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Biological consequences of global warming: is the signal already

The prospect that increases in atmospheric concentrations of greenhouse gases will have measurable effects on the earth's climate over the next few decades has attracted a vast research effort. Climatologists have faced two main challenges. The first has been to distinguish the signal of human-induced climate change from the noise of interannual and decadal natural variability. The second has been to predict probable climate scenarios for the future. Climate monitoring over the past century and long-term reconstructions of climate over the past millennium indicate that the earth is indeed warming up (Fig. 1)¹. Moreover, the recent patterns of warming and of changes in precipitation are generally consistent with the patterns predicted by global circulation models (Box 1)^{1–7}. Physical features of the earth's surface, such as sea ice and glaciers, also appear to be responding in a predictable way to the warming trends (Box 2)^{8–11}.

For ecologists, physiologists and land managers, the challenge is to predict the effects of human-induced climate and atmospheric change on species and on

Increasing greenhouse gas concentrations are expected to have significant impacts on the world's climate on a timescale of decades to centuries. Evidence from long-term monitoring studies is now accumulating and suggests that the climate of the past few decades is anomalous compared with past climate variation, and that recent climatic and atmospheric trends are already affecting species physiology, distribution and phenology.

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communities. These predictions can be broadly summarized into four categories (Fig. 2):

(1) Effects on physiology: changes in atmospheric CO₂ concentration, temperature or precipitation will directly affect metabolic and developmental rates in many animals, and processes such as photosynthesis, respiration, growth and tissue composition in plants.

(2) Effects on distributions: a 3°C change in mean annual temperature corresponds to a shift in isotherms of approximately 300–400 km in latitude (in the temperate zone) or 500 m in elevation. Therefore, species are expected to move upwards in

elevation or towards the poles in latitude in response to shifting climate zones.

(3) Effects on phenology: life cycle events triggered by environmental cues such as degree days might be altered, leading to decoupling of phenological relationships between species.

(4) Adaptation: species with short generation times and rapid population growth rates might undergo microevolutionary change *in situ*.

Changes in physiology, phenology and distribution of individual species will inevitably alter competitive, and other, interactions between species, with consequent feedbacks to local abundance and to geographic ranges (Fig. 2). It seems probable that at least some species will become extinct, either as a direct result of physiological stress or via interactions with other species. The important question is not if such changes will occur but how soon.

Recent analyses of long-term data sets indicate that some species are already responding to the anomalous atmosphere and climate of the 20th century. The examples reviewed here are not an exhaustive set, but have been chosen to represent the diversity of species and of habitats in which trends are becoming apparent. Although there is some evidence that adaptation *in situ* is taking place in some organisms¹², I have focused on studies showing changes in plant physiology and growth, and changes in species distributions and phenology. Some examples are more convincing than others owing to the quantity of data, strength of the trend or because alternative explanations are simply less plausible. However, there are some inevitable caveats in interpreting these studies. First, the nature of scientific publishing is such that positive trends are more likely to be both submitted and published than negative or inconclusive ones. Second, none of the studies represents a controlled experiment and thus different possible causes of the trends are confounded. Finally, the particular time intervals chosen for the data analyses can markedly influence the apparent strength of a trend. These caveats mean that no single study can be interpreted as unequivocal evidence for human-induced change. Instead, it is the increasing number of examples showing trends consistent with *a priori* predictions that is starting to become convincing.

Changes in plant physiology, productivity and growth

Photosynthesis and hence plant growth and productivity are directly affected by both temperature and atmospheric CO₂ concentration. Evidence is accumulating that plant growth in natural ecosystems has responded to recent trends in warming and to atmospheric changes, although it is difficult to separate the relative contributions of the two factors.

The concentration of atmospheric CO₂ has been increasing since the mid-1800s to the present day (Fig. 3)¹³. CO₂ concentration rises in winter and declines in summer, mainly in response to the seasonal growth of terrestrial vegetation. Since the early 1960s, the amplitude of this oscillation has increased by 20% in Hawaii and by 40% in the Arctic¹⁴. The increases are accompanied by phase advances of about seven days during the declining part of the cycle. Increasing

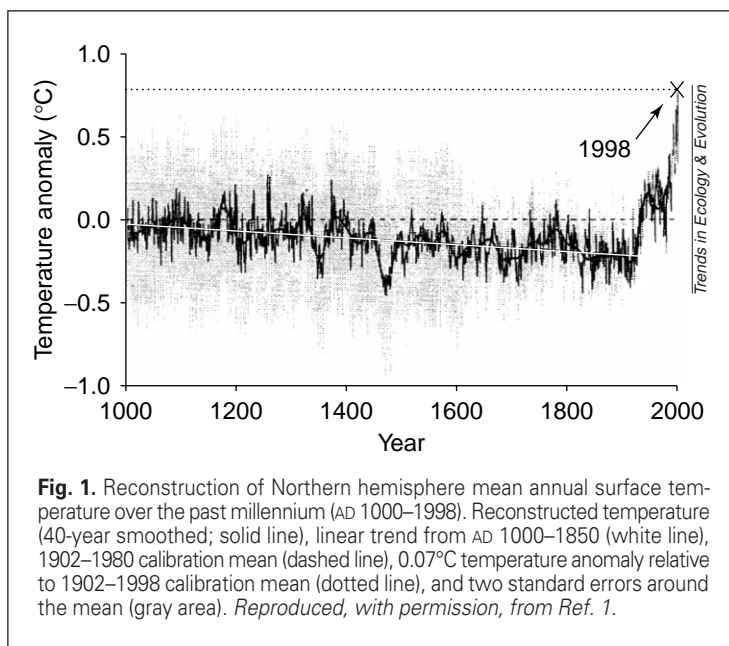


Fig. 1. Reconstruction of Northern hemisphere mean annual surface temperature over the past millennium (AD 1000–1998). Reconstructed temperature (40-year smoothed; solid line), linear trend from AD 1000–1850 (white line), 1902–1980 calibration mean (dashed line), 0.07°C temperature anomaly relative to 1902–1998 calibration mean (dotted line), and two standard errors around the mean (gray area). Reproduced, with permission, from Ref. 1.

assimilation of CO₂ by land plants is a probable explanation for this trend; this idea is supported by satellite data showing increased plant growth and a lengthening of the active growing season (1981–1991) in the Northern hemisphere¹⁵ (but see Ref. 16).

Tree-ring records at sites in both hemispheres indicate that increased growth rates have actually been occurring since the mid-19th century; that is, well before the recorded warming in the first half of the 20th century¹⁷. Therefore, although 20th-century warming has undoubtedly been important, the direct fertilization effect of increasing CO₂ concentration has probably also had an impact. The apparent CO₂ fertilization signal seems clearest in high elevation subalpine conifers, such as the bristlecone

Box 1. Climate scenarios for the future and some recorded 20th-century trends

Air temperature

Scenarios

Climate models predict that the mean annual global surface temperature will increase 1–3.5°C by 2100, with warming more pronounced at higher latitudes. Relatively greater increases are expected in winter than in summer, and in night-time versus daytime temperatures².

Trends

- Global mean surface temperatures have increased 0.6°C since the late 19th century, and by 0.2–0.3°C over the past 40 years. Recent warming has been greatest over continents between 40°N and 70°N (Ref. 2).
- Northern hemisphere temperature reconstructions from AD 1000 to the present day, based on a combination of tree-rings and ice cores, indicate that the 20th century has been anomalously warm, with the 1990s the warmest decade and 1998 the warmest year this millennium¹.
- The Antarctic Peninsula has warmed ~2.5°C between 1945 and 1990 (Ref. 3).
- The 0°C isotherm in tropical latitudes (15°N–15°S) has been upwardly elevated by approximately 110 m during the 1970s and 1980s⁴.
- The rise in the minimum temperature has occurred at a 50% greater rate than the rise in the maximum temperature in many regions, resulting in a decrease in the diurnal temperature range⁵.

Precipitation

Scenario

All climate models predict an increase in global mean precipitation, but some regions might get drier².

Trends

- There has been a small positive (1%) global trend in precipitation over land this century. Precipitation has increased over land at high latitudes in the Northern hemisphere, but has decreased since the 1960s over the subtropics and the tropics from Africa to Indonesia².
- Precipitation has increased ~10% across the contiguous USA since 1910. There has also been an increase in heavy and extreme daily precipitation events in the USA over the past 80 years (about one additional extreme precipitation event every two years)⁶.
- The length of the snow season and the snow amount in the Swiss Alps has decreased substantially since the mid-1980s (Ref. 7).

Box 2. Examples of recent changes to physical features of the earth

Sea levels

- The global sea level has risen by 10–25 cm over the past 100 years, which corresponds to the low end of model projections by the Intergovernmental Panel on Climate Change (IPCC) (15–95 cm) (Ref. 2).

Ocean warming

- Warming has been reported from transects in the Atlantic, Pacific and Indian Oceans, and near the poles; warming is consistent with the observed sea-level rise owing to thermal expansion. At some depths maximum warming has been equivalent to 1°C per century⁸.
- Increased water and air temperatures are associated with the increased frequency of coral bleaching events over the past two decades⁹.

Sea ice

- Arctic: there has been a nearly continuous, below normal summer sea ice coverage since 1990, with the decrease accelerated over the period 1987–1994. The extent of the ice pack was reduced by 9% in 1990–1995 compared with 1979–1989 (Ref. 10).
- Antarctic: of the nine ice shelves examined, the five most northerly shelves have retreated dramatically between 1945 and 1995 (Ref. 3).

Glaciers

- Glaciers in the European Alps have lost 30–40% of their surface area and approximately half their volume since the mid-1800s, with an additional loss of 10–20% of their remaining volume since 1980. Since the late 1980s, warming of alpine permafrost indicates acceleration by a factor of five to ten. Melting of ground ice also accelerated markedly from 1980–1990 compared with 1970–1980 (Ref. 11).

pine (*Pinus aristata*), where newly fixed carbon is primarily allocated to cambial growth; the CO₂ fertilization signal is less obvious in species where yearly biomass additions are apportioned more evenly among all plant parts¹⁸. Increasing CO₂ levels might also have altered stomatal density, and thus stomatal conductance in many species. Several studies have shown that the stomatal densities of plants collected recently are significantly lower than in herbarium specimens of the same species collected between 70 and 200 years ago¹⁹. These trends are consistent with the fossil record and with experimental studies using pre-industrial CO₂ concentrations.

Increasing yields in conifer plantations since the mid-1800s (Ref. 20), and acceleration of turnover rates and biomass of tropical trees since the 1950s (Refs 21, 22), have also been detected. Increasing biomass accumulation in forests has important implications for the current controversy as to where the ‘missing’ terrestrial carbon sink is located. Future climate change might be partially mitigated if CO₂ fertilization is already promoting forest growth, which, in turn, is sequestering carbon.

Significant positive and negative trends in phytoplankton abundance indicate that climatic changes might also be affecting productivity in the oceans, although large regional differences are apparent and warming surface temperatures appear to have had contradictory effects on nutrient upwelling. Phytoplankton abundance in the north east Atlantic and North Sea has apparently declined north of 59°N (1948–1995), possibly as a result of unusually cold waters spreading from the Arctic²³. The source of this water might include increased export of freshwater from melting ice and from permafrost. However, between 52 and 58°N phytoplankton abundance and season length have increased.

Changes in species distribution and abundance

Distributions and/or abundances of most species have been altered by human activities: most changes can be attributed to habitat loss or to habitat alteration. However, in a few cases, shifts in distribution are explained more parsimoniously by a correlation with a recent climatic trend, especially when the shift has been either towards the poles or upwards in elevation. Not unexpectedly, most of these examples are species (such as alpine and arctic plants) whose distributions are most obviously limited by

climate or organisms that are highly mobile at some stage of their life cycle (such as flying insects, birds and marine invertebrates). However, there are some instances of apparent shifts in distribution of less mobile species, such as terrestrial mammals, that are also correlated with recent climate trends.

Arctic and alpine plants

Distributions of the only two native vascular plants in Antarctica, *Colobanthus quitensis* (Antarctic pearlwort) and *Deschampsia antarctica* (Antarctic hair grass), appear to be limited by the number of degree days above 0°C and by the water supply during the short, cold growing season. At many

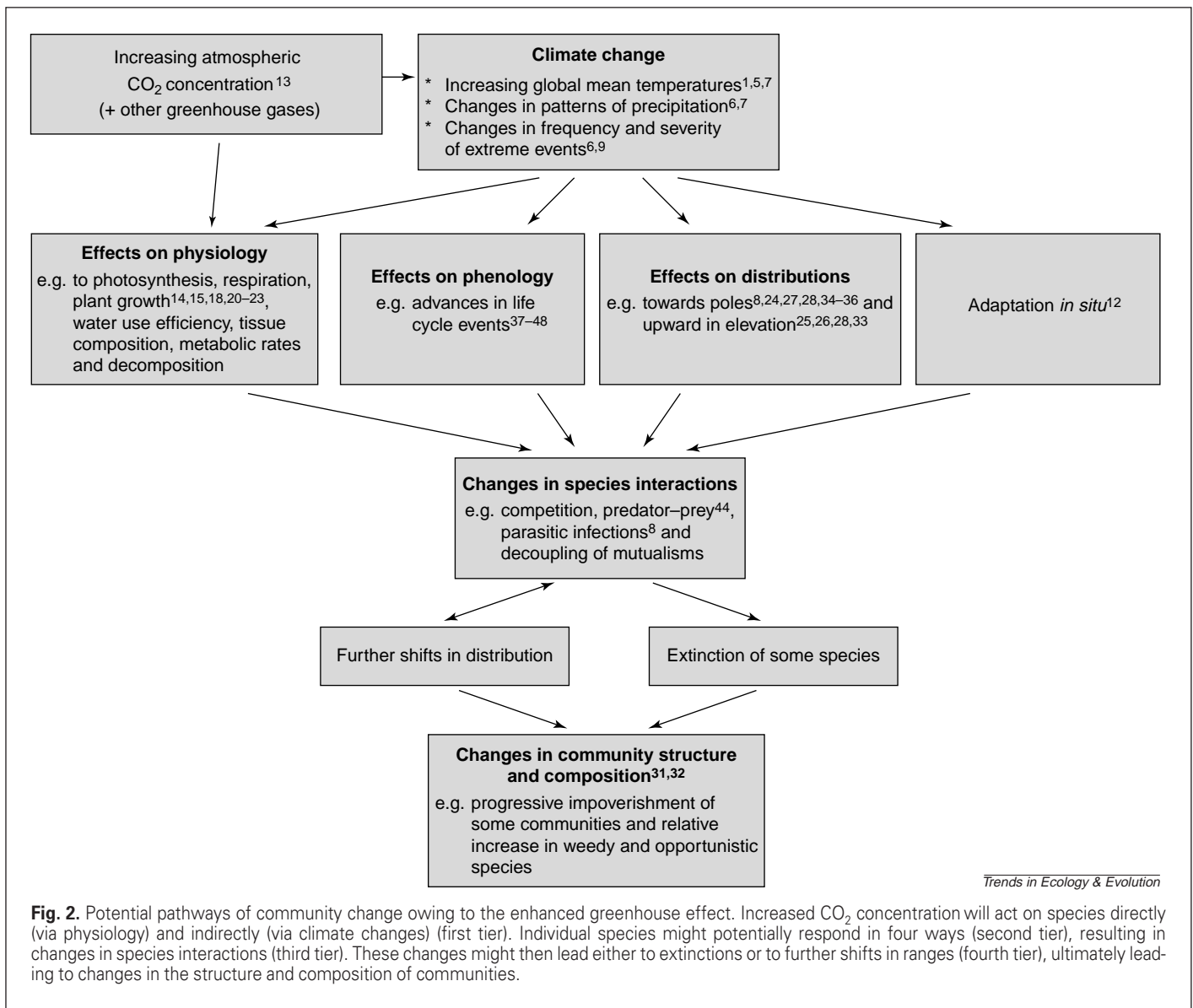
locations in maritime Antarctica, both species have shown dramatic increases in numbers from 1964–1990 as a result of greater seed germination and seedling survival²⁴. At Galindez Island, *D. antarctica* increased from 500 individuals in 1964, to 12 030 individuals in 1990; similar increases have been found at many other locations. Over this period, there have been a series of warm summers in the mid 1950s, early 1960s, early 1970s and mid-to-late 1980s, and winter temperatures have also increased substantially.

In alpine areas, upward movement of plant species has been widely reported. Tree establishment has increased in subalpine and in treeline stands, and in many regions young trees have been established at elevations or latitudes beyond the current treeline. Most locations in western North America, for example, show an upward expansion of the forest margin after 1890 with establishment peaks between 1920 and 1950 (Ref. 25). Compared with historical records, plant species richness on 30 peaks in the European Alps in 1992–1993 show increases at 70% of the sites, presumably because of upward colonization²⁶.

Flying insects

A recent survey of 35 non-migratory European butterfly species found that the ranges of 22 (63%) have shifted northwards by 35–240 km this century, with only two species (3%) having shifted south. Two-thirds of the species showing extensions at their northern boundary had southern boundaries that remained stable, thus, effectively expanding their range²⁷. In North America, a survey of 151 previously recorded populations of Edith’s checkerspot butterfly (*Euphydryas editha*) found significant latitudinal and elevational clines in extinction rates. Sites where populations had persisted were, on average, 2° further north than sites where populations had become extinct. Populations in Mexico were four times more likely to be extinct than those in Canada, and populations above 2400 m were significantly more likely to persist than those at lower altitudes²⁸.

In other arthropods, recent range shifts have serious implications for human health. Increases in mosquito-borne diseases have been reported in the highlands of Asia, Central Africa and Latin America⁸. *Plasmodium falciparum* malaria is a growing public health threat in the New Guinea highlands; in 1997, malaria was reported for



the first time up to 2100 m in the highlands of Irian Jaya and Papua New Guinea. Similar changes have been reported from Tanzania and from Kenya. Dengue fever, previously limited to about 1000 m in elevation in the tropics by the 10°C winter isotherm, has appeared at 1700 m in Mexico; *Aedes aegypti*, a vector of dengue fever and yellow fever viruses, has recently been reported at 2200 m in Colombia⁸.

Marine species

Rapid, and sometimes dramatic, responses of mobile marine species to the short-term sea surface temperature changes accompanying El Niño events indicate that these taxa will respond sensitively to ocean warming. Changes in the distribution and abundance of several taxa off the coast of California have been particularly well documented over the past few decades. The surface waters of the California Current warmed 1.2–1.6°C between 1951 and 1993; this warming was accompanied by a 70% decline in zooplankton abundance²⁹, possibly because of increased surface temperatures reducing the upwelling of cold, nutrient-rich waters to the surface (but see Ref. 23). One of the top predators in this system, the sooty shearwater (*Puffinus griseus*), suffered a 90% decline in abundance off western North America between 1987 and 1994, with a nine-month lag in response time to changing surface

temperatures³⁰. Whilst other influences, such as gill-net mortality and pollution, cannot be discounted, the coincidence of oceanic temperature increase in space and in time and the decrease in zooplankton abundance are suggestive of a direct causal relationship.

Two further studies of marine organisms associated with the Californian coast also provide evidence of recent climate-induced changes in community composition. Of 45 species of intertidal invertebrates surveyed in 1931–1933, and again in 1993–1994, the abundance of eight out of nine southern species increased, whereas five out of eight northern species declined; no trend was evident for cosmopolitan species. Annual mean shoreline ocean temperatures increased by 0.75°C from 1933 to 1994 at the same location, with mean summer maximum temperatures for 1983–1993 being 2.2°C warmer than for 1921–1931 (Ref. 31). In a second study, the composition of a Californian reef fish assemblage surveyed over a 20-year period (1974–1993), changed such that the proportion of northern, colder affinity species declined from approximately 50% to about 33%, and the proportion of warmer affinity southern species increased from about 25% to 35% (Ref. 32). The composition changes were accompanied by substantial (up to 92%) declines in the abundance of most species, with the northern species suffering the greatest

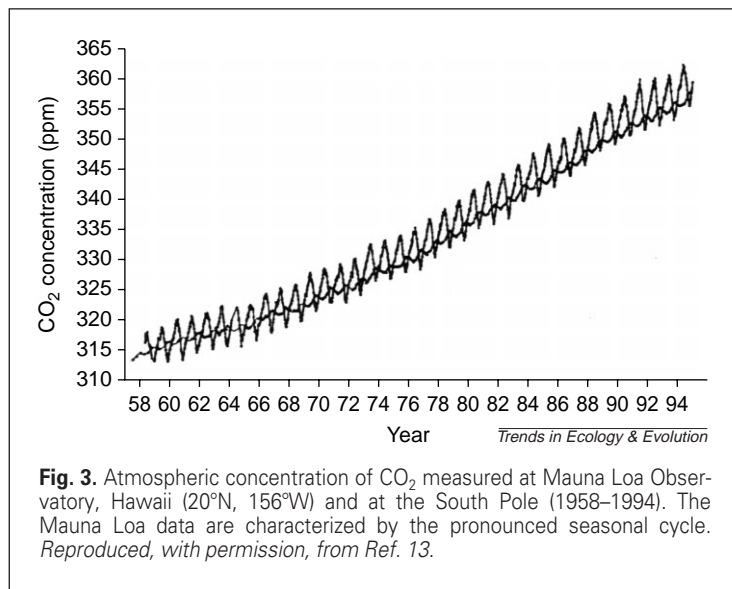


Fig. 3. Atmospheric concentration of CO₂ measured at Mauna Loa Observatory, Hawaii (20°N, 156°W) and at the South Pole (1958–1994). The Mauna Loa data are characterized by the pronounced seasonal cycle. Reproduced, with permission, from Ref. 13.

reductions. Concurrent declines of a similar magnitude were observed for several trophic levels of the benthic ecosystem further north, with the biomass of understory macroalgae decreasing by about 80%.

Terrestrial vertebrates

Ocean warming, especially in the tropics, might also be affecting terrestrial species. Enhanced evaporation from warm surface waters releases large amounts of water vapour. The latent heat released as this moisture condenses accelerates atmospheric warming and does so proportionately more at higher elevations⁴. In tropical regions, such as the cloudforests of Monteverde, Costa Rica, this process appears to result in an elevated cloud base and a decrease in dry season mist. Declines in the frequency of mist days have been strongly associated with synchronous population declines of birds, reptiles and amphibians on plots at 1540 m at Monteverde³³. Mist-day frequency is also negatively associated with upslope colonization of ‘cloud-forest intolerant’ bird species.

Poleward range expansions have been reported for birds in both Europe and the USA. The northern margins of 59 bird species with distributions in the south of Britain have moved further north by an average of nearly 19 km over a 20-year period (1988–1991 compared with 1968–1972) (Ref. 34). A survey of 24 bird species in the western USA, whose nesting distributions have expanded over the past three decades, found that 14 had shifted northward, compared with four moving southward, five moving westward and one radial expansion³⁵. This study hypothesized that most of the species have responded primarily to a decade-long increase in summer rainfall beyond their former ranges. A survey of small mammals in the southwest USA reported similar northward range expansion for 19 species from a variety of habitats³⁶.

Changes in life cycle timing

The life cycles of many organisms are strongly influenced by temperature and precipitation. In the future, warmer conditions are generally expected to advance phenological events such as flowering and fruiting in plants, and to hasten development time in those species that respond to cues such as degree days. Recently compiled data sets indicating advances in phenology in insects, birds, amphibians and plants provide the most compelling evidence yet for

the impact of human-induced climate change, simply because alternative explanations are generally less plausible.

Under a global rise in temperature, insects in particular are expected to pass through their larval stages faster and to become adults earlier. Five species of aphids recorded by the Rothamsted Insect Survey suction trap network in the UK have shown an advance in flight phenology of three to six days over the past 25 years³⁷. Mean temperatures in Britain have risen by 0.4°C over the same period. The date of peak flight for 104 species of the most common Microlepidoptera in The Netherlands (1955–1994) shows a trend towards earlier flight; the trend is strongest in the past two decades (1975–1994) where the date of peak flight has shifted earlier by an average of 11.6 days³⁸.

Among 65 British bird species surveyed from 1971 to 1995, significant trends towards earlier egg laying were found in 20 species (31%), with only one species laying significantly later³⁹. The shift towards earlier laying averaged 8.8 days (range 4–17 days). A subsequent, more extensive analysis of the annual median laying date of 36 British bird species over 57 years (1939–1995) found that 19 species (53%) show long-term trends, with laying dates becoming later in the 1960s and 1970s, and then earlier in the 1980s and 1990s (Ref. 40). Trends towards earlier reproduction, larger clutch sizes and more rapid development times have also been found in several long-term studies of individual bird species in Europe and the USA^{41–46}. Parallel trends in earlier reproduction have been reported for several British amphibians over the period 1978–1994, with every 1°C increase in maximum temperature corresponding to an advance in spawning date by nine to ten days⁴⁷.

Advances in the timing of flowering and of fruiting are also expected in the future, but, although anecdotal evidence abounds, few long-term data sets for plants have been analysed in detail. One exception is the phenological record kept by bee keepers in Hungary for the locust tree *Robinia pseudoacacia*, widely planted since the early 1700s for timber and honey production. Flowering dates in some parts of the species’ range have apparently advanced by three to eight days over the period 1851–1994, and this change is significantly correlated with average spring temperatures⁴⁸.

Conclusions

Recent analyses of long-term data sets indicate that the anomalous climate of the past century is already affecting the physiology, distribution and phenology of some species in ways consistent with theoretical predictions. Although natural variation, or nonclimatic factors, might be responsible for some of these trends, human-induced climate or atmospheric change is the most parsimonious explanation for many. The most convincing evidence comes from studies where intensive monitoring has occurred over an extended period^{22–24,37–40,42–46}; whereas the many studies where a single, recent ‘snapshot’ of distribution or of community composition has been compared with one in the past, are suggestive of climate-induced change, although more open to other interpretations^{26–28,31,32,34,35}. Further analyses of existing long-term data sets will be important to identify vulnerable species and communities⁴⁹. However, because such data sets are relatively rare, establishment of new baseline monitoring programs will also be important. Many of the trends reviewed here show accelerating rates of change over the past two or three decades, indicating that the following situations will become increasingly apparent in the relatively short term:

- The extension of species’ geographic range boundaries towards the poles or to higher elevations by progressive establishment of new local populations.

- The extinction of local populations along range boundaries at lower latitudes or lower elevations.
- Increasing invasion by opportunistic, weedy and/or highly mobile species, especially into sites where local populations of existing species are declining.
- Progressive decoupling of species interactions (e.g. plants and pollinators) owing to mismatched phenology, especially where one partner is cued by daylength (which will not change) and the other partner is cued by temperature.

Most of the trends apparent so far are those of individual species (second tier in Fig. 2). The cascading of these individual responses increasingly to affect the composition and structure of whole communities seems inevitable. The most sobering thought is that even if only a fraction of the examples reviewed here are indeed a result of the enhanced greenhouse effect, they have occurred with warming levels at only one-fifth, or less, of those expected over the next century.

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