

REVIEW SUMMARY

CLIMATE CHANGE

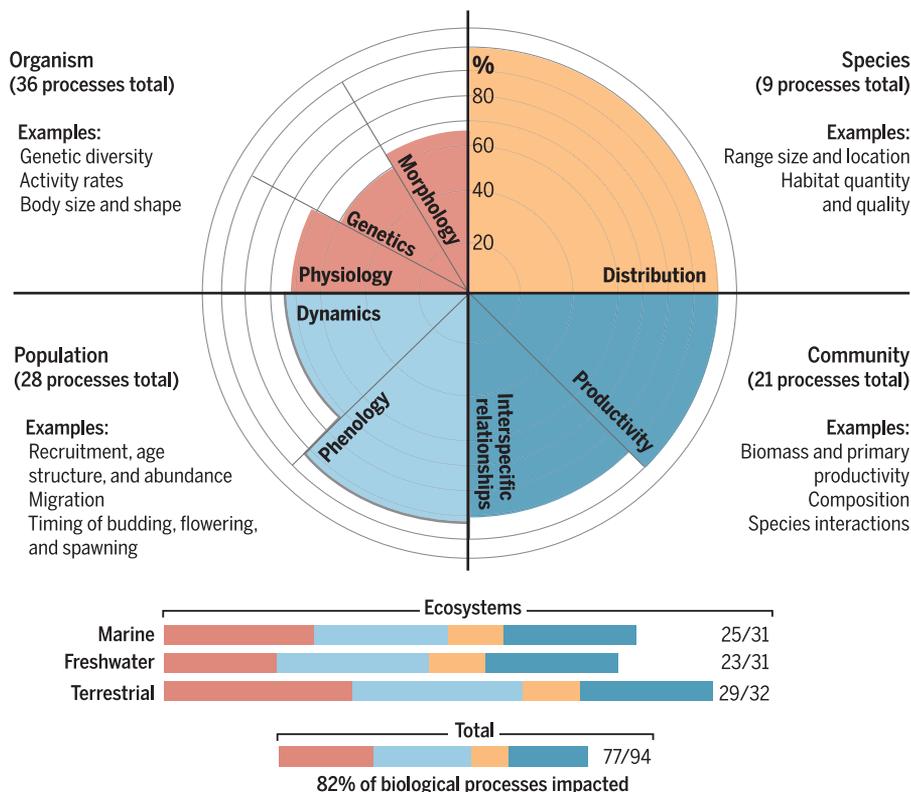
The broad footprint of climate change from genes to biomes to people

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BACKGROUND: Climate change impacts have now been documented across every ecosystem on Earth, despite an average warming of only ~1°C so far. Here, we describe the full range and scale of climate change effects on global biodiversity that have been observed in natural systems. To do this, we identify a set of core ecological processes (32 in terrestrial and 31 each in marine and freshwater ecosystems) that underpin ecosystem functioning and support services to people. Of the 94 processes

considered, 82% show evidence of impact from climate change in the peer-reviewed literature. Examples of observed impacts from meta-analyses and case studies go beyond well-established shifts in species ranges and changes to phenology and population dynamics to include disruptions that scale from the gene to the ecosystem.

ADVANCES: Species are undergoing evolutionary adaptation to temperature extremes,



Climate change impacts on ecological processes in marine, freshwater, and terrestrial ecosystems. Impacts can be measured on multiple processes at different levels of biological organization within ecosystems. In total, 82% of 94 ecological processes show evidence of being affected by climate change. Within levels of organization, the percentage of processes impacted varies from 60% for genetics to 100% for species distribution.

and climate change has substantial impacts on species physiology that include changes in tolerances to high temperatures, shifts in sex ratios in species with temperature-dependent sex determination, and increased metabolic costs of living in a warmer world. These physiological adjustments have observable impacts on morphology, with many species in both aquatic and terrestrial systems shrinking in body size because large surface-to-volume ratios are generally favored under warmer conditions. Other morphological changes include reductions in melanism to improve thermoregulation, and altered wing and bill length in birds.

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Broader-scale responses to climate change include changes in the phenology, abundance, and distribution of species. Temperate plants are budding and flowering earlier in spring and later in autumn. Comparable adjustments have been observed in marine and freshwater fish spawning events and in the timing of seasonal migrations of animals worldwide. Changes in the abundance and age structure of populations have also been observed, with widespread evidence of range expansion in warm-adapted species and range contraction in cold-adapted species. As a by-product of species redistributions, novel community interactions have emerged. Tropical and boreal species are increasingly incorporated into temperate and polar communities, respectively, and when possible, lowland species are increasingly assimilating into mountain communities. Multiplicative impacts from gene to community levels scale up to produce ecological regime shifts, in which one ecosystem state shifts to an alternative state.

OUTLOOK: The many observed impacts of climate change at different levels of biological organization point toward an increasingly unpredictable future for humans. Reduced genetic diversity in crops, inconsistent crop yields, decreased productivity in fisheries from reduced body size, and decreased fruit yields from fewer winter chill events threaten food security. Changes in the distribution of disease vectors alongside the emergence of novel pathogens and pests are a direct threat to human health as well as to crops, timber, and livestock resources. Humanity depends on intact, functioning ecosystems for a range of goods and services. Enhanced understanding of the observed impacts of climate change on core ecological processes is an essential first step to adapting to them and mitigating their influence on biodiversity and ecosystem service provision. ■

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REVIEW

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The broad footprint of climate change from genes to biomes to people

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Most ecological processes now show responses to anthropogenic climate change. In terrestrial, freshwater, and marine ecosystems, species are changing genetically, physiologically, morphologically, and phenologically and are shifting their distributions, which affects food webs and results in new interactions. Disruptions scale from the gene to the ecosystem and have documented consequences for people, including unpredictable fisheries and crop yields, loss of genetic diversity in wild crop varieties, and increasing impacts of pests and diseases. In addition to the more easily observed changes, such as shifts in flowering phenology, we argue that many hidden dynamics, such as genetic changes, are also taking place. Understanding shifts in ecological processes can guide human adaptation strategies. In addition to reducing greenhouse gases, climate action and policy must therefore focus equally on strategies that safeguard biodiversity and ecosystems.

Atmospheric concentrations of greenhouse gases from burning fossil fuels and deforestation are approaching levels that have not been detected in the past 20 million years (1). This has altered the chemical composition of the Earth's atmosphere, oceans, and fresh waters (2). As a result, temperatures

in the upper ocean and on land are now ~1°C higher than in preindustrial times, and temperature, wind, and precipitation regimes have become more variable and extreme (3, 4). These changes are having clear impacts on planetary biophysical processes, including desalinization and acidification of the world's oceans (5) and melting of permafrost, ice sheets, and glaciers (6, 7). Lakes and rivers have increased in temperature, altering seasonal patterns of mixing and flows (8).

Changing climate regimes have been an important driver of natural selection in the past (9) and, as in the past, species are responding to the current human-induced climate event in various ways. Previous reviews have covered many of the more obvious changes in species ranges, phenologies, and population dynamics (10–15) but have usually focused on one ecological system at a time. Here, we discuss the full range and scale of climate change effects on biota, including some of the less obvious disruptions observed in natural systems. We present examples of case studies of observed impacts across terrestrial and aquatic biomes and find evidence that climate change is now affecting most biological and ecological processes on Earth—spanning genetics, organismal physiology and life-history, population distributions and dynamics, community structure, and ecosystem functioning (Fig. 1 and table S1). People depend on intact, functioning ecosystems for a range of goods and services, including those associated with climate adaptation (16). Understanding the observed impacts of current climate change on core ecological processes is therefore an essential first step in humans planning and adapting to changing ecosystem conditions.

Although inherently different, marine, freshwater, and terrestrial realms share a common hierarchy of levels of biological organization, ranging from genes to organisms, populations, species, communities, and ecosystems. Broadly adapting from Bellard *et al.* (17), we screened the literature (supplementary materials) to evaluate evidence that climate change is affecting ecological components across different levels of biological organization, each of which comprises a core set of ecological processes (Fig. 1, fig. S1, and table S1). We identify a set of core ecological processes on Earth (32 in terrestrial and 31 each in marine and freshwater), which together facilitate ecosystem functioning that supports services to people (17). These processes include changes in genetic diversity (genetics), metabolic rates (physiology), body size (morphology), timing of migration (phenology), recruitment (population dynamics), range size (distribution), loss of synchronization (interspecific relationships), and biomass (productivity) (17). Because our main goal is to assess what processes are affected by climate change, we define “impact” on each process as an observed change in that process linked to climate change. We do not differentiate between “positive” (adaptive, buffering, or mitigating) and “negative” (stress or damage) responses because responses may be positive at one level of biological organization (such as genetic adaptation to climate change) but negative at another (such as reduced genetic variation and capacity to deal with other stressors). We then consider the relevance of the affected ecological processes in human systems and illustrate observed impacts to ecosystem services such as food and resource security (fisheries, agriculture, forestry, and livestock production), human health, and hazard reduction.

Ecological impacts of climate change

Organisms Genetics

There is now growing evidence that species are undergoing evolutionary adaptation to human-induced climate change. For example, between the 1960s and 2000s the water flea (*Daphnia magna*) evolved to cope with higher thermal extremes in the UK (18), and cornflower (*Centaurea cyanus*) life history traits have recently evolved in response to warmer springs across northern France (19). Other examples include the evolution of earlier migration timing in anadromous pink salmon (*Oncorhynchus gorbuscha*), with decreased frequency of incidence of a genetic marker that encodes for late migration (20). Time-series data that control for physiological acclimatization also show strong evidence for genetic responses to climate change. For example, Bradshaw and Holzapfel showed that genotypic values for the critical day length that induces diapause in the pitcher plant mosquito (*Wyeomyia smithii*) change with latitude, and that the latitudinal relationship has changed over the period from 1972 to 1996 (21). Onset of diapause now occurs later, which is consistent with a longer

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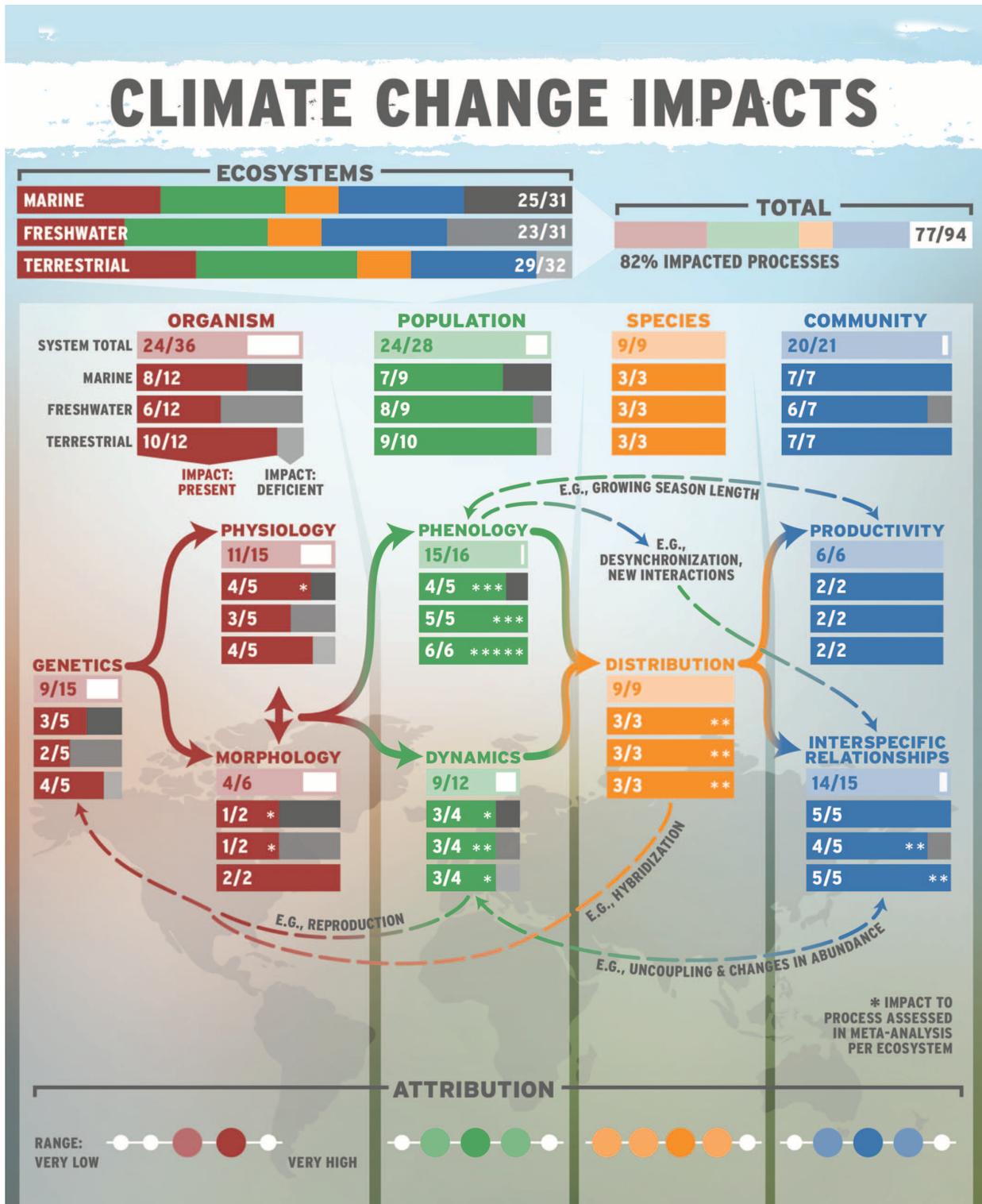
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growing season under warmer conditions. Oceanic phytoplankton have adapted to a temperature change of $+0.73^{\circ}\text{C}$ associated with 15 years of climate warming in the Gulf of Cariaco, Venezuela, by adjusting their thermal niche by $+0.45^{\circ}\text{C}$ (22). Although such evidence from small organisms with short generation times is accumulating, we found little documented evidence of evolutionary change from species with longer generation times such as birds, mammals, and trees (14, 23), although adaptation appears to be possible in some long-lived reef corals (24).

Changes in species ranges have altered or created new “hybridization zones” across the planet. For example, in North America, hybrid zones between black-capped (*Poecile atricapillus*) and Carolina chickadees (*P. carolinensis*) are shifting in response to warmer winter temperatures (25), and because the southern flying squirrel (*Glaucomys volans*) has expanded its range northward in eastern North America, it is now hybridizing with the northern flying squirrel (*G. sabrinus*) (26). In North American rivers and streams, hybridization between invasive rainbow trout (*Oncorhynchus mykiss*) and native cutthroat trout (*O. clarkia*) has increased in frequency as the former expand into warming waters (27). Such hybridization events have also been observed in some marine fishes, such as the coastal West Coast dusky cob (*Argyrosomus coronus*), and are expected to increase as species shift their ranges poleward in response to rapidly warming ocean conditions (28).

Physiology

Many species display temperature-driven trait plasticity in physiological processes such as thermal optima (29). Whereas some responses, such as acclimation to high temperatures, maximize fitness, others can reflect failure to cope with temperature stress and other climate-mediated changes. These responses can occur within a generation or between generations through maternal or epigenetic effects (30).

There is some observational evidence that warming has affected temperature-dependent sex determination (TSD) of species in marine and terrestrial systems. Snake pipefish (*Entelurus aequoreus*) in the northeastern Atlantic have altered their operational sex ratios and reproductive rates as a consequence of warmer sea surface temperatures (31). Most evidence for impacts on TSD in marine systems, however, is derived from experimental studies, which provide strong support for TSD changes in sea turtles and various fish species (32, 33). In terrestrial and freshwater systems, TSD has been implicated in masculinization and feminization, respectively, of lizard and turtle populations (34, 35).

In marine systems, physiological responses to both climate warming and changing ocean conditions are widespread (36, 37). Matching field and laboratory data for the eelpout (*Zoarces viviparus*) show increased metabolic costs associated with warming in the North and Baltic Seas (38). In aquatic systems, warming increases oxy-

gen demand but decreases oxygen content of the water, resulting in substantial metabolic costs (39). Although climate change per se does not cause acidification of the oceans, both arise directly from higher atmospheric carbon dioxide, and experimental evidence has raised concerns regarding negative effects of ocean acidification on calcification, growth, development, and survival of calcifying organisms (12). For example, acidification has led to extensive shell dissolution in populations of the pteropod *Limacina helicina* in northwest North America and in the Southern Ocean off Antarctica (40, 41).

Morphology

Individuals in some species are becoming smaller with increasing warming because large surface-to-volume ratios are generally favored under warmer conditions (42)—a phenomenon that is linked to standard metabolic principles (43). In the Appalachian Mountains, six species of *Plethodon* woodland salamander have undergone, on average, an 8% reduction in body size over the past 50 years (44). Similarly, three species of passerine birds from the northeast United States show an average 4% decrease in wing length correlated with recent warming (45), and the long-distance migrant bird the red knot (*Calidris canutus*) is now producing smaller offspring with smaller bills, which reduces survival in juveniles because of altered foraging success on underground bivalves (46). In general, decreasing body size with warming is expected, but evidence from cold, high-altitude habitats suggests that increased primary productivity and longer growing seasons from warming have led to increased body size in some mammal species such as American marten (*Martes americana*) and yellow-bellied marmot (*Marmota flaviventris*) (47, 48). In South Australia, leaf width in soapberry (*Dodonaea viscosa*) has decreased compared with the ancestral condition documented under cooler temperatures 127 years ago (49). Other climate change impacts on morphology include color changes in butterflies, dragonflies, and birds (50–53) and pronounced changes in skull shape in the alpine chipmunk (*Tamias alpinus*) (54).

Population Phenology

For most species, migrations and life-history processes (such as budding and flowering in plants, hatching and fledging in birds, and hibernation in mammals) are closely tied to seasonal and interannual variation in climate, and there is now overwhelming evidence that both have been affected by climate change (10, 37, 55, 56). Across marine, freshwater, and terrestrial ecosystems, spring phenologies have advanced by 2.3 to 5.1 days per decade (10, 57). A combination of climate warming and higher atmospheric CO_2 concentrations has extended the growing period of many plant populations (58). In a large global analysis, which included 21 phenological metrics such as leaf-off and leaf-on dates and growing-season length, plant phenologies were found to have shifted by more than 2 standard deviations

across 54% of Earth’s land area during the past three decades (59).

In marine and freshwater systems, advances in the timing of annual phytoplankton blooms—the basis for many aquatic food webs—have occurred more rapidly than temporal shifts in terrestrial plants (37, 60). Such changes in plankton phenology have been attributed to increases in water temperatures, reduction in the duration of ice cover, and the alteration of the seasonal duration of thermal stability or stratification of the water column.

Shifts in spawning times have been documented for 43 fish species in the northeast Pacific Ocean from 1951 to 2008, with earlier spawning associated with increased sea surface temperature and later spawning associated with delays in seasonal upwelling of nutrients toward the ocean surface (61). Similar impacts on breeding have been observed in terrestrial and marine bird species (62).

Changes in the timing of migration events have been extensively documented, including advances in spring arrival dates of long-distance migratory bird species in Europe, North America, and Australia (63–65). Similarly, long-term data on many amphibians and mammals have shown advancements in spring and delays in autumn migration (66–68) and altered peak calling periods of male amphibians (67–69). In the largest meta-analysis to date of phenological drivers and trends among species in the southern hemisphere, 82% of terrestrial data sets and 42% of marine data sets demonstrated an advance in phenology associated with rising temperature (70).

Abundance and population dynamics

Acute temperature stress can have severe negative effects on population dynamics such as abundance, recruitment, age structure, and sex ratios. Meta-analyses across thousands of species report that ~80% of communities across terrestrial, freshwater, and marine ecosystems exhibited a response in abundance that was in accordance with climate change predictions (10, 70). In a meta-analysis of marine species, 52% of warm-adapted species increased in abundance, whereas 52% of cold-adapted species decreased (71). Temperature spikes may cause mass mortality of key ecosystem engineers in both temperate and tropical oceans. Excessive heat kills canopy-forming macroalgae in temperate marine systems (72) and causes bleaching and mass mortality of corals in the tropics (73). Reductions in sea ice extent have caused declines in abundances of ice-affiliated species in the Arctic [for example, ivory gulls (*Pagophila eburnea*), ringed seals (*Pusa hispida*), and polar bears (*Ursus maritimus*) (74)] whereas in some cases, such as on Beaufort Island in the southern Ross Sea, the loss of ice from receding glaciers resulted in increased abundances of Adélie penguins (*Pygoscelis adeliae*) (75). In the United States, the bull trout (*Salvelinus confluentus*) has lost >10% of its spawning grounds in central Idaho over the past 13 years because of increased water temperatures (76), while the brown trout (*Salmo*

trutta) has lost habitat in the Swiss Alps (77). In western Canada, reduced survival of adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*) has been observed with increased water temperatures (78), and in eastern Canadian lakes, golden-brown algae dramatically increased in abundance as water temperature increased 1.5°C during the latter part of the 20th century (79). Some of the best evidence for climate-change impacts on the abundance of terrestrial species comes from analyses of bird population trends derived from systematic monitoring schemes in Europe, with warm-adapted species having increased in abundance on average since the 1980s and cold-adapted species having declined (80).

Climate change can increase the abundance of temperature-sensitive disease vectors, with subsequent effects on disease outbreaks. In the African Serengeti, there is some evidence that a combination of extreme weather, high abundances of ticks carrying *Babesia*-piroplasm, and suppressed immunity to canine distemper virus led to widespread mortality of lions (*Panthera leo*) (81). In marine systems, field evidence shows that corals are increasingly susceptible to white band disease at higher temperatures, leading to declines in two of the most important reef-building acroporid (branching) corals in the western Atlantic (82).

Species Distribution

One of the most rapid responses observed for marine, freshwater, and terrestrial species is a shift in their distributions to track optimal habitat conditions (71, 83, 84). Across land and aquatic ecosystems, species have expanded their leading (cold limit) edge by 19.7 km per decade, with marine species expanding by 72 km per decade compared with 6 km per decade in terrestrial species (37). The distributions of many marine taxa have shifted at higher velocities than those of terrestrial taxa (37) because areas with rapid changes in climate extend across broader regions of the ocean than on land, and connectivity in marine environments tends to be high (85). To illustrate this point, corals around Japan have shifted their range by up to 14 km per year over the past 80 years (86), and in waters off the southeast coast of Australia, intertidal invertebrate species have shifted their geographic distributions polewards at an average rate of 29 km per decade (87). Where connectivity allows for dispersal, some freshwater fishes are capable of shifting at rates comparable with those of marine and terrestrial taxa (88), but mean shifts by river fishes in some regions have been insufficient to compensate for measured temperature rises (89).

There has been a consistent overall trend for tropical, warm-adapted species to expand their ranges into environments previously dominated by temperate cold-tolerant species (“tropicalization”) (90). A similar phenomenon has been documented in the Arctic, where boreal fish communities have responded to warming in the Barents Sea by shifting northward, resulting in a

high turnover in Arctic fish communities (“borealization”) (91). Similarly, on land, increased minimum temperatures have driven rapid changes in the range size (as well as distribution) of Swedish birds, with northern species retracting and southern species expanding northward (92).

In addition to latitudinal changes, many observed shifts in species distributions have occurred across elevation gradients. In the mountains of New Guinea, birds have shifted their distributions upslope by 95 to 152 m from 1965 to 2013 (93). A similar upslope shift was observed in recent decades in mountainous stream-dwelling fish in France (89), North American plants (94), and Bornean insects (95). An analogous response has been the shift to deeper, colder waters among some marine fishes (91).

In some cases, species have shown no response or even downhill shifts in their distributions (96) or increased frequency of range disjunction rather than poleward or upward range shifts (97). Savage and Vellend (98) found upward range shifts in North American plant species and an overall trend toward biotic homogenization from 1970 to 2010, but their study also documents considerable time lags between warming and plant responses (99, 100). Delayed community responses to increasing temperature may be in part due to the buffering effects of microhabitats (101, 102) and possibly moisture, which is a critical, but less often studied, driver in the redistribution of species (103). For example, Crimmins *et al.* observed downhill movements for North American plants under climate change over an 80-year period, which they attribute to changes in water balance rather than temperature (104).

Community Interspecific relationships

As a by-product of the redistribution of species in response to changing climate, existing interactions among species are being disrupted, and new interactions are emerging (105, 106). These novel biotic interactions can exacerbate the impacts of abiotic climate change (107, 108). Woody plants are invading arctic and alpine herb-dominated communities in response to rapid warming in recent decades, leading to secondary shifts in distribution of other plants and animals (92). In the Sierra Nevada Mountains of California, Tingley and Beissinger found high levels of avian community turnover during the past 100 years at the lowest and highest elevations (109), and in Greece, Sgardeli *et al.* found similar patterns of temperature-driven turnover in butterfly communities (110). There are surprisingly few studies of observed impacts of climate change on competitive interactions (108). In one example from Sweden, Wittwer *et al.* found that among four bird species occupying the same ecological guild, resident birds were able to adapt to warmer temperatures and out-compete the sole long-distance migrant, *Ficedula hypoleuca* (111).

New interactions among species can also lead to trophic disruptions such as overgrazing. In western Australia, for example, overgrazing of

subtropical reefs by the poleward spread of tropical browsing fish has suppressed recovery of seaweeds after temperature-induced mortality (112). These types of trophic disruptions are escalating, with range shifts by tropical herbivorous fishes increasing herbivory rates in subtropical and temperate coastal ecosystems where seaweeds are the dominant habitat-forming taxa (90).

Phenological mismatches have been observed between butterflies and their annual host plants, with the plants dying before the insect larvae were ready to enter diapause (113). Similarly, an analysis of 27 years of predator-prey data from the UK showed asynchronous shifts between the tawny owl (*Strix aluco*) and its principle prey, the field vole (*Microtus agrestis*), which led to reduced owl fledging success (114). In Lake Washington, United States, spring diatom blooms advanced by over 20 days since 1962, resulting in predator-prey mismatches with their main grazer, the water flea (*Daphnia pulicaria*), and population declines in the latter (60). In Canadian Arctic lakes, asynchronous shifts in diatom blooms resulted in generalist water fleas being replaced by more specialist species (115). At higher trophic levels, warming has affected the fry and the juvenile life-history stages of lake char (*Salvelinus umbla*) via direct impacts on their zooplankton and vendace (*Coregonus alba*) food sources (116).

Productivity

Changes in productivity are one of the most critical impacts of climate change across aquatic and terrestrial ecosystems (117, 118). In marine systems, climate-mediated changes in chlorophyll-*a* concentrations as a proxy of phytoplankton biomass have been highly variable (119). Depending on location, these include both dramatic increases and decreases in abundance as well as changes in phenology and distribution of phytoplankton over the past several decades. In a global study of phytoplankton since 1899, an ~1% decline in global median phytoplankton per year was strongly correlated with increases in sea surface temperature (120), whereas in the Antarctic Peninsula, phytoplankton increased by 66% in southern subregions and decreased by 12% in northern subregions over a 30-year period. These conflicting observations in the Antarctic are in part linked to changes in sea surface temperature but also changes in ice cover, cloudiness, and windiness, which effect water-column mixing (121).

In deep tropical freshwater lakes dominated by internal nutrient loading through regular mixing, warmer surface waters confer greater thermal stability, with reduced mixing and return of nutrients to the photic zone, substantially decreasing primary productivity (122), phytoplankton growth (123), and fish abundance (122). In contrast, eutrophication effects are exacerbated by higher temperatures in shallow lakes, resulting in increased productivity and phytoplankton and toxic cyanobacteria blooms (124).

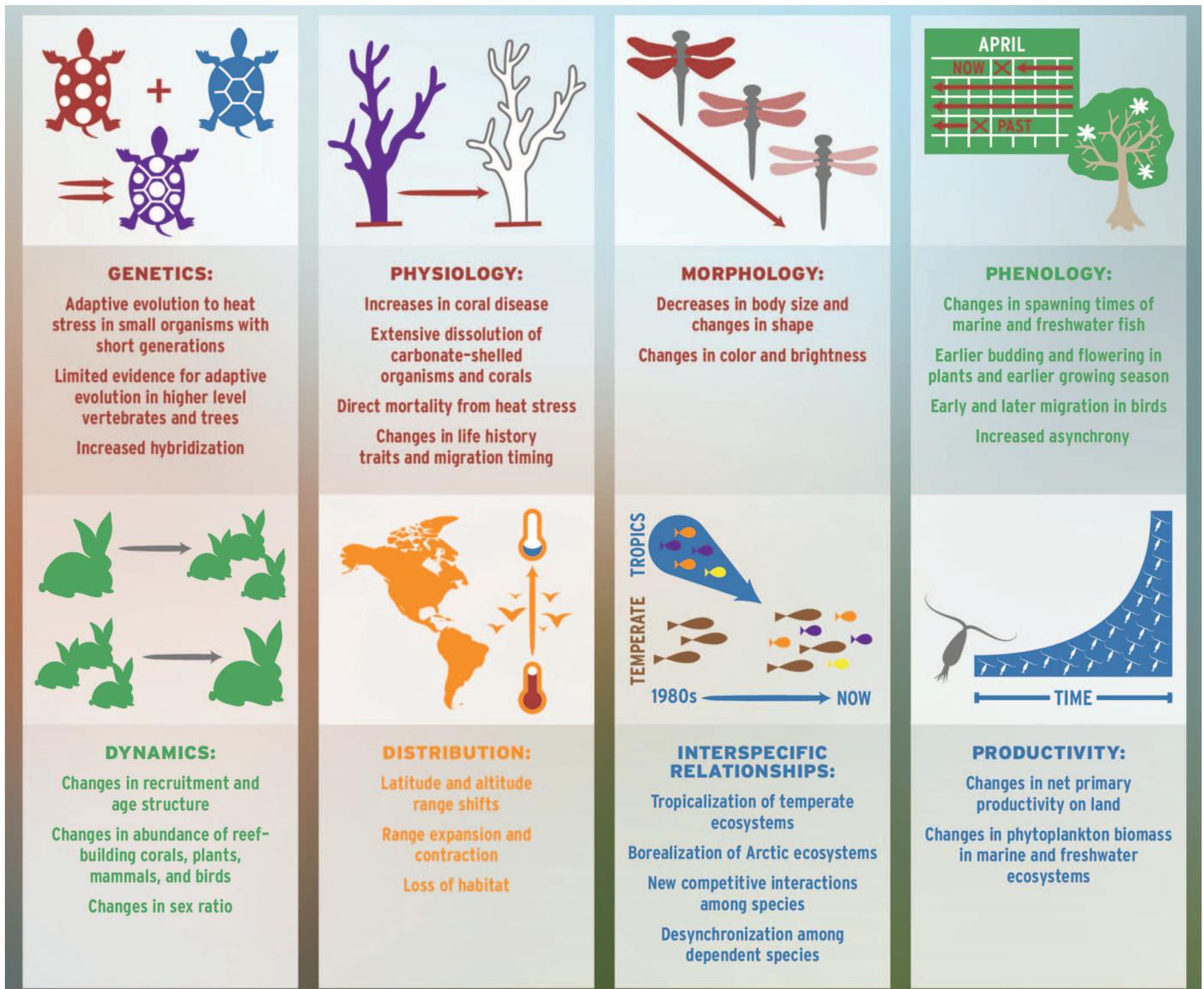


Fig. 2. Climate impacts on ecological processes. Examples of ecological components and processes affected by climate changes across marine, freshwater, and terrestrial ecosystems (fig. S1 and table S1).

Globally, terrestrial plant growth has increased with increasing temperatures and CO₂ levels. This may in part explain the on average 6% increase in net primary productivity (NPP) from 1982 to 1999 (125), although these changes in NPP may also be related to natural variation in El Niño–La Niña cycles (126). However, responses are highly variable, and some terrestrial systems are not experiencing increased productivity owing to either extreme temperatures or lack of water. Severe short-term droughts in climatically stable rainforest environments are unusual but in recent years have increased in frequency. These events have led to changes in forest canopy structure in Amazonia (127) and decreases in above-ground woody and leaf biomass in the Congo basin (128). Across large expanses of the Amazon, there has been an overall reduction in above-

ground biomass owing to increased climate variability over the past three decades (129).

Impacts across ecosystems

All three biotic realms (terrestrial, freshwater, and marine) are being affected by climate change, and the evidence summarized here reveals that these impacts span the biological hierarchy from genes to communities. Of the 94 processes considered, we found that 82% have evidence of impact by climate change, and this has occurred with just 1°C of average warming globally (Fig. 1). Impacts range from genetic and physiological changes to responses in population abundance and distribution (Fig. 2).

The fact that evidence is missing for some processes is more likely to reflect data deficiencies than the absence of any response to climate

change. We only considered field-based case studies that report changes in the processes through time. For many components, such as genetics (23) and physiology (29), there is strong evidence from experiments on a wide range of species that individuals and populations can and likely will respond to climate change. Thus, even though we found compelling evidence of widespread responses across the biological hierarchy, we still consider our discussion of impacted processes to be conservative. To illustrate this point, Box 1 shows the range of observed responses in the water flea *Daphnia*, which spans the entire hierarchy of biological organization.

Ecosystem state shifts

As ecological systems continue to accumulate stress through compromised ecological processes



Box 1. A complete hierarchy of climate change impact in one model system: the water flea *Daphnia*.

Combining time-series data with experimental approaches can lend insights to the breadth of climate change impacts. For water fleas of the genus *Daphnia*, for instance, there is evidence for responses to temperature at all levels of biological organization. *Daphnia* are important grazers in lakes and ponds (180). They adapt to temperature increase through genetic changes in thermal tolerance (18), body size, and life history traits (181, 182). In the laboratory, *Daphnia* exhibit phenotypic plasticity in physiology to changing temperatures [for example, hemoglobin quality and quantity (183) or metabolic activity (184)], behavior [such as swimming activity (184)], life history traits (185), and body size (182). *Daphnia* adjust their phenology (186) and abundance (187) in response to increases in temperature, which results in mismatches with phytoplankton dynamics (60). Warmer, drier weather over two decades can lead to expanded distributions and increased colonization capacity (188). Temperature influences interactions of *Daphnia* with predators (189) and parasites (190), and adaptation to increased temperature influences competitive strength (185). In the absence of fish, high abundances of *Daphnia* in +4°C heated mesocosms exert strong top-down control on phytoplankton (191).

either directly from climate change or interactively with other forced disturbances (discussion is provided in the supplementary materials), diminished resilience may lead to ecological regime shifts—in which one ecosystem state shifts to an alternative and potentially undesirable stable state. For example, some reefs are transitioning from coral- to algal-dominated states as a consequence of mass coral mortality (130),

whereas kelp forests are turning into rocky barrens in temperate seas (90, 131, 132). In lakes, climate change has increased the risk of regime shifts from clear-water to turbid states and increased the occurrence of cyanobacteria blooms (124). If sufficient community-based processes are affected at regional scales, wholesale biome shifts can occur such as has been observed in Alaska, where tundra is transitioning to boreal conditions (133). These are clear signs of large-scale ecosystem change and disruption, in which disequilibrium rapidly pushes the system into a new state (134).

Using ecology to better understand climate change impacts on human well-being

Threats to production

The impacts of climate change on marine fisheries have major consequences for human societies because these currently provide ~17% of the global protein for people (135). There is, however, no current consensus on the costs and benefits of the ongoing global redistribution of fisheries because trends are highly variable. In the Arctic, commercially important fish, such as Atlantic cod (*Gadus morhua*) and walleye pollock (*Theragra chalcogramma*), have increased in biomass primarily because of increases in plankton production from reduced sea ice (136, 137), whereas changes in fish biomass in the Southern Ocean are less clear (138). In Switzerland, which has experienced twice the average global temperature increase, trout catches have been halved over two decades because of rising temperatures in Alpine streams (77).

Changes in total marine productivity are not just attributed to abundance shifts but also morphological shifts. Indeed, some fish species appear to be shrinking, but attributing this solely to ocean warming is difficult because size-dependent responses can be triggered by commercial fishing as well as long-term climate change (139). However, long-term trend analyses show convincingly that eight commercial fish species in the North Sea underwent simultaneous reductions in body size over a 40-year period because of ocean warming, resulting in 23% lower yields (140). Reduced body size in fish is also being recorded in lakes and rivers throughout Europe and has been linked to increased temperature and climate-induced shifts in nutrient inputs (141, 142).

Impacts on plant genetics and physiology are influencing human agricultural systems. For example, yields in rice, maize, and coffee have declined in response to the combined effects of rising temperatures and increasing precipitation variability over past decades (143–145). Genetics is being used to counteract decreasing yields in some key crops such as wheat [for which, globally, yields have declined by 6% since the early 1980s (146)] through crossing domesticated crops with wild relatives to maintain the evolutionary potential of varieties (147). Yet, some important wild strains are also showing signs of impact from climate change. Nevo *et al.* documented high levels of genetic changes in the

progenitors of cultivated wheat and barley in Israel over the past 28 years (148). These wild cereals exhibited landscape-level changes in flowering time and a loss of genetic diversity in response to increasing temperatures.

Losing genetic resources in nature may undermine future development of novel crop varieties (149) and compromise key strategies that humans use to adapt to climate change. One such strategy is to use assisted gene flow, the managed movement of individuals or gametes between populations to mitigate local maladaptation in the short and long term (150). Where genetic introgression—the movement of genetic material from one species into the genome of another—can occur from unexploited natural populations to managed or exploited populations that are poorly adapted to warmer or drier conditions, adaptive changes may be facilitated (147), as in white spruce (*Picea glauca*), a tree commonly harvested for timber (151). Human-assisted evolution may also be a key strategy in maintaining reef-dependent fisheries by accelerating and enhancing the stress tolerance of corals (152).

Phenological changes due to milder winters are influencing crop and fruit production (153). Climate change has reduced winter chill events in temperate agricultural areas (154), which can desynchronize male and female flowers and trigger delayed pollination, delayed foliation, and reduced fruit yield and quality. To counter this, tree crop industries have developed adaptation measures such as low-chill cultivars with dormancy-breaking chemicals. For example, the “UFBest” peach requires four times fewer chill days than cultivars from more temperate climates (155). Advances in the timing of budding, flowering, and fruiting of plant species has induced earlier harvesting periods in some countries [such as Japan (156)].

Pollination is a key process linked to yields for a large number of crops. The short-lived, highly mobile insect species that provide pollination services to numerous crops have responded rapidly to changing climates by shifting their ranges throughout North America and Europe (157). Additionally, over the past 120 years, many plant-pollinator networks have been lost with overall decline in pollination services, which is attributed to a combination of habitat loss, pollution, and climate warming (158). Yet, observed changes in the phenology, abundance, and distribution of common pollinators have not been directly linked to declines in yields of animal-pollinated crops. This is likely due to limited data that directly link pollination services to crop yield over time and may, in part, reflect resilience provided by the diversity of insect species that pollinate many crops (159, 160). More specialized pollination systems are expected to be more vulnerable to climate change. Humans have adapted to the declines in native pollinators by transporting domesticated pollinators to crop locations.

Pest and disease threats

Climate-induced ecosystem-level changes, such as forest die-offs, have an obvious impact on

Table 1. Climate change consequences for humans. Affected ecological processes have direct consequences in food systems and human health.

	Organism	Population	Species	Community
	Genetics, physiology, morphology	Phenology, dynamics	Distribution	Interspecific relationships, productivity
Resource security	Rapid genetic adaptation to climate change in timber species	Increased herbivory on crops and timber by pests	Overall distribution shifts in marine and freshwater fisheries	Decline in plant-pollinator networks and pollination services
	Decreased crop yields in hot climates and increases in cool climates	Decreased genetic diversity and altered flowering time in wild cereals and novel crop varieties	Reduced range size or changes in pollinator abundance	Novel pests and invasive species
	Increased weed-crop competition and parasite-livestock interactions	Reduced fruit yields from fewer winter chill events		
	Decreased yield in fisheries from reduced body size	Reduced productivity in commercial fisheries		
Human health	Decline in reef calcifiers threatens coastal communities; loss of protection from storm surges and loss of food/protein sources	Increased costs and risk to subsistence communities from loss of sea ice and permafrost	Expanding and/or new distributions of disease vectors	Increased human-wildlife conflicts
	Rapid adaptation of disease vectors to new climatic conditions		Redistribution of arable land	Novel disease vectors

people, with a reduction in timber supplies and carbon sequestration, and changes in water quality and watershed volume (161–163). Several native insect species from North America, with no prior records of severe infestation, have recently emerged as severe pathogens of forest resources because of changes in population dynamics. These include the Aspen leaf miner (*Phyllocnistis populiella*), the leafblotch miner (*Micrurapteryx salicifoliella*), and the Janet's looper (*Nepytia janetae*), which have decimated millions of hectares of aspen, willows, and spruce-fir forests since the early 1990s (164). Known pests such as mountain and southern pine beetles (*Dendroctonus frontalis* and *D. ponderosae*, respectively) and spruce beetles (*D. rufipennis*) have recently expanded their distribution and infestation intensity on commercially important pine and spruce trees (161, 164). These outbreaks may increase in the future because hundreds of plant pest and pathogen species have shifted their distributions 2 to 3.5 km year⁻¹ poleward since the 1960s (165).

An emerging threat to human health under climate change is vector-borne disease (166). Vectors that have shifted their ranges and abundance can be found in marine, freshwater, and terrestrial systems. For example, in marine systems, unprecedented warming in the Baltic Sea led to emergence of *Vibrio* infections in Northern Europe (167, 168), a geographic locality that had limited prior occurrence of this water-borne bacterial pathogen. Mosquitoes (e.g., *Aedes japonicus*, *A. aegypti*, *A. albopictus*) are extending their distribution into areas that are much warmer than their original habitats. As a result of eco-

logical adaptation, mosquitoes have become more competent vectors for spreading diseases such as chikungunya, dengue, and possibly the emerging Zika virus (169). Last, in terrestrial systems Levi *et al.* found that the nymph stage of the Lyme disease-carrying blacklegged tick (*Ixodes scapularis*) exhibited an overall advancement in nymph and larvae phenology since 1994, shifting the timing of greatest risk for pathogen transfer to humans to earlier in the year (170).

Losing intact ecosystems and their function

Changes in ecological processes might compromise the functionality of ecosystems. This is an important consideration because healthy systems (both terrestrial and marine) sequester substantial amounts of carbon (171), regulate local climate regimes (172), and reduce risks associated with climate-related hazards such as floods, sea-level rise, and cyclones (173). In island and coastal communities, coral reefs can reduce wave energy by an average of 97% (174), and coastal ecosystems such as mangroves and tidal marshes buffer storms (175), while on land intact native forests are important in reducing the frequency and severity of floods (176). In many cases, maintaining functioning systems offers more sustainable, cost-effective, and ecologically sound alternatives than conventional engineering solutions (16).

Science and action in a warmer world

The United Nations Framework Convention on Climate Change (UNFCCC) and the recent COP21 agreement in Paris presently offer the best

opportunity for decisive action to reduce the current trajectory of climate change. This latter agreement set global warming targets of 1.5 to 2°C above preindustrial levels in order to avoid “dangerous climate change,” yet the current 1°C average increase has already had broad and worrying impacts on natural systems, with accumulating consequences for people (Table 1). Minimizing the impacts of climate change on core ecological processes must now be a key policy priority for all nations, given the adoption of the UN Sustainable Development Goals aiming to increase human well-being. This will require continued funding of basic science focused on understanding how ecological processes are interacting with climate change, and of programs aimed at supporting ecosystem-based adaptations that enhance natural defences against climate hazards for people and nature and ensure ongoing provision of natural goods and services (177).

We must also recognize the role that intact natural ecosystems, particularly large areas, play in overcoming the challenges that climate change presents, not only as important repositories for carbon but also because of their ability to buffer and regulate local climate regimes and help human populations adapt to climate change (16, 173). These systems are also critical for maintaining global biodiversity because the connectivity provided by large, contiguous areas spanning environmental gradients—such as altitude, depth, or salinity—will maximize the potential for gene flow and genetic adaptation while also allowing species to track shifting climate spatially (178).

The overriding priority of the UNFCCC is to set in motion a sustained global reduction in greenhouse gas emissions. This must be achieved alongside an improvement in our understanding of key ecological processes that form the foundation of biological and human systems, and in tandem with efforts to conserve the natural habitats in which such ecological processes operate.

It is now up to national governments to make good on the promises they made in Paris through regular tightening of emission targets, and also to recognize the importance of healthy ecosystems in times of unprecedented change (179). Time is running out for a globally synchronized response to climate change that integrates adequate protection of biodiversity and ecosystem services.

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SUPPLEMENTARY MATERIALS

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The broad footprint of climate change from genes to biomes to people

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Editor's Summary

Accumulating impacts

Anthropogenic climate change is now in full swing, our global average temperature already having increased by 1°C from preindustrial levels. Many studies have documented individual impacts of the changing climate that are particular to species or regions, but individual impacts are accumulating and being amplified more broadly. Scheffers *et al.* review the set of impacts that have been observed across genes, species, and ecosystems to reveal a world already undergoing substantial change. Understanding the causes, consequences, and potential mitigation of these changes will be essential as we move forward into a warming world.

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