

Ecological responses to recent climate change

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There is now ample evidence of the ecological impacts of recent climate change, from polar terrestrial to tropical marine environments. The responses of both flora and fauna span an array of ecosystems and organizational hierarchies, from the species to the community levels. Despite continued uncertainty as to community and ecosystem trajectories under global change, our review exposes a coherent pattern of ecological change across systems. Although we are only at an early stage in the projected trends of global warming, ecological responses to recent climate change are already clearly visible.

The Earth's climate has warmed by approximately 0.6 °C over the past 100 years with two main periods of warming, between 1910 and 1945 and from 1976 onwards. The rate of warming during the latter period has been approximately double that of the first and, thus, greater than at any other time during the last 1,000 years¹. Organisms, populations and ecological communities do not, however, respond to approximated global averages. Rather, regional changes, which are highly spatially heterogeneous (Fig. 1), are more relevant in the context of ecological response to climatic change. In many regions there is an asymmetry in the warming that undoubtedly will contribute to heterogeneity in ecological dynamics across systems. Diurnal temperature ranges have decreased because minimum temperatures are increasing at about twice the rate of maximum temperatures. As a consequence, the freeze-free periods in most mid- and high-latitude regions are lengthening and satellite data reveal a 10% decrease in snow cover and ice extent since the late 1960s. Changes in the precipitation regime have also been neither spatially nor temporally uniform (Fig. 1). In the mid- and high latitudes of the Northern Hemisphere a decadal increase of 0.5–1% mostly occurs in autumn and winter whereas, in the sub-tropics, precipitation generally decreases by about 0.3% per decade¹.

There is now ample evidence that these recent climatic changes have affected a broad range of organisms with diverse geographical distributions^{2–6}. We assess these observations using a process-oriented approach and present an integrated synopsis across the major taxonomic groups, covering most of the biomes on Earth. We focus on the consequences of thirty years of warming at the end of the twentieth century, and review the responses in (1) the phenology and physiology of organisms, (2) the range and distribution of species, (3) the composition of and interactions within communities, and (4) the structure and dynamics of ecosystems, highlighting common and contrasting features amongst the taxa and systems considered.

Phenology

Phenology—the timing of seasonal activities of animals and plants—is perhaps the simplest process in which to track changes in the ecology of species in response to climate change. Birds,

butterflies and wild plants, in particular, include popular and easily identifiable species and thus have received considerable attention from the public. As a result many long-term phenological data sets have been collected. Studies in Europe and North America have revealed phenological trends that very probably reflect responses to recent climate change^{7,8}. Common changes in the timing of spring activities include earlier breeding or first singing of birds, earlier arrival of migrant birds, earlier appearance of butterflies, earlier choruses and spawning in amphibians and earlier shooting and flowering of plants (Fig. 2). In general, spring activities have occurred progressively earlier since the 1960s (Table 1).

Some evidence also indicates a later onset of autumnal phenological events, but these shifts are less pronounced and show a more heterogeneous pattern. Studies reveal different proportions of bird species which advance, delay or do not change autumn migration⁹, and trends of leaf colouring of trees at neighbouring stations often show contradictory signals¹⁰. In Europe, for example, leaf colour changes show a progressive delay of 0.3–1.6 days per decade, whereas the length of the growing season has increased in some areas by up to 3.6 days per decade over the past 50 years^{8,11}. This extension of the growing season accords with the lengthening of 12 ± 4 days derived from satellite data¹² as well as with an advance in the seasonal cycle by 7 days and an increase in amplitude of the annual CO₂ cycle since the 1960s¹³.

Environmental links

In contrast with the climatic factors controlling autumn phenology, the climate signal controlling spring phenology is fairly well understood: nearly all phenophases correlate with spring temperatures in the preceding months. For birds, temperatures on the migration route are also important. Some spring events, such as egg-laying of several song birds and the start of the vegetation period in northern and central Europe, also correlate with the North Atlantic Oscillation (NAO) index, which quantifies winter climatic conditions^{5,14,15} (Fig. 2). An analysis of 50 years of data on 13 plant species in 137 localities revealed responses to the NAO in 71% of the total, with early-blooming and herbaceous species showing greater responses to winter warming than late-blooming and woody plants¹⁵. The temperature response of bird arrival may be modified by photo-

periodic control, genetic regulatory systems and/or population size. Phenological changes in birds and plants are often similar, as described in some cross-system studies^{16,17} (Fig. 2). However, the timing of change in different taxonomic groups is not always synchronous and may have profound ecological consequences. Earlier leaf unfolding, for example, generates a longer growing season but may also increase the risk of damage by a late frost (see also 'Complex Dynamics' below).

Variability and inconsistencies

Geographical differences are evident for both plants and birds, with delayed rather than earlier onset of spring phases in southeastern Europe, including later bird arrival in the Slovak Republic¹⁸ and a later start of the growing season in the Balkan region¹¹. Longer data series covering the last century also include periods of later onset¹⁶. There can also be differences in response to climate change between species at particular sites or with time of season. For plants, strong seasonal variation is reported with the highest advances in early spring (and notable advances of succeeding phenophases) and almost no response in summer and early autumn^{10,17}. Similarly, short-distance migrating birds, which tend to migrate early in the season, often exhibit a trend towards earlier arrival, whereas the later arrivals by long-distance migrants show a more complex

response, with many species not changing their arrival times or even delaying them^{7,19}.

Range shifts to keep up with climate change

It is generally agreed that climatic regimes influence species' distributions, often through species-specific physiological thresholds of temperature and precipitation tolerance^{20,21}. With general warming trends, these 'climate envelopes' become shifted towards the poles or higher altitudes. To the extent that dispersal and resource availability allow, species are expected to track the shifting climate and likewise shift their distributions poleward in latitude and upward in elevation. In some cases (for example, reef-building corals), range shifts in response to changing temperature may not occur if latitudinal distributions are also limited by other factors such as light⁴¹.

Many studies of the biological impacts of climate change have focused on species abundances and distributions in search of the predicted systematic shifts. Migratory species are among the best documented but often exhibit large fluctuations from year to year in their breeding sites, making it difficult to discern long-term range shifts^{22,23}. By contrast, range changes in more sedentary species follow from the slow processes of population extinctions and colonizations. This has made it easier to detect true geographic

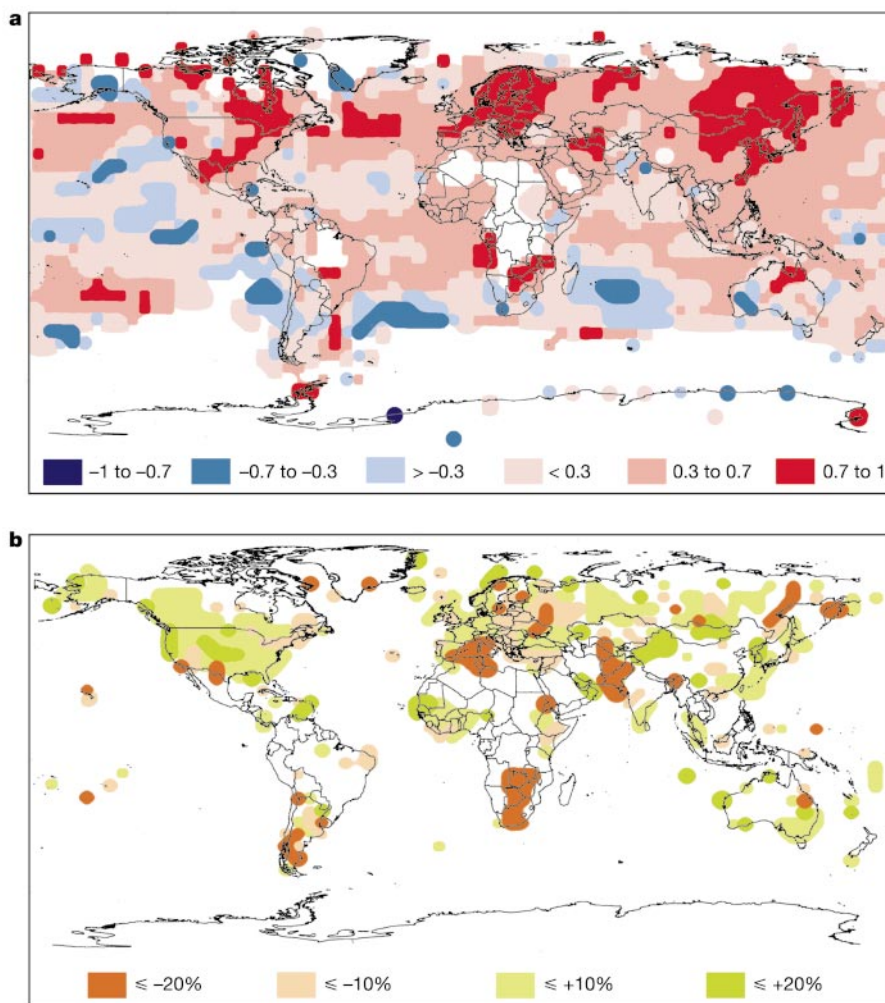


Figure 1 Spatial variability of annual trends in temperature and precipitation since 1976 relative to 1961 to 1990 normals (ref. 1, modified). **a**, Temperature (°C per decade); **b**, precipitation (% per decade).

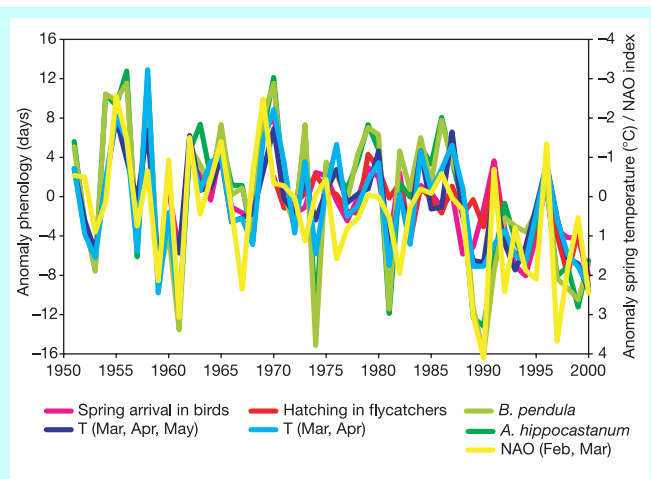


Figure 2 Anomalies of different phenological phases in Germany correlate well with anomalies of mean spring air temperature *T* and NAO index (by P. D. Jones, <http://www.cru.uea.ac.uk/cru/data/nao.htm>). Temperature taken from 35 German climate stations. Phenological phases used: spring arrival in birds, island of Helgoland, North Sea; hatching in flycatchers (*Ficedula hypoleuca*), Northern Germany; and mean onset of leaf unfolding of *Aesculus hippocastanum* and *Betula pendula*.

shifts in the latter group because change is more methodical and missing data have a smaller impact. It is now clear that poleward and upward shifts of species ranges have occurred across a wide range of taxonomic groups and geographical locations during the twentieth century^{2,4,6,23} (Table 2).

Factors affecting species distribution interact in complex ways, and it is not surprising that simple correlations with temperature changes are not always observed. Range shifts are often episodic rather than gradual or monotonic. In regions under the influence of El Niño/Southern Oscillation (ENSO), for example, change may happen rapidly during warm episodes, with ‘setbacks’ during cool periods. In addition, climatic extremes—related to natural oscillations and underlying long-term trends—are also important in driving the present range changes²³. Thus, rates of range shifts vary greatly among and within species, implying differential dispersal abilities. Whereas the magnitude of elevational shifts of alpine plant species lags behind the isothermal shift of 8–10 m per decade²⁴, butterflies appear to track decadal warming quickly^{25,26}, matching the upwards and northwards shifts of temperature isotherms²⁷ (compare data in Table 2).

Climate change and invasions

With climate change, non-native species from adjacent areas may cross frontiers and become new elements of the biota. When long distances have been covered, such movements have often been mediated by human activity. However, for species originating from habitats more suitable than the new location provides, a permanent establishment at the new locality may not be possible without changes in local conditions. An obvious possibility is that, while human activities promote species movement, their subsequent reproduction and spread at the new location imply altered site conditions due, for example, to climate change. The clearest

evidence for such a climate trigger occurs where a suite of species with different histories of introduction spread *en masse* during periods of climatic amelioration^{28,29}. Examples include warm-water species that have recently appeared in the Mediterranean and the North seas^{28,30,31} and thermophilous plants that spread from gardens into surrounding countryside^{29,32} (Fig. 3). Even in such remote places as some sub-Antarctic islands, it is estimated that introductions by humans over the last two centuries account for 50% or more of the higher-plant diversity³³ and a considerable proportion of the insect and mite faunas³⁴.

Climate-linked invasions might also involve the immigration of unwanted neighbours such as epidemic diseases. There is much evidence that a steady rise in annual temperatures has been associated with expanding mosquito-borne diseases in the highlands of Asia, East Africa and Latin America³⁵. Overall, trends of range changes show remarkable internal consistency between studies relating to glaciers, plant and insect ranges and shifting isotherms.

Community shifts

The assemblages of species in ecological communities reflect interactions among organisms as well as between organisms and the abiotic environment. We might expect, therefore, that rapid climatic change or extreme climatic events can alter community composition. In the Sonoran desert of the southwestern United States, for example, recent increases in woody shrub density, extinction of previously common animal species and increases in formerly rare animal species have been attributed to regional climatic shifts³⁶. Furthermore, some of the examples of range shifts mentioned earlier involve community-level changes^{29,37,38}. Changes in distribution are often asymmetrical with species invading faster from lower elevations³⁸ or latitudes³⁷ than resident species are receding upslope or poleward. The result is a (presumably transient) increase in species richness of the community in question as a consequence of the variability in rates at which species shift their ranges.

Observed changes at extremes of environmental and biological gradients

Rapid environmental warming has been reported over the last 30–50 years at a number of stations in the Antarctic, particularly in the Antarctic Peninsula region and on sub-Antarctic islands, along with changes in precipitation patterns^{39,40}. Likewise, tropical oceans have increased in temperature by 1–2 °C over the past 100 years⁴¹. Warming trends are punctuated in most oceans by fairly regular phenomena such as ENSO events, which induce anomalies both locally and temporarily; these phenomena have increased in size and duration over the past century⁴². Most climate projections reveal that this trend is likely to increase rapidly in the next 50 years⁴¹.

Antarctic terrestrial habitats and nearshore tropical marine communities reflect opposite extremes of environmental and biological variation on Earth. The warmth and stability of tropical oceans contrasts dramatically with the year-round low temperatures and rapid, unpredictable short-term variation typical on land in the Antarctic. Likewise, the rich biodiversity and trophic web complexity characterizing reef communities differ strikingly from the characteristics of the extremely simple communities of the Antarctic (Fig. 4). Both environments are experiencing extensive changes^{43,44}

Table 1 Evidence of recent advances in the timing of spring events

Taxon	Location	Observed changes	Period
Numerous plant species	Europe North America	Flowering and leaf unfolding occurring 1.4–3.1 days per decade earlier ⁸ Flowering and leaf unfolding occurring 1.2–2.0 (3.8) days per decade earlier ⁸	Past 30–48 years Past 35–63 years
18 butterfly species	UK	Earlier appearance by 2.8–3.2 days per decade ⁶²	Past 23 years
Amphibians	UK	Earlier breeding ⁶⁷	Past 25 years
Numerous bird species	Europe, North America	Earlier spring migration by 1.3–4.4 days per decade and breeding by 1.9–4.8 days per decade ^{7,22,83–86}	Past 30–60 years

Table 2 Recent latitudinal and altitudinal range shifts

Species*	Location	Observed changes	Climate link
Treeline	Europe, New Zealand	Advancement towards higher altitudes ^{87–89}	General warming
Arctic shrub vegetation	Alaska	Expansion of shrubs in previously shrub-free areas ⁹⁰	Environmental warming
Alpine plants	European Alps	Elevational shift of 1–4 m per decade ²⁴	General warming
Antarctic plants and invertebrates	Antarctica	Distribution changes ⁹¹	Liquid water availability and increased temperature
Zooplankton, intertidal invertebrate and fish communities	Californian coast, North Atlantic	Increasing abundance of warm-water species ^{92,97,93,94}	Warmer shoreline ocean temperature
39 butterfly species	North America and Europe	Northward range shifts up to 200 km over 27 years ^{25,95}	Increased temperatures
such as Edith's Checkerspot butterfly (<i>Euphydryas editha</i>)	Western United States	124 m upward and 92 km northward shift since the beginning of the twentieth century ^{25,26}	
Lowland birds	Costa Rica	Extension of distribution from lower mountain slopes to higher areas ⁹⁸	Dry season mist frequency
12 bird species	Britain	18.9 km average range movement northwards over a 20-year period ⁹⁶	Winter temperatures
Red fox (<i>Vulpes vulpes</i>), Arctic fox (<i>Alopex lagopus</i>)	Canada	Northward expansion of red fox range and simultaneous retreat of Arctic fox range ⁹⁷	General warming

* Where possible, numbers of species which showed a response to climate change are given.

and, lying at opposite extremes of environmental and biological gradients, generate different biological signals of climate change.

In Antarctic terrestrial ecosystems, visually dramatic examples of biological changes in response to climatic warming include the colonization by macroscopic plants (largely mosses) of previously bare or newly exposed ground and the rapid expansion in extent and numbers of the only two higher plants present on the continent^{43,45}. Commensurate with vegetational changes has been colonization by soil invertebrates. As yet there are few examples of Antarctic colonization by 'exotics' from lower latitudes, although some species have established themselves rapidly around several sources of geothermal warming⁴⁶ and there is an increasing number of human-mediated imports, particularly to the sub-Antarctic region.

Substantial impacts on community structure have been observed in coral reefs during periods of warmer than normal sea temperatures. Poised near their upper thermal limits, coral reefs have undergone global mass bleaching events whenever sea temperatures have exceeded long-term summer averages by more than 1.0 °C for several weeks^{41,47}. Six periods of mass coral bleaching have occurred

since 1979 and the incidence of mass coral bleaching is increasing in both frequency and intensity⁴¹. The most severe period occurred in 1998, in which an estimated 16% of the world's reef-building corals died⁴⁸. The impact of thermal stress on reefs can be dramatic, with the almost total removal of corals in some instances^{41,49–51}. In some cases (usually smaller or shorter thermal anomalies), thin-tissued, branching acroporid and pocilloporid corals have bleached and/or died preferentially, leaving more massive species like *Porites* spp intact. In other cases, all coral species have been largely removed^{51,52}. Estimates of how ecosystem species richness and community structure have changed after bleaching events are generally unavailable, but such changes are suspected to be large.

The combination of rising temperatures and ENSO variability has generated contrasting impacts in Antarctic terrestrial versus tropical marine ecosystems. Increasing temperatures have reduced the likelihood that Antarctic organisms will be exposed to their lower thermal limits, thereby allowing increases in both numbers and extent of populations previously at the edge of their range while also, in a few instances, increasing the risk of exposure to upper

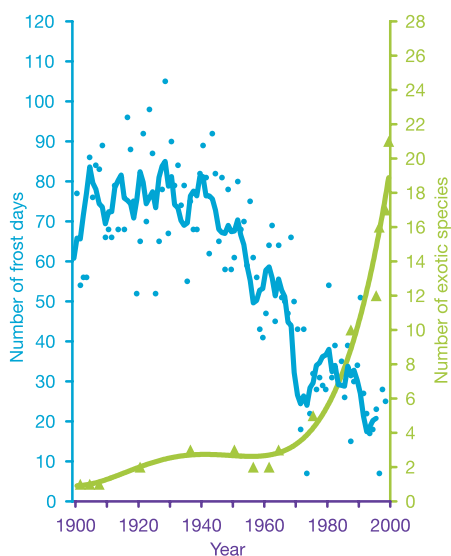


Figure 3 Vegetation shift from indigenous deciduous to exotic evergreen broad-leaved vegetation in southern Switzerland. The shrub layer is dominated by the growing number of spreading exotic evergreen broad-leaved species (see illustration) that

appear to profit from milder winter conditions, indicated here by the decreasing number of days with frost per year (the smoothed curve gives five year averages for the number of frost days per year)²⁹.

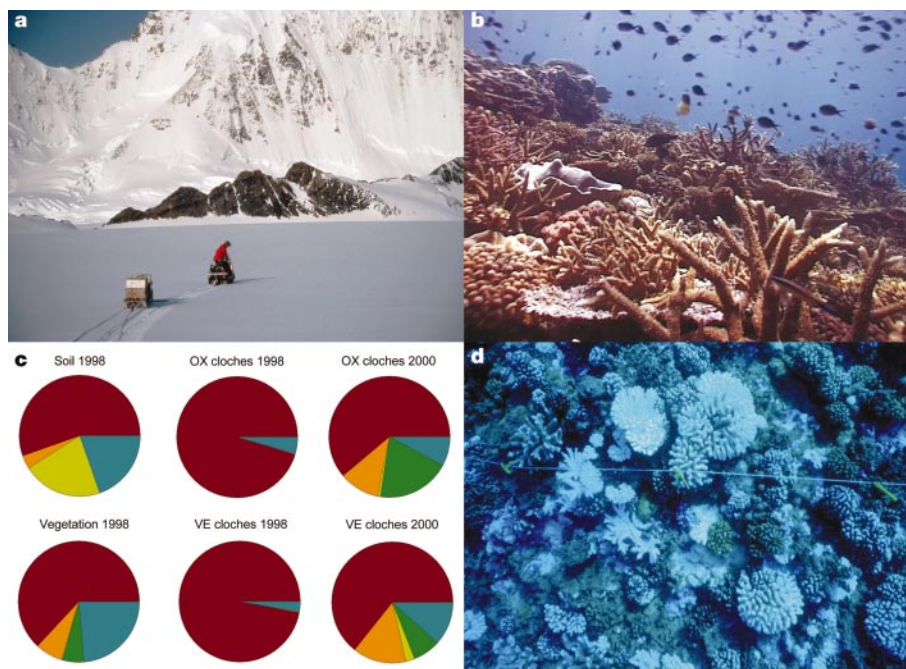


Figure 4 Different environments and their responses to warming. Biodiversity is low in terrestrial communities in Antarctica (a), but very high in nearshore marine communities in tropical oceans (b). The response of these communities to warming seems to differ. Manipulations of Antarctic soils by using Perspex cloches provided realistic simulations of climate change (temperature increase and exposure to different wavelengths of UV

radiation) by using different Perspex types, VE and OX, between 1998 and 2000. These led within 2 years to an increased diversity in soil nematode communities (colours indicate the proportional contribution of major genera), comparable to that found naturally in more developed microhabitats (c). However the increased occurrence of bleaching events on coral reefs (d) is likely to decrease abundance if not diversity.

thermal limits^{43,53,54}. In the tropics, anomalies of less than 1 °C may exceed physiological tolerances and result in large-scale coral bleaching (owing to physiological dysfunction and loss of crucial dinoflagellate symbionts) and subsequent mortality. Because of their need to cope with short-term and seasonal environmental variability, Antarctic biota generally occupy a wider physical niche than do organisms from more stable environments (such as marine tropical organisms). This difference is important in defining range boundaries and how species respond to environmental change⁵⁵.

Complex dynamics

Responses by individual species to climate change may disrupt their interactions with others at the same or adjacent trophic levels. When closely interacting or competing species display divergent responses or susceptibilities to change, the outcome of their interactions may be altered, as long-term data on both terrestrial and marine organisms indicate^{56,57}.

Recruitment success and trophic interactions in marine systems

Recruitment in fish populations has long been known to be a key process that is strongly influenced by climate variability⁵⁸. Variations in atmospheric circulation over the Bering Sea, through interactions with ocean currents, influence transportation of juvenile walleye pollock (*Theragra chalcogramma*) away from adults, affecting the intensity of cannibalism and, consequently, year class strength⁵⁹. Because walleye pollock is an important forage species for other fish, marine mammals and birds, its fluctuations in recruitment affect the whole Bering Sea food web. A Southern Ocean parallel involves krill (*Euphausia superba*), a key food source for higher predators (penguins and other seabirds, whales, seals) as well as a fishery target. Climate change is apparently affecting the reproductive grounds of krill, and consequently its recruitment, by reducing the area of sea ice formed near the Antarctic

Peninsula, which leads to both food web and human economic consequences^{58,60}.

The most widespread effects of climate on dynamics in marine systems appear, however, to be indirect. The persistence of positive anomalies of the North Atlantic Oscillation has, for instance, modified marine primary and secondary production⁵⁷. This may affect the availability of planktonic food for fish larvae, which determines the recruitment success and consequently the size of fish populations⁵⁸. Migration patterns and spatial distributions of large pelagic fish, such as bluefin tuna (*Thunnus thynnus*), can also be altered indirectly through climate-induced changes in prey abundance⁶¹. In upwelling systems, fish production appears to be controlled by enrichment, concentration and retention processes⁶², which are themselves governed by climatic factors. Because temperature increases should intensify upwelling, global fish production could decline because of a consequent reduction in the concentration and retention processes. Changes in the north-east Pacific ecosystem that support this hypothesis are already evident⁶³.

Human exploitation may further exacerbate the effects of oceanic warming on fish populations. In North Sea cod (*Gadus morhua*), for example, a long adult lifespan provides a buffer to occasional recruitment failures, but overfishing has truncated the age structure of the population and thereby increased vulnerability to the adverse effects of prolonged warming⁶⁴.

Species interactions in terrestrial systems

Direct climatic effects on development, spatial distribution, and species interactions are apparent in amphibians and reptiles, which, in common with other ectotherms, are heavily influenced by environmental conditions. Both temperature and humidity affect their reproductive physiology and population dynamics. Oogenesis and spermatogenesis in temperate amphibians and reptiles are dependent on seasonal temperature regimes. In the case of reptiles

there is particular interest in the effects of climate change on the population dynamics of species with temperature-dependent sex determination. In painted turtles (*Chrysemys picta*) offspring sex ratio is highly correlated with mean July temperature, and the production of male offspring would be potentially compromised even by modest (2–4 °C) temperature increases^{65,66}.

Winter warming has precipitated breeding season changes in some but not all species of amphibians in Britain⁶⁷. This variability has, in turn, altered temporal niche overlaps in breeding ponds with immediate consequences for trophic interactions. Thus, newts (*Triturus* spp.) are entering ponds earlier than before, whereas frogs (*Rana temporaria*) have not substantially altered their reproductive phenology. Embryos and larvae of early-breeding frogs are, therefore, exposed to higher levels of newt predation. Such examples illustrate the higher-order consequences of phenological responses to climate change described above. Especially dramatic indirect effects have been observed on the population dynamics of montane amphibian species³⁸. In Costa Rica and the western USA, sharp population declines have been linked with epidemic disease and changes in precipitation patterns related to recent warming^{38,68}. Further, frog population declines in Costa Rica have occurred simultaneously with those of anoline lizards (*Norops* spp.), both being associated with the same climatic patterns³⁸.

Delays in spring arrival by migratory birds may lead to increased competition for nest sites with species arriving earlier⁶⁹. Evidence also indicates that warmer spring weather in Europe has disrupted the synchrony between winter moth (*Operophtera brumata*) hatching and oak bud burst, leading to a mismatch between the peak in insect availability and the peak food demands of great tit (*Parus major*) nestlings^{70,71}. Such disharmonization of fine-tuned events may pose consequences for species interactions and the persistence of ecological communities across an array of ecosystems.

Extensive studies of large mammals indicate that climatic extremes appear to influence juvenile survival, primarily during winter, although not independently of population density^{15,72}. Increasingly warm winters associated with the NAO influence the development and fecundity of red deer (*Cervus elaphus*)⁷³ and Soay sheep (*Ovis aries*)⁷⁴ in Norway and the UK. The impact of such life history responses on population dynamics can occur years later when cohorts have reached reproductive maturity^{15,74} and may, as in the case of Soay sheep, occur only above certain population densities⁷⁵. On Isle Royale, USA, climate directly influences temporal dynamics at producer, herbivore and carnivore trophic levels⁷⁶, as well as indirectly through mediation of trophic interactions such as wolf predation and moose herbivory⁷⁷.

Knowns and unknowns

We have reviewed merely a portion of the enormous body of basic research on ecological and physiological processes that are sensitive to climatic variables such as temperature and precipitation. The evidence indicates that only 30 years of warmer temperatures at the end of the twentieth century have affected the phenology of organisms, the range and distribution of species, and the composition and dynamics of communities. These examples, spanning the previous century and encompassing most major taxa and ecosystems on Earth, provide linkages between recently observed changes in natural systems and twentieth century climate change. The mechanistic bases for the observed biotic responses to climate change have been well established through experimental and observational studies on the behaviour, ecology and physiology of many wild species. Such studies will continue to provide detailed mechanisms by which climatic change affects individual physiology, seasonal timing, population dynamics and geographic distributions.

However, the complexity of ecological interactions renders it difficult to extrapolate from studies of individuals and populations to the community or ecosystem level. We do not, for example, have a

clear understanding of the roles of short-term versus long-term environmental stochasticity and population-intrinsic processes in community dynamics and stability^{76,78}. Currently, the most relevant physical and temporal scales of ecological investigation are local and short-term (less than three decades). In contrast, climatology generally encompasses much larger spatial and temporal scales. As a consequence, it remains difficult to link population and community-level dynamics to the global-scale studies of atmospheric and oceanic processes^{23,79,80}.

As both ecological theory and conservation history have shown, the modern landscape provides little flexibility for ecosystems to adjust to rapid environmental changes. In contrast with historical responses and migration processes, species in many areas today must move through a landscape that human activity has rendered increasingly impassable⁸¹. As a result of the widespread loss and fragmentation of habitats, many areas which may become climatically suitable with future warming are remote from current distributions, and beyond the dispersal capacity of many species. Consequently, species with low adaptability and/or dispersal capacity will be caught by the dilemma of climate-forced range change and low likelihood of finding distant habitats to colonize, ultimately resulting in increased extinction rates. Furthermore, several case studies (especially in the marine environment) have indicated that climate change can reinforce the detrimental effects of human exploitation and mismanagement and push species and ecosystem tolerances over their limits. This is exemplified by the North Sea cod, which clearly illustrates the human economic consequences of such synergistic effects, as well as by the massive and direct impacts of climate change on coral reefs that may yield even more substantial social and economic impacts.

It is not simply the magnitude of change of global average temperature over the last century but the inherent asymmetry in change processes that complicates predictions of ecological responses, especially for complex systems. However, it is clear that communities are already undergoing re-assembly that is attributable to climate change, as several of the studies cited in this review demonstrate. The implications of such large-scale, consistent responses to relatively low average rates of climate change are large and the projected warming for the coming decades raises even more concern about its ecological and also socio-economic consequences. □

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