buskirk, and Ary A. Hoffmann</i>	433
Resource Exchange in the Rhizosphere: Molecular Tools and the Microbial Perspective <i>Zoe G. Cardon and Daniel J. Gage</i>	459
The Role of Hybridization in the Evolution of Reef Corals <i>Bette L. Willis, Madeleine J.H. van Oppen, David J. Miller, Steve V. Vollmer, and David J. Ayre</i>	489
The New Bioinformatics: Integrating Ecological Data from the Gene to the Biosphere <i>Matthew B. Jones, Mark P. Schildbauer, O.J. Reichman, and Shawn Bowers</i>	519
Incorporating Molecular Evolution into Phylogenetic Analysis, and a New Compilation of Conserved Polymerase Chain Reaction Primers for Animal Mitochondrial DNA <i>Chris Simon, Thomas R. Buckley, Francesco Frati, James B. Stewart, and Andrew T. Beckenbach</i>	545
The Developmental, Physiological, Neural, and Genetical Causes and Consequences of Frequency-Dependent Selection in the Wild <i>Barry Sinervo and Ryan Calsbeek</i>	581
Carbon-Nitrogen Interactions in Terrestrial Ecosystems in Response to Rising Atmospheric Carbon Dioxide <i>Peter B. Reich, Bruce A. Hungate, and Yiqi Luo</i>	611
Ecological and Evolutionary Responses to Recent Climate Change <i>Camille Parmesan</i>	637

Indexes

Cumulative Index of Contributing Authors, Volumes 33–37	671
Cumulative Index of Chapter Titles, Volumes 33–37	674