

Ecological Consequences of Recent Climate Change

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Abstract: *Global climate change is frequently considered a major conservation threat. The Earth's climate has already warmed by 0.5° C over the past century, and recent studies show that it is possible to detect the effects of a changing climate on ecological systems. This suggests that global change may be a current and future conservation threat. Changes in recent decades are apparent at all levels of ecological organization: population and life-history changes, shifts in geographic range, changes in species composition of communities, and changes in the structure and functioning of ecosystems. These ecological effects can be linked to recent population declines and to both local and global extinctions of species. Although it is impossible to prove that climate change is the cause of these ecological effects, these findings have important implications for conservation biology. It is no longer safe to assume that all of a species' historic range remains suitable. In drawing attention to the importance of climate change as a current threat to species, these studies emphasize the need for current conservation efforts to consider climate change in both in situ conservation and reintroduction efforts. Additional threats will emerge as climate continues to change, especially as climate interacts with other stressors such as habitat fragmentation. These studies can contribute to preparations for future challenges by providing valuable input to models and direct examples of how species respond to climate change.*

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Resumen: *El cambio climático global es frecuentemente considerado como una gran amenaza para la conservación. Sin embargo, el clima de la tierra ya se ha calentado 0.5° C a lo largo del siglo pasado y estudios recientes muestran que es posible detectar los efectos de un clima cambiante en los sistemas ecológicos. Esto sugiere que el cambio global puede ser una amenaza presente y futura para la conservación. Los cambios en las décadas recientes son aparentes a todos los niveles de organización ecológica: cambios poblacionales y de historia de vida, sesgos en el rango geográfico, cambios en la composición de especies en comunidades y cambios en la estructura y funcionamiento de ecosistemas. Estos efectos ecológicos pueden estar ligados a disminuciones poblacionales recientes y a la extinción de especies tanto en el ámbito local como global. A pesar de que es imposible probar que el cambio climático es la causa de estos efectos ecológicos, estos estudios tienen implicaciones importantes para la biología de la conservación. Ya no es seguro asumir que todo el rango histórico de una especie permanece apto. Al llamar la atención sobre la importancia del cambio climático como una amenaza actual para las especies, estos estudios hacen énfasis en la necesidad de esfuerzos de conservación contemporáneos que tomen en consideración el cambio climático tanto para esfuerzos de conservación in situ, como de reintroducción. Emergerán amenazas adicionales en tanto el clima continúe cambiando, especialmente al interactuar el clima con otros estresores como la fragmentación del hábitat. Estos estudios pueden contribuir en la preparación de desafíos a futuro al proveer datos valiosos para los modelos y encauzar ejemplos sobre las respuestas de las especies al cambio climático.*

Introduction

Global climate change is often viewed as a looming conservation problem. Possible future implications for conservation of species and communities have been widely

discussed (Markham 1996; Halpin 1997; Sala et al. 2000). Assessments based on computer models, paleoecological studies of past climate change, and small-scale experiments suggest that extensive disruptions of most ecological communities are likely under generally accepted climate scenarios (Intergovernmental Panel on Climate Change [IPCC] 1996).

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A growing number of studies suggest, however, that global climate changes may not just be a conservation problem for the future but may in fact be a current threat to species and ecosystems. I review the rapidly accumulating, direct documentation of changes in species and ecosystems linked to global climate change (Hughes 2000).

The Earth's climate has warmed 0.3° to 0.6° C over the last 100 years (IPCC 1996). The rate of change has varied, with warming occurring most rapidly during the periods 1925–1944 and 1978–1997 (Jones et al. 1999). Although an average increase of 0.5° C is significant for many physiological and ecological systems, this single value understates the magnitude of the changes to which species have been exposed. Temperature changes vary geographically and tend to be greatest during the coldest months (Easterling et al. 1997). Between 1950 and 1993, for example, winter minimum temperatures rose almost 3° C and spring maximum temperatures increased 1.4° C in the northern hemisphere (Easterling et al. 1997). Changes in precipitation have also occurred (IPCC 1996).

The observation that climate is already changing has promoted reevaluation of long-term data sets. A number of high-profile papers have resulted, establishing a plausible link between recent changes in climate and observed changes in species and communities (e.g. Parmesan 1996; Brown et al. 1999; Parmesan et al. 1999; Pounds et al. 1999; C. D. Thomas & Lennon 1999). Given the unavoidable constraint on establishing a definitive causal link between large-scale climate patterns and species and communities, the overall picture provided by the combination of these studies is needed to best evaluate the insights this emerging body of work can provide to conservation biology.

The Role of Climate in the Ecology of Species

Climate has far-reaching effects on species and ecosystems (Andrewartha & Birch 1954). The direct effects of temperature on the physiology of organisms are well documented, and many mechanisms of action have been identified (Wieser 1973; Woodward 1987; Wood & McDonald 1996). Some effects of temperature may present unexpected challenges to conservation. For example, the sex of developing turtle embryos is determined by environmental temperature (Bull 1980). Painted turtle (*Chrysemys picta*) eggs raised under warmer conditions produce female offspring, whereas males are produced under cooler conditions (Janzen 1994). Interannual differences in the sex ratio of offspring produced are explained largely by variation in mean temperature in July (Janzen 1994). Janzen's evidence indicates that under some climate-change scenarios, painted turtles will suffer local extinctions in the near future, solely as a result

of the skewed sex ratio and resulting demographic problems created by a warming climate.

Precipitation levels also have direct effects on species. Water stress is one of the prime determinants of the distribution of different vegetation types (Woodward 1987). Natural systems can change rapidly in response to changes in precipitation. Distributions of ponderosa pine forest (*Pinus ponderosa*) and piñon-juniper woodland (*Pinus edulis* and *Juniperus monosperma*) in New Mexico are sensitive to moisture levels that vary with elevation (Allen & Breshears 1998). Data from aerial photos taken between 1935 and 1975 show a rapid change (2 km in <5 years) in the distributions of these two communities in response to a regional drought (Allen & Breshears 1998). Precipitation in the form of snow can have negative effects on browsing and grazing animals such as muskoxen (*Ovibos moschatus*) and deer, making it more difficult for them to find food and avoid predators (Forchhammer & Boertmann 1993; Post & Stenseth 1999).

For many species, climate has indirect effects through the sensitivity of habitat or food supply to temperature and precipitation. For example, increases in winter snow depth on Isle Royale associated with the North Atlantic oscillation result in grey wolves (*Canis lupus*) hunting in larger packs (Post et al. 1999). These larger packs reduce the population size of moose (*Alces alces*), which in turn allows higher productivity of balsam fir (*Abies balsamea*) (Post et al. 1999). Likewise, warming climate may allow northward expansion of red fox (*Vulpes vulpes*), which outcompetes arctic fox (*Alopex lagopus*) (Hersteinsson & Macdonald 1992).

Climate variability and the frequency and magnitude of extreme events may also be changing (IPCC 1996; Easterling et al. 2000). Species and ecosystems respond to events such as storms (Mehlman 1997), drought (Grant 1986; Allen & Breshears 1998), and periodic, complex climate shifts such as the North Atlantic oscillation and the El Niño southern oscillation (ENSO) in the Pacific (Barber & Chavez 1983; Chavez et al. 1999).

The response of species to interannual or geographic variations in climate are well documented. Responses to long-term directional trends in climatic conditions such as those experienced in recent decades are most relevant to understanding the conservation implications of global climate change now and in the future.

Recent Ecological Changes and the Link to Climate Change

Changes in Populations and Reproductive Biology

Climatic warming during the past century may have significant effects on the population and reproductive biology of organisms. Recent population dynamics of dippers (*Cinclus cinclus*) in southern Norway have been heavily

influenced by climate, especially a trend toward warmer winters which appears to allow easier access to foraging streams and subsequent increases in population size (Sæther et al. 2000). In Germany, Pied Flycatchers (*Ficedula hypoleuca*) have undergone long-term changes in reproductive success associated with a springtime warming of 1.3° C (Winkel & Hudde 1997). Both clutch size and the number of surviving offspring were higher in warmer springs (Winkel & Hudde 1997), and a population breeding in Finland increased egg-laying effort in recent, warmer years (Järvinen 1994). Reed Warblers (*Acrocephalus scirpaceus*) in southern Germany have also shown a greater tendency to produce young early in the season as spring temperatures have warmed (Bergmann 1999). In contrast, the average clutch size of arctic-breeding geese declined during the warming period from 1951 to 1986 (MacInnes et al. 1990).

The abundance of Sooty Shearwaters (*Puffinus griseus*) declined by 90% off western North America between 1987 and 1994 (Veit et al. 1996, 1997), associated with a rapid warming of the California current. Periodic changes in ocean temperature such as those associated with El Niño have widespread ecological effects (Barber & Chavez 1983). Increases in nearshore water temperatures along the California Coast are associated with significant changes in the population sizes of intertidal invertebrates (Barry et al. 1995). The role of atmospheric warming in determining the frequency and magnitude of these changes remains uncertain (IPCC 1996).

In the Antarctic, temperature increases have caused dramatic changes in ice cover, which in turn have had far-reaching effects on animals such as penguins (Taylor & Wilson 1990; Fraser et al. 1992; R. C. Smith et al. 1999). This warming trend is the likely explanation for the increase in numbers of individuals and populations of terrestrial plants in the Antarctic since the mid-1960s (R. I. L. Smith 1994).

Recent climate change is linked to both increases and declines in population size. The implications for conservation of the direction of change will depend on the species and the effects on community interactions. Rapid declines in population are of direct concern. Increases in valued species (Dennis & Shreeve 1991) will likely be offset by population increases in groups such as invasive exotics (Bergstrom & Chown 1999; Dukes & Mooney 1999), disease vectors (Lindgren et al. 2000), and agricultural pests (Cammell & Knight 1992; Whittaker & Tribe 1998; Tenow et al. 1999). Negative effects of further increases in already abundant, aggressive species will likely overwhelm any benefits of climate change.

Changes in Phenology

A number of studies have documented long-term changes in phenology which may be caused by global change

(Table 1). In the United Kingdom, systematic data on bird nesting has been collected for 60 years. From 1971 to 1995, 78% of 65 species examined started breeding earlier (Crick et al. 1997). Within individual species, there were significantly earlier breeding dates, averaging 9 days earlier in the spring (Crick et al. 1997). Temperature and precipitation explain most of the variation in the timing of breeding (Crick & Sparks 1999).

Studies of the population biology of individual bird species also support this trend toward earlier breeding (Table 1). Great Tits (*Parus major*) in the United Kingdom and Germany now breed up to 10 days earlier than in 1970, when the region's spring warming trend began (Winkel & Hudde 1997; McCleery & Perrins 1998). In the Canadian Arctic, breeding of Snow Goose (*Chen caerulescens*) and Canada Goose (*Branta canadensis*) populations advanced by 30 days from 1951 to 1986 (MacInnes et al. 1990), whereas Mexican Jays (*Apelocoma ultramarina*) in Arizona started nesting 10 days earlier between 1971 and 1997 (Brown et al. 1999).

One of the best examples of phenological change in a single species is the advance in breeding date in Tree Swallows (*Tachycineta bicolor*). Dunn and Winkler (1999) used nest records collected across much of the Tree Swallow's range to document a shift in breeding date of 5–9 days earlier in the season between 1959 and 1991. Laying date was correlated with local temperatures and changed most rapidly during the 1960s and 1980s (Dunn & Winkler 1999). This example emphasizes that phenological changes within a species influenced by local conditions can produce patterns at continental scale.

Long-term data on the timing of bird migration is also available. In New York, records of spring arrival for 76 species of migrating landbirds date back to 1903 (Oglesby & Smith 1995). Over a 90-year period, 39 species arrived significantly earlier, 35 species showed no significant changes, and only 2 species arrived later in the spring (Oglesby & Smith 1995). In Wisconsin, arrival of birds during spring migration and date of first song has become significantly earlier over the past 61 years for 8 species, whereas only 1 species has started arriving later (Bradley et al. 1999). An additional 7 species have shown trends toward earlier arrival. For some European passerines, fall migration is also occurring later in the season (Gatter 1992; Bezzel & Jetz 1995).

Changes in phenology are not limited to birds (Table 1). Records of British butterfly species indicate that timing of the first observation has changed along with climate (Sparks & Carey 1995; Sparks & Yates 1997). The time of appearance of crop pests has also been monitored in many areas. Analysis of data from the Rothamstead Insect Survey Network in Great Britain shows that, over 25 years, the flight period of five species of aphids has become 3–6 days earlier (Fleming & Tatchell 1995).

Table 1. Ecological changes attributed to recent climate change.^a

<i>Variable observed</i>	<i>Species observed</i>	<i>Change</i>	<i>Time span^b (years)</i>	<i>Reference</i>
Geographic range	59 bird species	18.9 km	20	C. D. Thomas & Lennon 1999
Geographic range	Edith's checkerspot butterfly	92 km	100	Parnesan 1996
Geographic range	speckled wood butterfly	88-149 km	55	Hill et al. 1999
Geographic range	22 butterfly species	35-240 km	30-100	Parnesan et al. 1999
Elevational range	9 plant species	70-360 m	70-90	Grabherr et al. 1994
Breeding range	Adelie Penguin	3 km	10	Taylor & Wilson 1990
Flowering date	6 wildflower species	19.8 days	50	Oglesby & Smith 1995
Flowering date	36 species	8.2 days	61	Bradley et al. 1999
Flight period	5 aphid species	3-6 days	25	Fleming & Tatchell 1995
Spawning date	2 frog species	14-21 days	17	Beebee 1995
Breeding migration	3 newt species	35-49 days	17	Beebee 1995
Breeding date	20 bird species	8.8 days	25	Crick et al. 1997
Breeding date	3 bird species	3-9 days	25	Winkel & Hudde 1997
Breeding date	Pied Flycatcher	13 days	24	Slater 1999
Breeding date	Tree Swallow	5-9 days	33	Dunn & Winkler 1999
Breeding date	Great Tit	11.9 days	27	McCleery & Perrins 1998
Breeding date	2 bird species	30 days	35	MacInnes et al. 1990
Breeding date	Mexican Jay	10.1 days	27	Brown et al. 1999
Migration date	4 bird species	11.9 days	50	Mason 1995
Migration date	39 bird species	5.5 days	50	Oglesby & Smith 1995
Migration date	American Robin	14 days	19	Inouye et al. 2000
Migration date/first song	19 bird species	4.4 days	61	Bradley et al. 1999
End of hibernation	yellow-bellied marmot	23 days	23	Inouye et al. 2000
Growing season	Europe	10.8 days	34	Menzel & Fabian 1999
Growing season	northern hemisphere	12 ± 4 days	9	Myneni et al. 1997
Growing season	northern hemisphere	7 days	20	Keeling et al. 1996

^aOnly examples where the magnitude of change was estimated are included; some papers may have discussed additional species for which estimates of the rate of change could not be calculated. Means for studies with multiple species may include species showing no response or response counter to that predicted by climate warming.

^bLength of record examined.

Breeding of amphibians is also starting earlier in the spring. Based on 17 years of data on frogs and newts in the United Kingdom, Beebee (1995) showed that migration of breeding ponds and spawning dates has occurred 2-7 weeks earlier in recent years (Beebee 1995).

The first appearance of spring wildflowers and the leafing out of trees is strongly correlated with annual variations in climate, although long-term directional trends are not always evident (Fitter et al. 1995; Sparks & Carey 1995). Oglesby and Smith (1995) found that the flowering dates of spring wildflowers in New York showed a directional trend consistent with climate warming during this century. In 6 of the 15 species with available data, blooming had advanced at a rate of 20 days per 50 years, and no species flowered significantly later (Oglesby & Smith 1995). In Wisconsin, 10 plants began flowering significantly earlier between 1936 and 1998, and none flowered significantly later in the season (Bradley et al. 1999). There was a trend toward early flowering in an additional 15 plants, whereas eleven species showed nonsignificant trends toward later flowering (Bradley et al. 1999).

At first glance, it may seem that changes in phenology are relatively benign. Indeed, these results even indicate that many species have some capacity to respond rapidly to climate changes by altering the timing of life-his-

tory events. For some species, shifting activities to a cooler time of year may be a sufficient response to climate change. But it is not safe to assume that this will be a general pattern. Timing of life-history events depends on factors besides temperature, and a shift in phenology may disrupt important correlations with other ecological factors. Species that regularly move between habitats may need to adjust to climate changes that are occurring at different rates in different areas, such as between high and low elevations (Inouye et al. 2000).

Plant-animal interactions such as pollination and seed dispersal depend on synchrony between species. Species depend on the appearance of specific foods at critical times (Fitter et al. 1995; Sparks & Carey 1995; Sparks & Yates 1997). For many systems, species will respond to climate change at similar rates and maintain synchrony (Buse & Good 1996), whereas for other species the loss of synchrony may have detrimental effects. In the Netherlands, warmer springs have resulted in a mismatch between the time of peak availability of insects and the peak food demands of nestling Great Tits (Visser et al. 1998). In this population, the birds have not begun breeding earlier, even though consistent warming over 23 years has resulted in the peak availability of the insects they eat occurring 9 days earlier (Visser et al. 1998). Disruptions such as this will reduce the ability of

threatened species to cope with other environmental stresses.

Changes in Geographic Range

Climate is an important determinant of geographic range for many species (Andrewartha & Birch 1954; Iverson & Prasad 1998; Venier et al. 1999). Recent northward movements of species' range boundaries consistent with climate warming have been observed in birds (Thomas & Lennon 1999), mammals (Payette 1987; Hersteinsson & Macdonald 1992), and butterflies (Dennis 1993; Parmesan 1996; Hill et al. 1999; Parmesan et al. 1999).

Northward expansion of bird species in North America and Europe has been widely observed over the past 50 years (Kalela 1949; Williamson 1975; Brewer 1991; Johnson 1994; Burton 1995; Root & Weckstein 1995). Although numerous factors have been proposed that might explain these range expansions, C. D. Thomas and Lennon (1999) present compelling evidence linking northward movements of British birds to climate change. The authors compared the breeding ranges of birds in 1968–1972 to ranges in 1988–1991. Of 59 species occupying southern Great Britain, the northern boundary of their ranges shifted an average of 19 km to the north (including those species showing no changes or southward retractions). Birds confined to the north (42 species) showed little change in the southern boundary of their ranges (C. D. Thomas & Lennon 1999). This comparison shows that the northern and southern range boundaries of species are not equally sensitive to climate change. By statistically controlling for changes in total range size, Thomas and Lennon also provide evidence that the northward shift in range is not simply a result of an overall expansion of species into the central part of the island (C. D. Thomas & Lennon 1999).

Parmesan et al. (1999) examined changes in the northern range boundaries of 52 species of European butterflies over the past 30–100 years. The northern boundaries of geographic ranges showed northward shifts in 34 species, southward shifts in 1 species, and no change in the remaining 17 species. The southern boundaries of species' ranges were more stable over time. Of 40 species for which Parmesan et al. had appropriate data, 9 shifted north, 2 moved south, and 29 remained stable. Changes in other environmental factors, especially land use, also influence the distribution and abundance of butterflies (Pollard & Eversham 1995). Although explanations not linked to climate cannot be ruled out, Parmesan et al. (1999) omitted from analyses species with large habitat losses or gains or species known to have been severely affected by habitat alteration. Parmesan et al. (1999) also assert that habitat loss has actually been higher in the north than the south, indicating that in this case habitat loss is not driving changes in species' ranges.

In mountains, climate changes more rapidly with elevation (about 1° C per 160 m) than it does with latitude (about 1° C per 150 km; IPCC 1996), so rapid changes in montane communities are expected as climate changes. Grabherr et al. (1994) surveyed montane plants on 26 mountain summits in the Swiss Alps and compared species distributions to historical records. The relationship of species richness to elevation showed a pronounced shift to higher elevations over the past 40–90 years, consistent with the effects of warming (Grabherr et al. 1994). For 9 species for which they have more detailed records, the rate of upward shift was estimated to be 1–4 m per decade. These movements were slower than the 8–10 m per decade expected based solely on the change in mean temperature over the last 90 years and may indicate that these plants are unable to respond successfully to more rapid climate change (Grabherr et al. 1994).

Other montane habitats may also be showing the effects of climate change. Dieback of montane trees (Hamburg & Cogbill 1988; Fisher 1997) are consistent with the effects of warming climate. Climate change in the montane cloud forests of Costa Rica (Still et al. 1999) have been accompanied by the loss of many cloud-forest species and invasion by species from lower elevations (Pounds et al. 1999). Parmesan (1996) also documented an upward shift of 124 m in the distribution of Edith's checkerspot butterfly, primarily in the Sierra Nevada mountains.

Community- and Ecosystem-Level Changes

Broad patterns of terrestrial vegetation types are determined largely by a combination of temperature and precipitation (Woodward 1987; IPCC 1996). Vegetation is sensitive to changes in temperature occurring on the scale of years and decades (Jacoby et al. 1996). Experimental studies indicate that plant communities are also sensitive to the direct effects of higher carbon dioxide (CO₂) concentrations (McLeod & Long 1999). Changes in climate associated with the rise in CO₂ may in part explain recently observed changes in arctic (Oechel et al. 1993; Chapin et al. 1995), temperate (Hamburg & Cogbill 1988; Brown et al. 1997; Alward et al. 1999), and tropical (Phillips 1996) plant communities.

Changes in precipitation patterns in the arid regions of the southwestern United States have resulted in a shift at some sites from arid grassland to desert shrubland, accompanied by the local extinction of several formerly abundant species of animals (Brown et al. 1997). In the shortgrass steppe of northeast Colorado, average temperatures have risen 1.3° C since 1970, largely because of a rapid increase in nighttime temperatures (Alward et al. 1999). Measurements of the annual net primary productivity of the dominant native grass in this habitat, *Bouteloua gracilis*, reveal a significant decline

over this period. *Bouteloua gracilis* accounted for 90% of the groundcover in this ecosystem, and the magnitude of the decline in productivity (about one-third for each 1° C of warming) suggests that major disruptions in both ecosystem structure and functioning could result from further warming (Alward et al. 1999). Broadleaf plants showed the opposite trend in primary productivity and increased in abundance over time (Alward et al. 1999). The shift in species composition from drought- and grazing-tolerant grass to intolerant forbs could also reduce the value of these areas for livestock grazing. Exotic species responded favorably to warming, raising the possibility of further invasions of the community by non-native weeds (Alward et al. 1999).

At an ecosystem level, increased activity of northern vegetation has been detected in measurements of global CO₂ concentration (Keeling et al. 1996). Seasonal growth of plants, especially in the high latitudes of the northern hemisphere, results in a pattern of decreasing atmospheric CO₂ levels in summer as photosynthetic activity removes CO₂, followed by increasing CO₂ in winter as plants respire and vegetation decays. Interannual differences in the amplitude of the CO₂ cycle correlate with temperature changes over the past 35 years, suggesting that plant growth at the ecosystem and global scales are sensitive to temperature (Keeling et al. 1996). Since the early 1960s the amplitude of this seasonal CO₂ cycle has increased by as much as 40%, suggesting increased activity of terrestrial vegetation over time (Keeling et al. 1996). This has occurred during a period of increasing temperatures, especially in the northern spring (Jones et al. 1999). The changes in the CO₂ cycle likely reflect a combination of increased plant growth and increased respiration (Chapin et al. 1996; Keeling et al. 1996).

Some of the change in primary productivity can be attributed to longer growing seasons evident from several independent data sources (Table 1). The phase of the CO₂ cycle has shifted approximately 7 days earlier in the spring, indicating an increase in the length of the growing season (Keeling et al. 1996). Likewise, meteorological satellites over the northern hemisphere measure changes in reflectance showing an increase in the growing season of approximately 12 days since the early 1980s, primarily due to an advance in the onset of spring by about 8 days (Myneni et al. 1997). Finally, observations of plant phenology in Europe suggest a 10.8-day lengthening of the growing season, including an advance in spring of 6 days and a delay in autumn of 4.8 days (Menzel & Fabian 1999). These independent methods provide a surprisingly consistent picture, strengthening the conclusion that growing seasons are getting longer (Table 1).

Long-term data on lakes in the northern hemisphere reflect the ongoing trend toward a warmer climate. Moderating winter climate is clearly reflected in records

of lake-ice phenology (Anderson et al. 1996). Data from the Experimental Lakes Area of northwestern Ontario reveal a 2°-C increase in air and water temperatures since the late 1960s (Schindler et al. 1990, 1996a). Associated with this warming are changes in both physical and biological characteristics of lakes.

Significant increases in nearshore ocean-water temperatures have occurred over the last 60 years in California. Barry and colleagues (1995) compared detailed records of the invertebrates of the rocky intertidal zone collected in the early 1930s to data collected at the same sites in the 1990s. Forty-five of the most abundant species were classified as being near either the southern or northern limit of the range or as being cosmopolitan in distribution. Over 60 years, eight of the nine southern species increased in abundance, and five of the eight northern species declined, but cosmopolitan species showed no overall trend (Barry et al. 1995). Although average water temperatures increased 0.75° C overall, this underestimates the increased heat stress northern species suffered, as maximum summer temperatures increased by 2.2° C. Near-shore ocean warming is also implicated in similar changes in the reef-fish assemblage off southern California, where southern species have tended to replace northern ones (Holbrook et al. 1997).

Open-ocean ecosystems have also responded to temperature changes on several scales (Aebischer et al. 1990; Hayward 1997). Surveys off southern California since 1951 have shown an 80% decrease in the biomass of macrozooplankton in conjunction with a long-term increase of 0.8–1.5° C in ocean surface temperature (Roemich & McGowan 1995). Declining zooplankton may in turn be responsible for declines in species at higher trophic levels, such as sea birds (Veit et al. 1996, 1997). Similar changes have also been detected in the North Sea (Aebischer et al. 1990). Long-term data are needed to distinguish between the effects of long-term climate trends and periodic events such as El Niño (McGowan et al. 1998; Mullin 1998).

The Risk of Extinction

The contribution of climate change to future extinctions depends on how quickly species can respond to change. Ongoing climate change is an additional source of stress for species already threatened by local and global environmental changes, increasing the risk of extinction.

Concerns have been raised about possible global declines in amphibian populations (Blaustein & Wake 1990). Population sizes of amphibians are sensitive to fluctuations in the amount and timing of precipitation. Drastic declines in populations of frogs in Puerto Rico are correlated with recent years of low precipitation (Stewart 1995). Recent climate change may be directly responsible for the extinction of the golden toad (*Bufo*

periglenes) from the Costa Rican cloud forest (Pounds & Crump 1994; Pounds et al. 1999). The sudden extinction of this species was associated with unusually warm and dry conditions that also resulted in the local extinction of the harlequin frog (*Atelopus varius*) and drastic declines in populations of other species (Pounds & Crump 1994; Pounds et al. 1997). The failure of populations to recover from the rapid declines that occurred in the late 1980s suggests that long-term changes in climate are responsible (Pounds et al. 1997; Still et al. 1999).

Global warming may also be indirectly linked to amphibian declines resulting from UV radiation (Blaustein et al. 1995). Increasing temperatures are associated with decreases in dissolved organic carbon in lakes, which result in increased penetration of UV-B radiation (Schindler et al. 1996b). This effect may lead to greater increases in exposure to UV-B radiation than would be associated with decreases in stratospheric ozone alone (Herman et al. 1996; Schindler et al. 1996b).

Climate acts locally, and its effects will be most apparent on the level of populations and metapopulations. Parmesan (1996) provides a clear picture of what may become a familiar pattern. Shifts in a species' range under climate change will occur in part as a result of an increase in the probability of more southerly populations going extinct. In western North America, Edith's checkerspot butterfly (*Euphydryas editha*) is distributed in discrete populations that undergo periodic extinctions and recolonizations (Harrison et al. 1988). Climate is known to play an important role in determining the persistence of populations (Singer & Thomas 1996; C. D. Thomas et al. 1996). Parmesan (1996) used museum specimens and other historical records to locate and re-survey 151 sites that had once hosted populations of Edith's checkerspot. Population extinction rates were higher in the southern part of the species' historic range and at low elevations (Parmesan 1996). The result of this nonrandom pattern of extinctions was a shift in the species' distribution of 124 m upward in elevation and approximately 92 km north over the same time period that isotherms in western North America shifted 105 m upward and 105 km north (Parmesan 1996; Parmesan et al. 1999; Parmesan 2001). The recognition of the role of local extinctions and the importance of metapopulation dynamics in range shifts in response to climate change is especially relevant given the local focus of many conservation efforts. Global extinctions as a result of climate change can be expected, as demonstrated by the fate of the golden toad. But loss of local, familiar species and species serving important ecological roles may become the rule. This becomes a problem for conservation biology because stakeholders value local species and because lost species are most likely to be replaced by exotic, invasive species (Dukes & Mooney 1999).

Biotic Changes and Global Climate Change

The twentieth century saw an increase in the human population from 1.6 billion to over 6.0 billion. Human effects on the environment have increased at least as fast as population, so the ecological systems described here have been subject to rapid changes in many aspects of their environments in addition to changes in climate.

None of the ecological studies reviewed here can demonstrate that climate change has *caused* the recent changes in species and communities described (Hughes 2000). Indeed, most authors have gone to considerable effort to point out alternative explanations for these patterns. These studies do present plausible arguments for recent climate change as a primary agent of the ecological changes observed. Perhaps the strongest support for the role of climate change comes from the remarkable consistency in the types and magnitude of changes observed across multiple studies (Table 1).

The strengths of individual studies can provide important guides for future analyses. Significant regional differences exist in both past and expected future climate changes (IPCC 1996). Analyses need to incorporate local climate records when used to interpret recent ecological changes. For example, four boreal species of small mammals in the central plains of North America expanded southward during the 1960s and 1970s (Frey 1992). This may appear to contradict the general trend of poleward expansion described here, but in fact regional climate data show a marked trend toward cooler temperatures from the 1930s to the 1980s (Frey 1992). Likewise, in England, the present warming trend was preceded by a period of cool spring temperatures lasting into the 1970s, and laying dates of birds reflect this pattern (Crick & Sparks 1999).

Although studies of individual species contribute to the overall argument that recent climate change is having effects, analyses of groups of organisms or entire communities provide more powerful tests. Ecosystems are dynamic systems that show variation over time, even in the absence of human disturbance. Thus, even in the absence of climate change, we expect some species to move poleward, some to breed earlier, and others to increase or decrease in population size. This problem will be compounded if studies that show results consistent with climate change are more likely to be published. Several of the studies presented here address this potential problem by analyzing changes in all members of a taxon within a region and find an overall change consistent with the predicted effects of global climate change, even after averaging in species showing no changes or changes counter to those predicted (Oglesby & Smith 1995; Crick et al. 1997; Parmesan et al. 1999; C. D. Thomas & Lennon 1999). In addition, those datasets that provide continuous records of how ecological variables have changed will be most convincing, whereas those data-

sets providing only a “snapshot” of conditions in the past compared with current conditions will be most subject to alternative explanations (Hughes 2000).

Climate Change and Conservation

Even as the significance of these results for global-change biology may still be argued, the implications for conservation and resource management are clear. Together, these studies emphasize that conservation scientists need to look at climate change as a current, not just a future, threat to species. Although a causal link to climate cannot yet be rigorously demonstrated, the consistent patterns indicate that the prudent course for conservation is to take these changes seriously. Certainly, cases such as the extinction of the golden toad are of immediate concern, but changes in climate need to be taken into account as a possible factor contributing to declines in other species.

Planning for the conservation of particular species or communities should take into account the fact that climate change is ongoing. The assumption that conditions in the historic range of a species are still present will be increasingly challenged. Additions to ongoing conservation efforts include (1) explicit analysis of climatic responses, including recent changes in climate, when decisions are made about where to reintroduce species (Lindenmayer et al. 1991; Pearce & Lindenmayer 1998); (2) evaluation of physiological responses to climate to ensure that in situ conservation efforts are directed at appropriate sites (J. A. Thomas et al. 1999); (3) recognition of the importance of relatively small changes in climate to species reproduction and survival, with emphasis on the need for conserving microclimatic variation within habitat types (Weiss et al. 1988; Kindvall 1996; J. A. Thomas et al. 1999); and (4) increased efforts to monitor invasive species from warmer climates and slow migration to higher latitudes or elevations (Dukes & Mooney 1999).

The available evidence indicates that changes in the Earth's climate will likely continue and even accelerate over the next 50–100 years (IPCC 1996). Accurate predictions of how species and ecosystems will respond to climate change will assist in preparing for future conservation challenges. The direct observations of species' responses to climate change that I have reviewed will complement models, small-scale experiments, and paleoecology studies in several ways. First, predictions of ecological models can be evaluated by simulating recent ecological changes in much the same way climate models have been evaluated by simulating recent climate. Second, ecologically relevant climate variables can be identified for future models. Variables such as dry-season mist frequency (Pounds et al. 1999), minimum spring temperature (Alward et al. 1999), or temperature in spe-

cific months (Beebee 1995; Sparks & Yates 1997; Brown et al. 1999) are ecologically important but not obvious targets of modeling efforts. Third, the amount and seasonality of precipitation is likely to be at least as important as temperature in determining the distribution and abundance of organisms. To date, predictions of changes in precipitation are less reliable than those for temperature. Coping with this uncertainty will increase the challenges associated with managing species under changing environmental conditions. Fourth, empirical studies should emphasize the importance of the indirect effects of climate on species (McKone et al. 1998; Visser et al. 1998; Buse et al. 1999). Of special concern for conservation are possible changes in the abundance and range of pests and pathogens (McNulty et al. 1998; Harvell et al. 1999; Lindgren et al. 2000).

Although models provide guidance about the types and magnitude of changes to be expected, the studies I have reviewed provide direct examples of what conservation biologists can expect to see in the coming decades and identify areas where further research is needed.

These studies demonstrate the wide range of responses that species may have to climate changes, including shifts in geographic range and in timing of life-history events. An obvious gap to date is the dearth of studies examining evolutionary changes. The calculations of Janzen (1994) of the evolutionary potential of turtles provides a good example of a starting point. The amount of genetic variation within populations and the heritability of responses to climate-based selection will vary greatly and will have enormous implications for the rate of evolutionary change (Billington & Pelham 1991; Hairston 1996; Rodríguez-Trelles & Rodríguez 1998; Hayes & O'Connor 1999). Creative efforts are needed, perhaps taking advantage of stored seeds and natural seed banks, repeating physiological measurements of thermal response from published studies, or examining genetic changes in species exposed to thermal pollution from power plants.

The rate at which species' boundaries can change is thought to be of key importance to understanding how species will respond to climate change. Past efforts have focused on trying to infer rates of change from fossil pollen or other indirect indicators. Studies of the type I have reviewed provide a direct measure of the minimum rate at which species' boundaries can change. The ability of butterflies to move 35–240 km during a period when isotherms shifted 120 km shows that many species are capable of matching the recent rate of climate change (Parmesan et al. 1999), but it doesn't preclude faster change. Additional work is needed to understand factors limiting the rate at which geographic range shifts.

Studies of groups of species show that most, but not all, species are responding to climate change; attention

needs to be directed toward those species not responding. These species may be less sensitive to temperature than those showing responses. But the alternative, that these species are unable to respond to even moderate warming, has different and more ominous implications for conservation.

European birds and butterflies have shown rapid northward expansion but little range contraction in the south (Parmesan et al. 1999; C. D. Thomas & Lennon 1999; but see Parmesan 1996). The short-term implication is that species may not immediately be forced out of the southern part of their ranges by climate. Instead, interspecific interactions with competitors and invasive exotic species moving north may be the mechanism of species loss (Hersteinsson & Macdonald 1992; Burton 1995). Future work should determine which characteristics make species most likely to respond quickly to climate change.

The overall picture that emerges is that conservation biologists need to add another source to the long list of stressors that may be causing population and species decline. These results add to the urgency of earlier calls to consider climate change when planning for conservation and to consider the interactions between climate change and other stressors such as habitat fragmentation (Markham 1996; Halpin 1997). This will be especially true for species dependent on unusual and localized combinations of climatic conditions. Even without demonstrating a causal link to anthropogenic climate change, we now have the best estimates to date of how quickly species and ecosystems can change. These contributions to our understanding of how species and communities react to global climate change will improve assessments of future threats to ecological systems.

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