Biological Impacts of Climate Change

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Introductory article

Article Contents

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Based in part on the previous version of this eLS article 'Biological Impacts of Climate Change' (2009) by John P McCarty, L LaReesa Wolfenbarger, James A Wilson.

Climate has far reaching impacts on biological systems. Survival and reproduction depend on how well adapted individuals are to local climate patterns. Climate change can disrupt the match between organisms and their local environment, reducing survival and reproduction and causing subsequent impacts on populations or species' distributions across geographic regions. Changes in climate may benefit some species and cause extinction for others. Cumulatively, it will alter biological communities and the functioning of ecosystems. Changes to ecosystem functions can in turn increase or decrease the rate of human-driven climate change. In addition to effects of climate variables such as temperature and precipitation, plants may respond directly to rising concentrations of CO_2, while aquatic species cope with changes in water chemistry as greenhouse gasses dissolve in water. The earth is already experiencing sufficient climate change to affect biological systems; well-documented changes in plant and animal populations are related to recent climate change. Predicting future biological impacts of climate change remains a formidable challenge for science.

Introduction

Emission of carbon dioxide, methane and other greenhouse gasses is a primary driver of current and future human-caused climate change (IPCC, 2014). Biological systems respond not only to the resulting changes in climate but also directly to changes in atmospheric concentrations of greenhouse gasses and to secondary effects such as rising sea levels and changes in water chemistry.

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One of the fundamental lessons from the science of ecology is that patterns of climate strongly influence the distribution and abundances of living organisms. Climate describes weather patterns for a given location over an extended period of time (e.g. 10+ years). Climate is not just the average conditions of temperature and precipitation but also the seasonal and annual weather variation, including the frequency and severity of extreme events such as storms or drought. The earth's climatic patterns are now changing and human activities are major contributing factors driving these changes (IPCC, 2014). The types of impacts climate change will have on living systems have far reaching consequences for natural ecosystems and the people who depend on the goods and services that ecosystems provide.

The distribution of the general types of plants and animals, or biomes, around the world can be predicted with some accuracy from climate patterns. General climate patterns are in turn generated by atmospheric circulation patterns caused by differential heating of the earth's surface, which determine the temperature and precipitation patterns in a given area. Relatively minor changes in the overall heat balance of the earth can change atmospheric circulation and result in local climate changing more dramatically than indicated by the degree of average warming. For example, a 1°C increase in average temperature can translate into significantly longer growing seasons, greater number of extremely hot days, and changes in the patterns and intensity of precipitation (Melillo *et al.*, 2014). In addition, a 1°C increase in global average temperature will result in some geographic regions experiencing much greater than 1°C warming, while other regions show little or no warming. This has been observed with the warming of recent decades where the arctic has warmed much more quickly than the global average (IPCC, 2014). **See also: Ecosystem Concepts: Introduction**; **Plant Physiological Responses to Climate and Environmental Change**

Climate changes of this magnitude have already been observed to impact species and entire biological communities (McCarty, 2001, Rosenzweig *et al.*, 2008). Ongoing and future climate changes will have far reaching effects on biological systems, including humans. Each species is likely to respond differently to changes in climate. For some species, climate will remain within

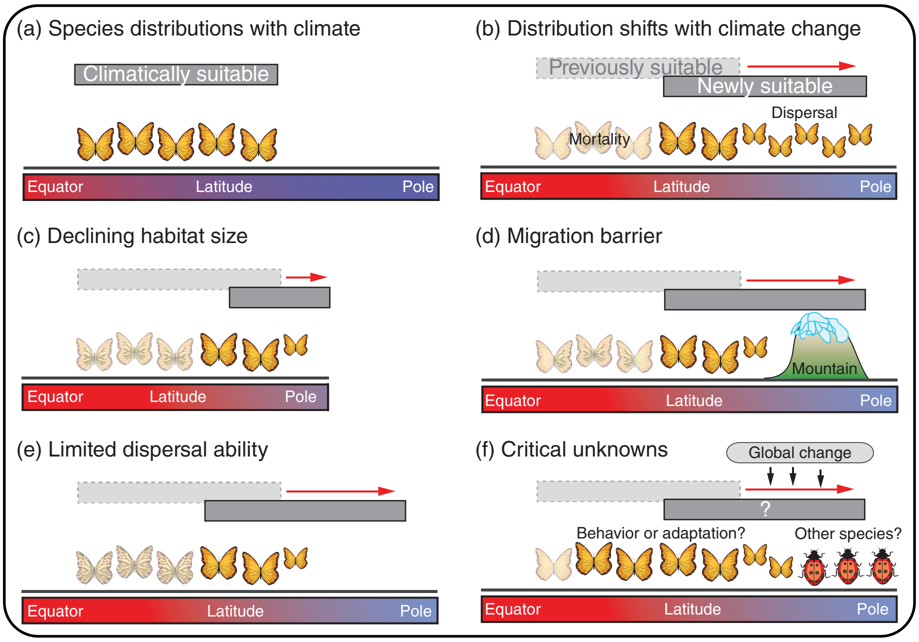

Figure 1 The current geographic range of species is limited to areas with a suitable climate (a). As climate changes and the areas with suitable climate shift towards the poles, species will respond in different ways. For some species, geographic distributions might shift to track changes in suitable climate, with little change in the overall size of their range (b). However, for other species the area of suitable habitat may decline (c), or their ability to shift their geographic range to take advantage of new areas may be limited by physical barriers such as mountains or bodies of water (d) or restrictions on the movement of individuals that limit the ability to disperse (e). However, other factors besides climate can influence future geographic distributions. For example, some species will evolve to adapt to new climatic conditions and remain in their current geographic range, while interactions with competitors, predators and pathogens might prevent species from using areas with newly suitable habitat (f). Finally, species that are unable to respond adequately to new climatic conditions or whose suitable habitat becomes too small (c) will go extinct. Reproduced with permission from Lambers (2015) © The American Association for the Advancement of Science.

the existing range of tolerances. If a local climate shifts outside the species' range of tolerances, one of three responses will occur: adaptation (environmental or genetic change), relocation or extinction (**Figure 1**).

One of the great challenges for biology today is to try to understand how future changes in climate will impact biological systems. Progress towards this goal depends on understanding the underlying mechanisms as to how individuals and species respond to changes in climate, examining biological responses to recent climate changes and integrating this information in experiments and models to try to understand how complex biological systems will interact under future changing climate conditions.

How Climate Impacts Life

The basic components of climate – temperature and moisture – have pervasive impacts on organisms. Physiological processes define life, and at the most basic level these are chemical reactions. As such, they are subject to the unavoidable relationship between temperature and the speed of chemical reactions. While the rates of simple chemical reactions increase as temperature increases, physiological processes respond in a more complex manner. This typically involves a thermal optima where the reaction proceeds most quickly. Physiological processes proceed more slowly at temperatures above or below the thermal optimum. Most physiological processes are also water-based. All organisms face a major challenge: maintaining an appropriate water balance and temperature range for life-sustaining physiological processes while living in environments that are too wet/dry and too cold/warm.

The climate where an organism lives dictates the specifics of this challenge, and organisms have evolved numerous adaptations to cope with hostile environments. Organisms are exposed to not just the average temperature and moisture conditions but also the variability associated with seasons and with extreme events. Plants and animals cope with variation in the environment in many ways. Some animals move to different geographic areas to avoid severe conditions (e.g. migration). Both plants and animals can reduce activity when conditions are too severe: torpor in animals and senescence in plants. **See also: Fundamentals of Water Relations and Thermoregulation in Animals**; **Ecology of Water Relations in Plants**

Climate and individuals

The physiologic health or condition of individuals acts as the link between the habitat and population dynamics. Individuals poorly suited for their habitat may not obtain enough energy to maintain themselves in good condition and may forego reproduction completely or until conditions in the habitat improve.

Climate can impact survival and reproduction for animals that are able to regulate their body temperature within a narrow range even as the surrounding air temperature varies, including endotherms such as birds and mammals. As the temperature of the environment decreases relative to body temperature, individuals need to expend energy to stay warm and may eventually reach the point where they can no longer generate enough heat to maintain body temperature. If individuals cannot move to a warmer environment or obtain needed energy, they may die. At the other extreme, as environmental temperature rises above body temperature, individuals need to expend energy and often significant amounts of water, to stay cool. Once again if surrounding temperatures rise too high, the individual will no longer be able to regulate the body temperature and could die. Even if environmental temperatures do not reach the extremes that cause death, the energy required to maintain internal conditions is no longer available for other important activities such as reproduction.

Climate also has profound effects on the survival and reproduction of ectotherms: animals such as amphibians, reptiles and insects that are unable to regulate their body temperature independently of the surrounding temperature of the environment. For these species, the rate of physiological processes determined by body temperature depends upon ambient temperature. As ambient temperature rises the rate of physiological processes increases in a nonlinear fashion and increases more rapidly when initial temperatures are low. For example, a rate may triple across a temperature of 10–20°C but may only double from 20 to 30°C. Although ectotherms have a limited ability to avoid the physiological consequences of changing environmental temperature, they have evolved a broad assortment of strategies for coping with a broad range of climate conditions. **See also: Thermoregulation in Vertebrates; Vertebrate Metabolic Variation**

As an adaptation to harsh environmental conditions, especially cold temperatures, some ectotherms become inactive during unfavourable seasons of years, and climate change will significantly alter the energy expenditures and body condition of these organisms. Body condition in ectotherms is tightly bound to reproductive output, timing to maturity and survival during inactive periods. Unlike hibernation in mammals, where individuals can regulate body temperature independent of ambient temperature, ectotherms cannot. Because their hibernating metabolic rate is dependent on ambient temperature, warmer winters will cause ectotherms to utilise more energy during hibernation than colder winters. For example, common toads (*Bufo bufo*) in the United Kingdom have shown a decline in body condition associated with increasing temperatures which is also associated with decreased annual survival (Reading, 2007). In addition, when ectotherms use more energy to hibernate during warming winter, they emerge from hibernation in poorer condition, which reduces reproduction. **See also: Hibernation: Endotherms; Hibernation: Poikilotherms; Thermoregulation in Vertebrates: Acclimation, Acclimatization and Adaptation**

Aquatic species are also sensitive to temperature. Distributions of many species are limited by water temperatures. The tolerance limits for some species can be quite narrow. Corals, for example, can lose their symbiotic alagal partners with warming on the order of 1°C, resulting in bleaching that stresses or even kills coral (Doney *et al*., 2012). In addition, the dissolved oxygen levels decline as water temperature rises, placing an additional limit on some species. Antarctic icefish (Notothenioidei: Channichthyidae) provide an extreme example of how trade-offs between temperature and dissolved oxygen availability impact aquatic organisms. This group of fish has lost functioning haemoglobin due to the loss of the gene that produces the β-subunit of the haemoglobin protein (Cocca *et al*., 1995). This mutation would normally prove to be lethal, resulting in the metabolic asphyxiation of the individual because nonfunctional haemoglobin cannot carry oxygen to the body's tissues to support aerobic metabolism. However, the fact that they live in extremely cold Antarctic waters results in low metabolic rates and a substantial reduction in oxygen demand. Indeed, the waters are so cold that icefish depend on several physiological adaptations to help them survive, including antifreeze proteins in their blood. Icefish live within a few degrees of their upper, lethal temperature limit and if these fish were ever exposed to warmer waters their metabolism, and consequently their oxygen demand, would increase resulting in their death (Bilyk and DeVries, 2011; Beers and Sidell, 2011). Currently, the waters surrounding Antarctica have increased in temperature from 0.17°C to ~1°C over the last 50 years and are predicted to increase by another 2°C throughout the next century (Clarke *et al*., 2007).

Plant physiology is also sensitive to temperature range and moisture balance. Temperature and moisture interact to determine the rate of photosynthesis, the physiological process in which plants meet their energy needs and use the sun's energy to synthesise carbohydrates from carbon dioxide and water. Because plants have limited ability to regulate internal temperatures or to avoid temperature extremes, many species become inactive during seasons when conditions are unfavourable. Therefore, climate determines the length of the growing season and the nongrowing season when plants lack the necessary moisture for photosynthesis or when temperatures drop below the freezing point of water.

The response of plants to global change is complicated by the fact that one of the primary greenhouse gasses, carbon dioxide, is also the key building block in photosynthesis. Rising concentrations of carbon dioxide will increase rates of plant productivity, but only when sufficient water and nutrients are available. The net impact of global change on photosynthesis will vary regionally, with water limitations and extreme temperatures counteracting the positive impacts of higher carbon dioxide concentrations in many areas. **See also: Ecology of Water Relations in Plants; Photosynthesis: Ecology; Plant Physiological Responses to Climate and Environmental Change; Plant Responses to Elevated CO_2**

Climate and populations

A population consists of a collection of individuals, and population size changes due to reproduction, immigration, mortality and emigration of these individuals. As such, a population can only grow when net individual reproduction and immigration is greater than mortality and emigration, and decreases when the opposite occurs. Population size is influenced by a complex interaction of direct and indirect factors that change the energy budget of individuals living in a population. Simply put, direct factors are those that are abiotic and reflect changes to a population due to thermal stress, extreme weather or changes in precipitation. Indirect factors represent changes to the biotic environment, typically manifested as changes in biotic interactions due to resource availability, community composition and structure and predation pressure.

Most species have resolved the challenges associated with a specific range of climate conditions, and the occurrence of these conditions constrains the geographic range of a species. Outside of this range, factors driving populations down – mortality and emigration – will overwhelm reproduction and immigration, and populations will die out. In some cases, the correlation between specific climate conditions and the limits of geographic range can be quite close. Classic examples where climate limits geographic range include plants such as wild madder (*Rubia peregrina*) whose northern limit in Europe corresponds closely to where January temperatures remain approximately 4.5°C and saguaro cactus (*Carnegiea gigantea*) in Arizona where the range is limited to areas where daily temperatures consistently rise above freezing (Begon *et al*., 2006). The distribution of most species is influenced by a more complex combination of factors, though climate may still play a role. For example, the distribution of Northern Bobwhite (*Colinus virginianus*) in North America is explained in part by a combination of temperature and precipitation (Matthews *et al*., 2007; **Figure 2**).

Although unfavourable climate can eliminate populations, favourable climate is not a guarantee that populations will occur or persist. Additional environmental conditions besides climate may be unfavourable, or geographic barriers may exist that prevent members of the population from ever reaching a given geographic region. **See also: Range Limits**

Climate and interactions among species

Individuals interact with members of other species in a variety of ways. These include interactions among parasites, disease organisms, predators and prey and competition over common resources as well as mutually beneficial interactions such as flowering plants producing nectar for the animals that pollinate their flowers. Through these interactions species may influence the population size and even the geographic range of other species. Interactions among species in a community can produce indirect links between a population and climate. For example, rush moths (*Coleophora alticolella*) in England tolerate the direct effects of climate associated with high elevations sites, but the plants on which the caterpillars feed do not produce enough seeds at high elevation, thereby limiting the range of the moth to low elevation sites with abundant food for caterpillars (Randall, 1982). Differences among species in their abilities to cope with changes in climate can shift the balance between competitors or allow new predators, pathogens or parasites to invade a species range. **See also: Coexistence; Community Ecology: An Introduction; Interspecific Competition; Interspecific Interaction; Predation (Including Parasites and Disease) and Herbivory**

Climate and communities and ecosystems

The community of plants and animals in a given area emerges from the responses of individual species to climate and other physical factors. The species-specific nature of the factors limiting ranges means that biological communities do not respond to climate as cohesive units but rather are assemblages that reflect the tolerances of their component species. These assemblages of species are both familiar and have emergent properties such as diversity and productivity. As climate changes it is probable that assemblages of species that are now familiar will be broken up as species that respond to new environmental conditions in different ways. New assemblages will then emerge with their own characteristics and properties. **See also: Community Ecology: An Introduction**

Communities in turn are linked with the nonliving environment in ecosystems. Within an ecosystem, the flow of energy and matter among organisms is constrained by the ability of plants to capture the sun's energy in a form that can be used by other organisms. In this way, energy balance forms the link between individual condition, population dynamics and ecosystem functioning. Likewise, these higher-level processes that emerge from ecosystems have far reaching implications for humans through their impacts on nutrient, air and water cycles. **See also: Ecosystem Concepts: Introduction; Photosynthesis: Ecology**

Observations of the Biological Impacts of Climate Change

The earth's climate has been in a state of change for most of the history of life, and ample evidence exists to show how biological systems respond to changes in temperature and moisture. We know from fossils and other remains of long dead organisms that biological systems have undergone dramatic changes in response to past changes in climate. **See also: Palaeoclimatology; Palaeoenvironments**

Since the mid-twentieth century, climate has been changing rapidly relative to previous periods. Global mean temperatures have increased by about 0.85°C since 1880 and this warming has occurred unevenly across the globe (IPCC, 2014). Temperatures over land are warming faster than over oceans, and warming of the arctic is occurring almost twice as fast as the global average.

Other changes in the environment follow from this warming. Polar regions have had extensive warming of air and surface ocean temperatures. This has led to a decrease in the extent of Arctic sea ice, especially during summer. Similarly, ice mass has been lost from the Greenland ice sheet and the northern Antarctic Peninsula (IPCC, 2014). In the Northern Hemisphere, the extent of snow cover in the spring months of March and April has declined at a rate of 1.6% per decade since the mid-twentieth century (IPCC, 2014). These changes both reflect a changing climate and can impact species that are dependent on ice and snow or whose life cycles are timed to a predictable spring thaw.

The magnitude of recent changes are sufficient for scientists to observe how biological systems respond to ongoing climate change. Researchers have turned to long-term datasets to understand how climate change is impacting biological systems. Some of the longest running quantitative records of biological systems are observations of seasonal biological events. In many areas of the globe, records of the timing, or phenology, of events such

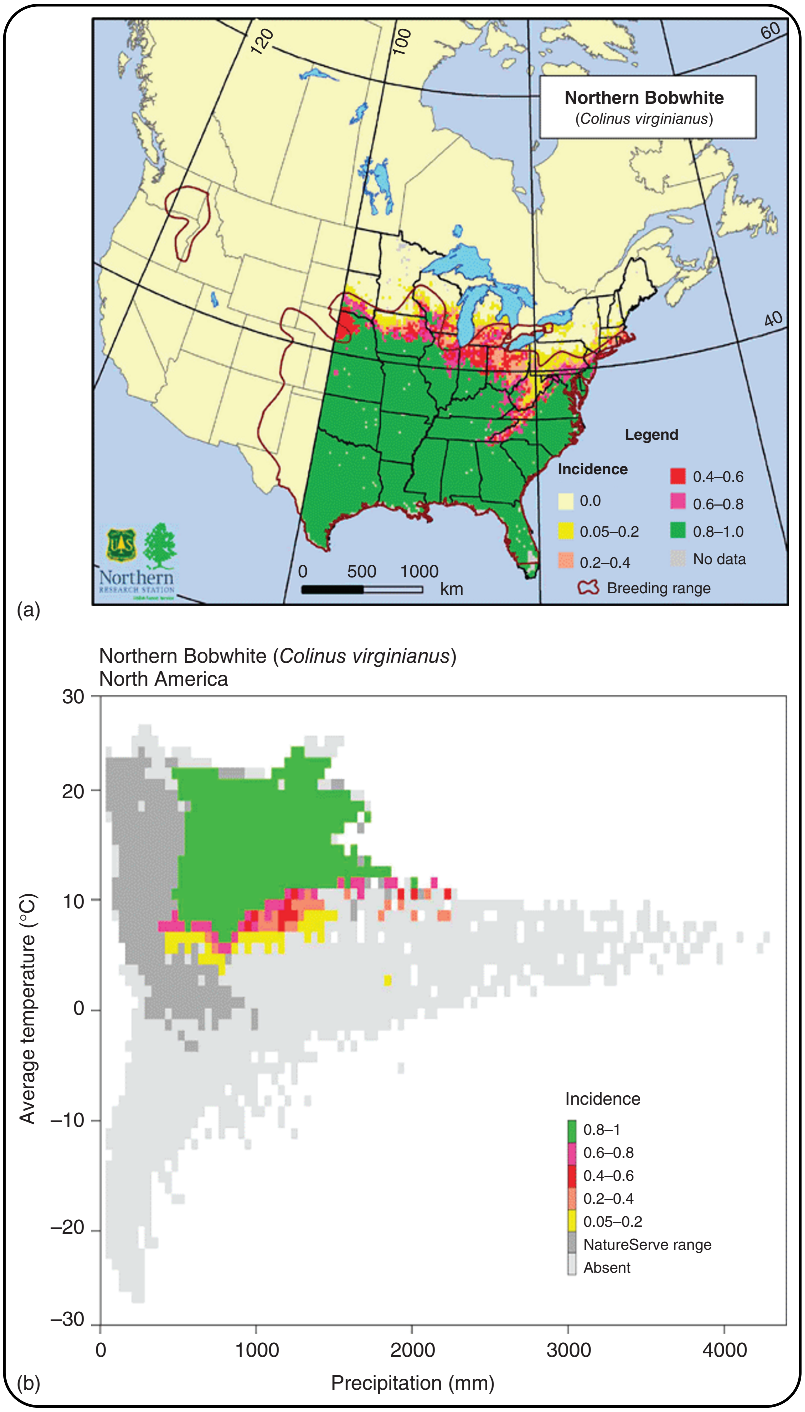

Figure 2 Much of the geographic range of species can be explained by climate. In the example shown above, Northern Bobwhites are widespread across the southern two-thirds of the eastern United States. (a) The map shows their geographic range and relative abundance based on the North American Breeding Bird Survey. USDA Forest Service scientists evaluated the geographic distribution of Northern Bobwhite (and 146 other bird species) against information about the climate and vegetation in the eastern United States. The importance of different climate and habitat variables in explaining geographic range depends on the bird species. (b) Illustration shows the combination of temperature and precipitation found in the eastern United States. The coloured cells indicated the combinations of temperature and precipitation where Northern Bobwhites are found, while the light grey squares represent combinations of temperature and precipitation found in the eastern United States where Northern Bobwhites are absent. Reproduced from Matthews *et al.* (2007) © USDA Forest Service.

as when birds migrate and when leaves or flowers appear in the spring go back decades or more. These data provide strong evidence for widespread changes in the timing of biological events linked to the climate changes experienced over the same time period. For example, Terry Root and her colleagues conducted a review of 64 studies of biological events associated with the onset of spring in 694 species of plants and animals; the results indicated that spring phenological events like migration and flowering have been occurring earlier at a rate of 2–7 days every decade (Root and Hughes, 2005). Globally, the documented changes in biological systems are consistent with the changes in climate observed during these same decades (Rosenzweig *et al*., 2008). **See also: Climate Change Impacts: Insects**; **Climate Change Impacts: Birds**

Not all species will be able to cope with climate change by tracking favourable conditions because the changing climate might exceed the capacity of individuals to alter the timing of activity. Desert-dwelling ground squirrels face extreme heat during summer months and also low water availability. As a result, ground squirrels enter a period of seasonal inactivity (aestivation) during the summer months to decrease energetic demands. However, as summers become warmer and precipitation decreases, the length of the inactive season will increase while the wet season, when squirrels obtain food for aestivation, shortens. Piute ground squirrels (*Spermophilus mollis*), from the western United States, have been shown to enter aestivation early in response to early spring drought. If the drying trend continues to increase, these animals may not acquire sufficient energy resources during the shortened growing seasons to aestivate over the longer dry months (Steenhof *et al*., 2006).

Changing phenology may not always track favourable conditions if it disrupts or decouples species interactions or other biotic factors that influence populations. For example, Marmots in the mountains of Colorado spend the winter hibernating and emerge from hibernation when air temperature warms. As air temperatures have increased, marmots have been emerging from hibernation 23 days earlier than they did in 1976. However, because winter precipitation in the form of snow is increasing, deep snow is still on the ground preventing plants from growing. Therefore, marmots must use their limited fat reserves for longer periods in spring while at the same time they have increased energetic demands and are preparing for reproduction (Inouye *et al*., 2000).

Geographical ranges of species have expanded and contracted as climate factors have changed over the past decades. Historic datasets show that geographic ranges of many northern hemisphere species are shifting northward at rates consistent with observed climate change. A recent meta-analysis examined the results from studies of looking at changes in latitudinal distribution of taxonomic groups covering 764 species in Europe, North America and Chile and found that the groups had shifted away from the equator at a median rate of 16.9 km per decade (Chen *et al*., 2011). Overall, the distance moved corresponded to the expected change given the rate of climate warming. However, the distance moved varied among species groups and some groups were not moving fast enough to keep up with the pace of climate change. In mountainous regions an analogous shift has been documented with species spreading to higher elevations where temperatures are cooler at a median rate of 11.0 m per decade (Chen *et al*., 2011). These range expansions lead to a homogenisation of alpine plant communities and a decrease in specialised communities, particularly in alpine tundra associated with mountain peaks (Jurasinski and Kreyling, 2007). Marine species are also altering their ranges to compensate for increased water temperatures. Globally, marine species have shifted their distribution 30.6 ± 5.2 km per decade (Sydeman *et al*., 2015). Most range shifts seem to be associated with an attempt to maintain their presence in cooler waters and have therefore resulted in more polar shifts, or, when polar movements are not possible (i.e. movement is blocked by the presence of land), then species may move to deeper waters. **See also: Alpine Ecosystems**; **Marine Communities**

Most species are likely to respond to changing conditions in more than one way. For example, pacific walrus use sea ice as a place to rest between foraging trips, a location to molt their skin, and as a safe location to give birth to their young (Jay *et al*., 2012). In response to earlier ice break up in spring and later ice formation in fall, walruses now begin their spring migration about 1 month earlier and return in the fall a month later (MacCraken, 2012). In addition, populations in the Chukchi Sea have shifted their range to more northern latitudes in June and July, while during September and October walruses forage closer to shore than historically documented. Even with these adjustments, the loss of sea ice has contributed to young and adult females to haul out in large numbers onto the shore (Jay *et al*., 2012; MacCraken, 2012).

In some cases it appears that changes in climate have overwhelmed species' abilities to respond. Amphibians living in the mountains of Central America may provide a window into what the future might hold (Pounds *et al*., 2006). The Monteverde region of Costa Rica is world famous for its cloud forest and diverse community of frogs. Declines in populations of these frogs have been well documented in recent decades and include the extinction of the golden toad (*Bufo periglenes*). Population decline and species loss are linked to the changing climate, including a reduction in misty days; a defining feature of cloud forests, but the full explanation is much more complex. Warmer night time temperatures produce ideal growing conditions for a chytrid fungus (*Batrachochytrium dendrobatidis*) that infects amphibians and sometimes kills them. Frogs stressed by warmer and drier climate are less able to resist fungal infection. As a result, populations decline and populations and species go extinct (Pounds *et al*., 2006).

Responses of a few key species to climate change may result in far reaching consequences for entire ecological communities. Corals are sensitive to ocean warming, which contributes to bleaching. In addition, increases in atmospheric CO_2 concentrations result in more acidic ocean waters as CO_2 dissolves in water. These more acidic conditions make it more difficult for corals to secrete their skeletons (Doney *et al*., 2012). Loss of corals and the physical structures they create will result in disruption of the entire community dependent on this habitat. These changes are already impacting many of the world's reef systems and global impacts are projected in the coming decades (Frieler *et al*., 2013). An analogous change has been observed along the temperate coast of Australia where extreme warming starting in 2011 resulted in the loss of kelp forests and the community that depends on the kelp (Wernberg *et al*., 2016).

Within 2 years, the kelp forest community had been replaced by tropical and subtropical species along 100 kms of the coast.

In addition to changes in populations and biological communities, earlier spring warming and changes in summer climate have produced significant changes in the fundamental energy dynamics of ecosystems. Satellite and ground-based observations show that over the past 30 years the thermal potential growing season in northern ecosystems has become 10.5 days longer; however, limited moisture and light has limited the ability of plants to take advantage of the warmer conditions so the growing season when photosynthesis occurs has lengthened by 6.7 days (Barichivish *et al*., 2013). For some ecosystems this has been accompanied by an increase in net primary productivity as well. Globally, satellite data measuring leaf-area index shows that an overall 'greening' of the earth's surface has occurred during the growing season, indicating that plants produce more leaves (Zhu *et al*., 2016). Models indicate that this increase is driven by the fertilising effect of CO_2 combined with changes to climate, changes to nitrogen cycling and other variables. Analogous changes are seen in aquatic systems (Burrows *et al*., 2011) where spring events such as migrations and plankton blooms have occurred 4.4 ± 1.1 days earlier (Poloczanska *et al*., 2013).

Trying to Understand the Future

Biological responses to future climate change will depend on the rate and magnitude of continued climate change. Sophisticated models of the earth's climate system incorporate our best understanding of the variables that interact to drive the earth's climate, but a fundamental uncertainty for predicting climate change is how human behaviour will influence the increase in atmospheric greenhouse gas concentrations. The Intergovernmental Panel on Climate Change (IPCC) presents the most comprehensive and authoritative synthesis of possible outcomes by examining several leading climate models and incorporating a range of 'scenarios' for future greenhouse gas concentrations. The IPCC's 2014 report suggests that warming will continue and accelerate during the twenty-first century. The average global temperature by the end of this century is projected to increase 0.3–4.8°C or more beyond what was experienced during 1986–2005 (or approximately 0.9–5.4°C above pre-industrial levels), depending on how human emissions of greenhouse gases change (IPCC, 2014). As with past change, actual changes in temperature experienced by plants and animals will vary. Alpine and polar regions have experienced the greatest change in climate and will likely continue to show dramatic effects of global warming. **See also: Biotic Response to Climatic Change**

Methods for studying the biological impacts of climate change – models and experiments

One approach to understanding complex interactions among species and a changing environment is to take what we know about how species respond to climate (**Figure 2**) and combine that information with output from global climate models to forecast how species or communities might respond to future conditions. For example, the USDA Forest Service has detailed information about where different forest types currently exist (Prasad *et al*., 2007; **Figure 3**). By analysing these distributions in relation to environmental variables, predictive models can be generated that approximate the distribution currently observed ('current modelled' in **Figure 3**). By then, incorporating forecasts of how those environmental variables will change under scenarios of incorporating with low or high rates of climate change, the figure distributions of the forest types can be generated. In the case shown in **Figure 3**, spruce/fir forests currently exist in northern United States but the models suggest that future conditions will no longer be suitable for that forest community. Although these models do not predict whether species will be able to respond to climate change successfully, they can provide insights into how potential habitat for different species might shift under different climate conditions.

Another approach to understanding complex interactions is to expose current communities to conditions they might expect in the future. For example, experiments can alter temperature, moisture levels, concentrations of carbon dioxide in the surrounding air and various combinations of these and other variables (**Figure 4**). This approach can be especially useful for understanding how changes in different aspects of the environment can interact to influence biological systems. For example, the Aspen FACE (Free-Air Carbon Dioxide Enrichment) experiment exposed trembling aspen (*Populus tremuloides*) and other trees to higher concentrations of carbon dioxide as well as the air pollutant ozone to understand impacts on forest productivity and ecosystem function (Karnosky *et al*., 2003). The TasFACE project employed similar technology to expose native grasslands in Tasmania, Australia to increased levels of CO_2 and then added treatments including infra-red heaters to mimic higher temperatures expected in 2050, (Hovenden *et al*., 2014; **Figure 4**). **See also: Global Carbon Cycle**; **Climate Change Impacts: Vegetation**

Effects of increasing carbon dioxide on biological systems

Most of our attention is focused on changes in climate driven by increasing concentrations of carbon dioxide in the atmosphere. However, carbon dioxide can have other effects on biological systems that will contribute to changes in the coming decades.

Carbon dioxide plays a key role in photosynthesis. Photosynthesis rates can be higher as carbon dioxide concentrations increase. Whether plants are able to take advantage of the enrichment of the atmosphere with carbon dioxide will depend on whether they have the other resources, such as water and nutrients, to support increased productivity. The TasFACE experiments (**Figure 4**) demonstrated that variation in seasonal rainfall was a factor that determined how grasslands respond to elevated CO_2, in part because of interactions between rainfall in the cool months and limited nitrogen (Hovenden *et al*., 2014). Other anthropogenic factors can also influence these patterns. For example, the aspen trees in the Aspen FACE project that were grown under higher concentrations of carbon dioxide grow faster, whereas those exposed to increased ozone grow slower (Karnosky *et al*., 2003; **Figure 4**). When exposed to both carbon

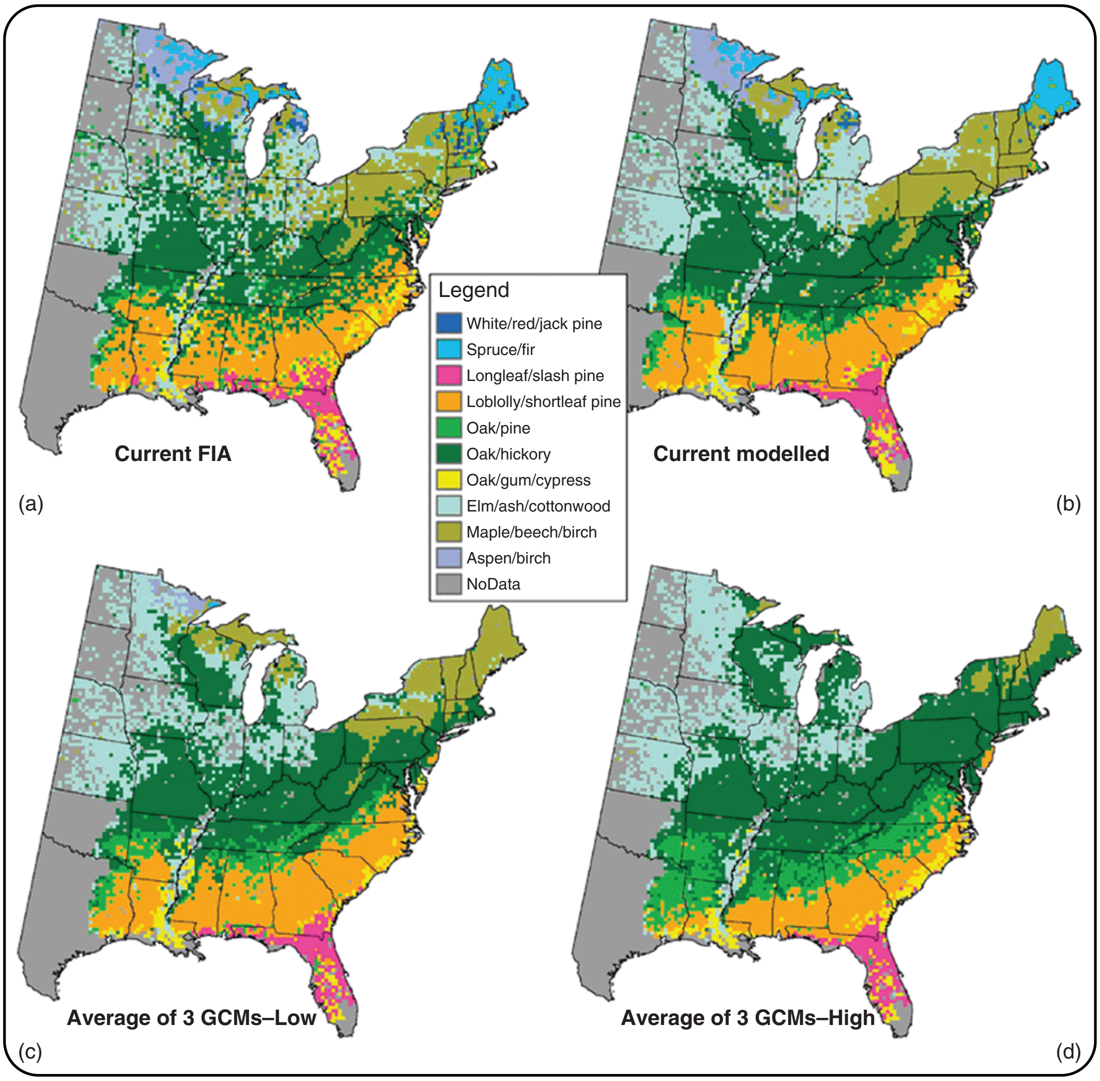

Figure 3 Mathematical models provide one approach for helping us understand how changes in climate will impact biological systems. These maps show the current geographic range of forest types as well as modelled output based on current climate and two scenarios of future climate. Current forest types (panel a) are based on the USDA Forest Service's Forest Inventory Analysis (FIA) data. Information about the geographic range of 134 tree species was evaluated against 38 environmental variables to generate predictive models. The utility of the models can be evaluated by inserting current climate conditions into the models and comparing the output (panel b) to current distributions of forest types (panel a). The general correlation between the actual current FIA data and the modelled current distributions indicates that much of the variation where the forest types occur can be explained by combinations of climate variables. This correlation also suggests that the Forest Service model can be used to model potential habitats under future climate conditions. The scientists took the output from three widely used global climate models under two scenarios used by the Intergovernmental Panel on Climate Change. The 'Low' scenario assumes that emissions of greenhouse gasses will be significantly reduced, while the 'High' scenario assumes that current emission trends will continue. Panels (c) and (d) show how the potential habitat for forests might change in the future. Note in particular the loss of potential habitat for northern forest types such as Spruce-Fir forests that are currently found in the northern tier of states but which might disappear in the future. Reproduced from Prasad *et al.* (2007) © USDA Forest Service

dioxide and ozone the effects on growth were neutralised. Indirect effects on trees appeared when trees were exposed to higher levels of carbon dioxide by impacting insects that live and feed on the trees and by altering the competitive balance between aspen and sugar maple trees (*Acer saccharum*). Not all plants in a community will be equally able to respond to increased carbon dioxide. Plants that are able to respond may have a competitive advantage in communities. In the grasslands of North America, this might lead to invasion of grasslands by trees and shrubs as woody plants gain an advantage over grasses. Exposure to higher levels of CO_2 during growth can also change the nutrient levels of plants in ways that could have implications for the animals that eat them. In Australia, the leaves of rainforest trees grown under elevated CO_2 contained lower levels of nitrogen and other nutrients (Kanowski,

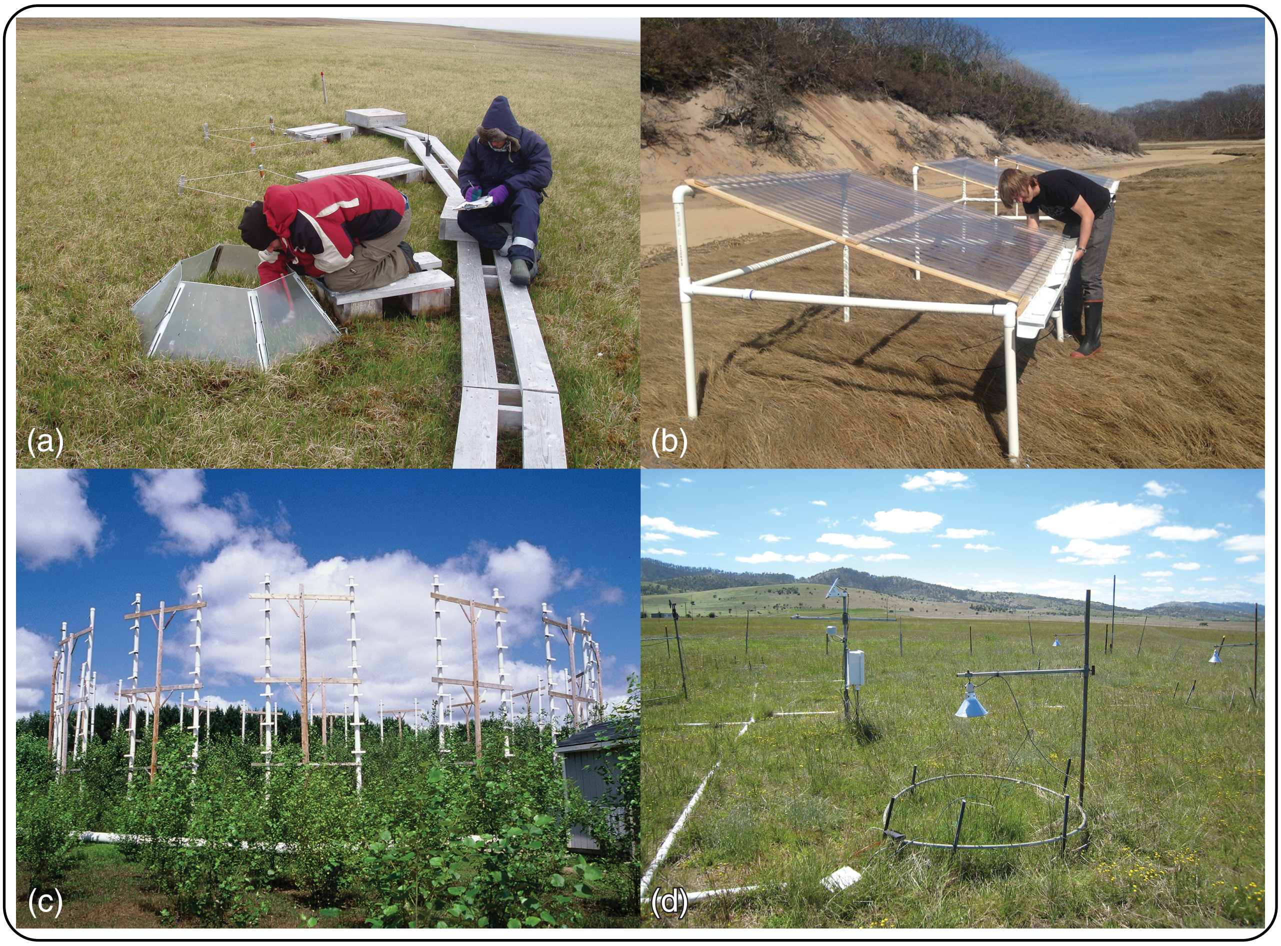

Figure 4 Experimental approaches for studying the effects of climate change on biological systems. (a) Species may respond directly to warming associated with climate change. Open Top Chambers are designed to passively warm vegetation plots with a simple, inexpensive system that can be replicated across many sites as part of the International Tundra Experiment (ITEX; Elmendorf *et al.*, 2012). Reproduced with permission from R Hollister. (b) Changes in precipitation patterns can be manipulated using shelters such as these deployed in a salt marsh as part of study to study the response of ecosystem processes such as plant growth and nutrient cycling. Reproduced with permission from H Emery. (c) Plants may respond directly to changes in concentrations of greenhouse gasses such as carbon dioxide. The Aspen FACE (Free Air Carbon Dioxide Enrichment) Experiment exposed trembling aspen trees in the open under carbon dioxide levels similar to those expected to occur late in the twenty-first century. The pipes surrounding the growing trees release carbon dioxide, mimicking the effects of altered atmosphere in a field setting where plants interact with each other and with other environmental variables in a natural setting. Photo by JP McCarty. (d) The TasFACE experimental system combines the FACE technology with infrared heaters to simulate warming and altered atmospheric gasses simultaneously. Reproduced with permission from M Hovenden.

2001). A decline in the nutritional value of the leaves in turn raises concerns about the impacts on the native marsupials that feed on the leaves. **See also: Photosynthesis: Ecology**; **Plant Physiological Responses to Climate and Environmental Change**; **Ecophysiological Responses of Plants to Air Pollution**

Increased carbon dioxide in the atmosphere is also having far reaching direct effects on the world's oceans. Carbon dioxide is soluble in water and decreases its pH by forming carbonic acid. Oceans have become more acidic in recent years as atmospheric carbon dioxide levels have increased. The average pH of the ocean has decreased from a pre-industrial level of 8.20 to 8.11 and could fall to 7.8 by 2100 (Feely *et al*., 2009). Many aquatic organisms are sensitive to the acidity of water. For example, the carbonate shells of marine animals can dissolve in acidic water. Increased acidity will further stress coral reef communities that are already suffering the effects of warmer water temperatures. **See also: Climate Change and Biogeochemical Impacts**; **Global Carbon Cycle**

Range shifts in response to climate change

As climate changes, the geographic range of some species will shift to track changes in climatic conditions (**Figure 1**). The total area occupied by a species might increase, decrease or remain constant. The potential for the range of species to move with the climate will depend on whether there is a net gain or loss of area with a suitable climate. Some species whose ranges are currently limited by climate may expand into suitable areas whereas the potential range of other species will shrink. At a local scale, suitable climate conditions may disappear entirely. This might be most dramatic in mountains where the potential shift in habitats to higher elevations is limited by the height of the mountains or near the poles where sea ice habitat will disappear. Within a given area some species will be lost as the climate becomes unsuitable but other species will be added as climate becomes favourable for them. Across North America, changes in climate will result in both gains and losses of birds (Langham *et al*., 2015; **Figure 5**). In addition, the species within a community are likely to respond differently so the composition of communities will change.

Another key factor will be the balance between how fast climate shifts and how quickly species can respond. How far individuals or seeds and other propagules can spread or move will limit changes in geographic range or migration (**Figure 1**). Freshwater plants and animals may have even more limited abilities to colonise new habitats as lakes and streams warm. Although we might predict distributions of highly mobile species to change quickly, a suitable habitat may depend not just on climate conditions but also on the presence or absence of other species or resources. Barriers to movement also exist in the form of mountains and water bodies (or land in the case of aquatic species). Finally, much of the earth's surface has been transformed by human activities, and the ability of populations of plants and animals to colonise new areas in a human-dominated landscape is uncertain. **See also: Dispersal: Biogeography**; **Range Limits**

Evolution in response to climate change

Changes in behaviour, timing of life history events (phenology), selective use of more hospitable microhabitats within the existing range and changes in physiology can all help species adjust to variations in climate. For some species, these capabilities already exist in individuals and responding to climate change will be relatively straightforward (i.e. phenotypic plasticity). In other cases, the characteristics that determine the climate tolerance of a species will involve a more fundamental, genetically based change (evolution).

The rate at which populations evolve or undergo change in its genetic make-up will determine whether a species can adapt to new climatic conditions. Although evolution can happen rapidly, not all species will be equally able to evolve in the face of climate change. For evolution to occur rapidly, genetic variability in traits of interest needs to exist in the population; otherwise the rate of change would depend on a suitable mutation arising, an extremely rare event. Furthermore, small or declining populations are less likely to adapt to changing environments due to their low levels of genetic variation. The rate at which evolutionary change could proceed is also a function of the time between generations. Long-lived species such as trees will evolve more slowly than species with short generation times such as insects. **See also: Adaptation and Constraint: Overview**; **Adaptation and Natural Selection: Overview**; **Natural Selection: Responses to Current (Anthropogenic) Environmental Changes**; **Evolutionary Responses to Climate Change**

Extinction in response to climate change

Not all species will be able to respond to changes in climate. Species that are unable to respond quickly enough will go extinct. Estimates of the risk of extinction due to climate change vary, but the magnitude of extinctions could be immense. One recent meta-analysis synthesised 131 published estimates of extinction risks and concluded that 7.9% of species were at risk of extinction although, depending on the assumptions used, some authors produced estimates as high as 50% (Urban, 2015). Extinction risks were greatest in South America, while fewer species in North America and Europe are considered to be at higher risk. Arctic species may also be at greater risk, both due to the faster warming experienced at high latitudes, and the structural changes associated with loss of sea ice.

Climate changes may increase the extinction rates of species already at risk. Small populations will have limited potential to evolve in response to new conditions. Climate change may also exacerbate the very conditions that placed species at risk in the first place. For example, invasive species, disease and parasites pose a threat to many populations, and the changing climate may facilitate the invasion of new threats into the range of species at risk. Invasive species are defined in part by their ability to colonise new areas and would be expected to expand their ranges quickly in response to climate change. This pattern has already been observed in alpine areas of Australia, where warming temperatures have allowed invasive, non-native mammals including rabbits and horses, to access areas where they had previously been excluded (Hughes, 2003). Lack of suitable habitat places many species at risk of extinction. If climate change reduces habitats further, species may be unable to recover from the loss and will go extinct. This threat is exacerbated by the fact that current conservation efforts may miss many of the species that will be at risk from climate change in the near future (Langham *et al*., 2015). **See also: Biodiversity–Threats**; **Extinction**

Climate – ecology feedbacks

Climate clearly impacts biological systems but biological systems can also influence climate by changing the amount of heat absorbed from the sun, releasing water vapour and altering the levels of carbon dioxide and other greenhouse gasses in the atmosphere. The impact of this feedback on climate is a considerable source of uncertainty for projecting future effects of climate change on biological systems. Plants, both on land and in the ocean, absorb carbon dioxide from the atmosphere during photosynthesis. Some of the carbon trapped this way is transferred to higher trophic levels when animals eat plants, some remains bound up in living or dead plant matter and some is released back into the atmosphere when dead plant material decays. The balance between absorption of carbon dioxide from the atmosphere and its release back into the atmosphere has significant effects on the composition of the atmosphere and, ultimately, the climate.

Behaviour of these so-called feedback loops is difficult to predict. Warming climate may extend the growing season in some areas, leading to more carbon dioxide being removed from the atmosphere. Whether this has an impact on climate will depend

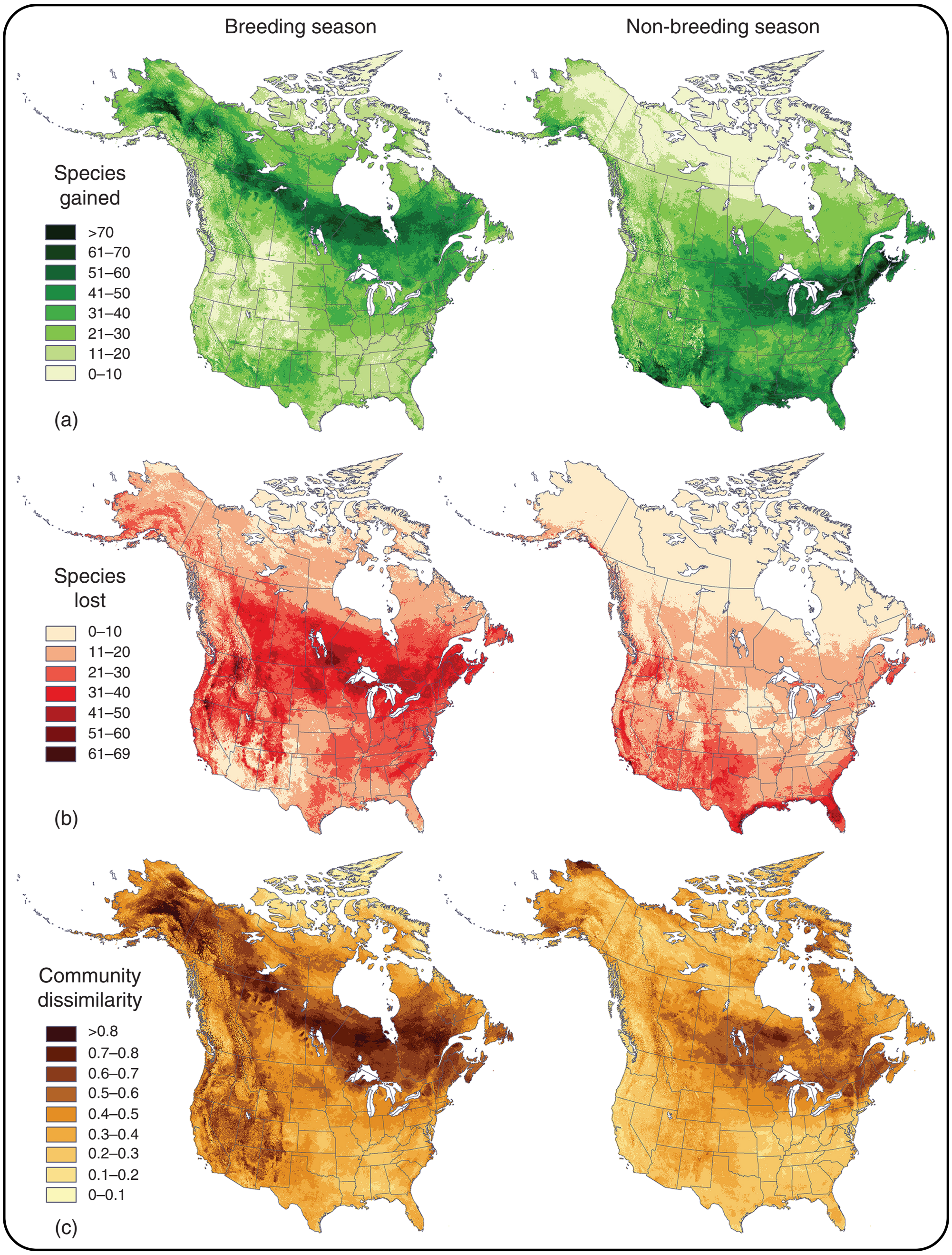

Figure 5 As climate changes, the community of species present in a given area is also expected to change. Langham *et al.* (2015) modelled the possible changes in the geographic distributions of 588 North American bird species by 2080 under one possible emission scenario (SRES A2). Impacts vary both geographically and between the breeding and nonbreeding seasons. As expected, most areas are projected to lose species of birds during both the breeding and nonbreeding season (a). At the same time, areas will gain new species as the distributions of breeding birds shift north and as species that currently winter further south remain in the region during the nonbreeding season (b). The overall change in community composition, represented here by the Bray–Curtis dissimilarity index, demonstrates the change in the local composition of communities expected, especially in the north and the mountainous regions of western North America (c). Reproduced from Langham *et al.* (2015) under the terms of the Creative Commons Attribution License.

on whether the carbon remains trapped in plant material or is released into the atmosphere.

Climate change has the potential to disrupt current stores of carbon trapped in plant matter and actually increase carbon dioxide in the atmosphere. In the Arctic, vast stores of carbon are stored in peat and other plant material. As the permafrost layer thaws, this material could decay at a faster rate, releasing the stored carbon in the form of carbon dioxide and even more potent greenhouse gases such as methane. **See also: Global Carbon Cycle; Climate Change and Biogeochemical Impacts**

Summary

There is little doubt that the earth's climate will continue to change in ways that impact biological systems. While recent and future changes in climate patterns are driven by an overall global warming trend, it is important to remember that biological systems interact with local climate patterns, not the global average. Understanding future impacts of climate change is not a simple matter of asking how biological systems respond to 2 or 4°C changes in temperature, but the more complicated task of how 2 or 4°C or more °C warming of the earth's system will impact the climate patterns where the biological system of interest resides. **See also: Global Change – Contemporary Concerns**

It is clear from both ancient and recent climate change that while some species will adapt to new climate conditions, not all species will have the ability to respond to changes in climate. Extinctions will occur; current communities of species may disassemble as species respond differently to rapid climate change; new species' assemblages will emerge. The fates of those species faced with the rapid changes in climate expected in the coming decades are uncertain, but their extinction will result in permanent, cascading changes to the ecosystems that provide human societies with goods and services we depend on and value.

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