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Observed Impacts of Climate Change on Biodiversity

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ABSTRACT

There is strong scientific evidence that climate change is already impacting plant and animal populations, and model projections indicate that the current trends are likely to continue over the coming century. This synthesis reviews the observed effects of climate change on biodiversity, drawing on key findings from the primary scientific literature. Case studies covering a broad taxonomic and geographical range have been selected to provide examples of recent studies on these impacts including poleward and upslope shifts in distribution, changes in disease risk, phenological responses, coral bleaching, and regional and global impacts across taxa.

INTRODUCTION

Evidence from the fossil record (Mayhew et al. 2008; Edie et al. 2018; Nogués-Bravo et al. 2018) demonstrate that changes in climate can have a profound influence on the myriad of species that comprise Earth's biodiversity. Predicted climate change over the coming century is therefore likely to have a significant influence on biodiversity (Rinawati et al. 2013; Bellard et al. 2014). Through this synthesis, students will review some of the main ways that climate change affects natural systems. Case studies have been selected to provide examples of observed impacts from the recent past, including poleward and upslope shifts in distribution, changes in disease risk, phenological responses, and coral bleaching.

The physical science of climate change is covered in the NCEP module *The Global Carbon Cycle and Climate Change* (available from <https://ncep.amnh.org>). The focus of this module is on the impacts of climate change on biological systems (see Box 1 for an overview). The scope of the module is to deal with responses of wild biological species and ecosystems, but not impacts on agricultural systems (see Wheeler and von Braun 2013; Kumar 2016) or human health (see Franchini and Mannucci 2015; Kreslake et al. 2016). There are a number of excellent extensive reviews of climate change impacts on biodiversity, notably Pecl et al. 2017, Bellard et al. 2012, Foden et al. 2013, and a book-length treatment by Pearson (2011). Rather than try to duplicate these reviews, this synthesis distills key findings from the primary literature into easily understandable summaries of a selection of case studies. Case studies were selected to give a fairly broad range of taxonomic (e.g., birds, insects, fish, and plants) and geographical (e.g., North and Central America, and Australia) examples.

POLEWARD DISTRIBUTION SHIFTS

One of the expected impacts of climate change on biodiversity is a shift in species' distributions toward the poles (i.e., northward shifts in the northern hemisphere, and southward shifts in the southern hemisphere). This is because climates generally get cooler moving away from the equator, so particular climate regimes will be expected to move toward higher latitudes under climate change. Hitch and Leberg (2007) provide a good example showing northward shifts in the breeding distributions of North American birds as a result of climate change. Birds provide especially good subjects for investigating shifts in species distributions because: 1) birds distributions are generally well-known (especially in North America), with observations having commonly been made over a long



Box 1. Climate change: impacts on nature

At its 7th Plenary session in 2019, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) developed a critical assessment report on the condition and direction of the natural world and the implications of these trends. Notably, this assessment incorporated evidence from a wide range of sources and perspectives, including Indigenous and local knowledge, and therefore represents a more global and comprehensive synthesis. The following list summarizes some of the main conclusions of the IPBES plenary report regarding impacts of climate change on biodiversity:

- Climate change is a direct and substantial driver of changes in nature that also interacts with and magnifies the impacts of other drivers, such as land use change, overexploitation, pollution, and invasive species.
- Human activity has led to an increase in global temperature by 1.0°C compared to pre-industrial levels, an increase in frequency and intensity of extreme weather events in the past 50 years, and an increase in sea level by over 3 mm a year for the last 20 years. These changes have altered species distributions, population and community structure and dynamics, and ecosystem functioning.
- The impacts of climate change are predicted to accelerate in coming years, with exponentially worsening effects on biodiversity and ecosystem functioning. Effects will vary regionally, with tropical ecosystems facing particularly large declines in biodiversity due to the combination of climate change with land-use change and exploitation of fisheries.
- A global warming estimate of 1.5°C to 2°C is projected to cause a decline in range size for the majority of terrestrial species, which in turn will heighten the risk of global extinctions. Studies indicate that at 2°C warming, 5% of species will be at risk of extinction due to climate change. Local population extinctions are already well established and widespread.
- Nearly half of threatened land mammals (other than bats) and a quarter of threatened birds have potentially already been negatively impacted by climate change in some part of their range. The number of threatened species is predicted to increase due to climate change.
- The ability for species to respond to climate change will depend on their abilities to disperse, move to favorable conditions, or evolve.

time period, meaning that temporal dynamics can be studied; 2) bird ranges are known to be strongly associated with temperature (e.g., Root 1988); and 3) most birds have good dispersal capacity, enabling them to move around the landscape to track suitable climate conditions.

For their assessment, Hitch and Leberg (2007) used data from the U.S. Geological Survey's North American Breeding Bird Survey (BBS). The BBS is a very large initiative whereby trained observers annually record birds present along 3,500 roadside survey routes in the continental United States, southern Canada, and northern Mexico. The researchers tested for shifts in distributions using data recorded during the periods 1967–1971 and 1998–2002. To exclude possible confounding effects from large elevation gradients that would be expected to show upslope distribution shifts (see next section), Hitch and Leberg (2007) restricted their evaluation to central and east North America, thus leaving out the Rocky Mountains in the west. They also chose to exclude game birds, because their distributions have been greatly influenced by direct human interference, and to also exclude species dependent on aquatic habitats, since these were unlikely to be well sampled by the roadside surveys.

An important part of the study was to ensure that the analyses distinguished between general range expansions and true northward range shifts. Only assessing the northern range margins of species could result in the appearance of a northward range shift, when in fact the species is generally expanding, resulting in both a northward shift at the northern margin and a southward shift at the southern margin. While a true northward range shift in the northern hemisphere is most likely to have been caused by climate change, a general range expansion could be caused by other factors, such as changes in land use or increased supplemental feeding. An apparent general expansion could also



result from increased survey effort in the later years. To get around these potential problems, Hitch and Leberg (2007) asked whether northern range margins were moving north, and/or if southern range margins were moving south. Because few species have both their northern and southern range margins included within the geographical scope of the BBS, the researchers divided bird species into those whose northern range margin was included and those whose southern margin was included. The authors also required that range margins were at least 200 km from the edge of the area sampled by the BBS to ensure that any shift in range would have been detected by the survey.

The results of the analysis showed that northern range margins had moved northward by a statistically significant average of 2.3 km per year. However, results for the southern range margins did not show a statistically significant shift to the south. Hitch and Leberg (2007) thus concluded that their results show a northward shift in sampled bird distributions over recent decades. The results are similar to those from a comparable study undertaken in Britain, which showed that the northern (but not southern) range margins of many species of birds had moved north by an average of 18.9 km over a 20-year period (Thomas and Lennon 1999). Since it is very difficult to identify other factors that could have caused northward range shifts consistent across many species and two continents, climate change is implicated as the most likely explanation.

An interesting question raised by this case study is why are southern range boundaries not also moving north? A response concerns the way that analyses of range shifts utilize presence and absence data: a small population colonizing a new area will be recorded as a 'presence', but 'absence' will not be recorded until population density has dropped to a level whereby the species is no longer detected. In effect, a single individual moving into a new area may be recorded as a range expansion and can be more readily detected over a short time span, but all individuals have to move out of an area in order for a contraction to be recorded, a much longer process. Thus, it is much easier to detect a range shift at the leading edge, as opposed to trailing edge, of the distribution (Thomas et al. 2006). For instance, a similar study by Brommer et al. (2012) looking at the range shifts of 148 bird species in Finland also found a poleward shift in the northern range margins by 1.1–1.3 km/year. However, despite using repeated surveys over multiple decades, the change in southern range margins was not significant (Brommer et al. 2012). In order to observe range contractions, it is therefore preferable to study abundance data, as opposed to presences and absences (see, for example, Foden et al. 2007; Howard et al. 2014).

MARINE POLEWARD DISTRIBUTION SHIFTS

Terrestrial poleward distribution shifts have been well documented in a wide range of taxa (Hickling et al. 2006; Mason et al. 2015). However, poleward distribution shifts as a result of climate change are happening even faster in marine species, with an estimated range expansion of 72 km/decade (Poloczanska et al. 2013). Marine species are both more sensitive to climatic changes and more adept at colonizing new regions than terrestrial species, enabling them to expand their ranges on a wider spatial scale (Pinsky et al. 2020).

The ability for marine species to shift and/or expand their ranges can depend on a number of intrinsic factors, including rates of reproduction and dispersal abilities (O'Connor et al. 2011). For many marine species with a sedentary adult life stage, range shifts occur during the mobile larval stage. These larvae can disperse over great distances, producing juvenile "vagrants" that have moved beyond their typical range boundaries (Cowen and Sponaugle 2009). Many vagrants fail to survive because they are faced with temperatures outside their normal range; however, with ocean temperatures



increasing, more vagrants may be able to survive beyond their typical boundaries.

Ocean currents also play a critical role in shifting distributions, particularly when combined with changing ocean temperatures (see Ling et al. 2008; Beaugrand 2009; Johnson et al. 2011). The East Australian Current, for example, moves southward along the coast of Australia, carrying warm water as well as larval organisms (Booth et al. 2007). Effects of climate change have driven an increase in both the temperature and flow rate of this current (Ridgway 2007), driving warmer water temperatures further south. This has provided potential opportunity for vagrants to expand their ranges poleward.

Fowler et al. (2018) used a long-term monitoring study to show how distributions of tropical reef fishes in southeastern Australia are responding to changes in the East Australian Current. From 2006 to 2016, Fowler et al. (2018) monitored tropical reef fishes in three southeastern monitoring locations in Australia: Jervis Bay, Narooma, and Merimbula. They conducted multiple underwater surveys per year at each site and recorded and identified observed reef fish species. These survey results were then compared to those conducted by Booth et al. (2007) from 2003 to 2005. Fowler et al. (2018) found that 30 tropical reef fish species had vagrants present in regions beyond the southern poleward boundary of their last reported location. This indicates that warmer temperatures are enabling vagrants to increase overwinter survival beyond their normal boundaries and may lead to established populations of adults in new southern regions.

This will be important to monitor, as tropical fish can have various impacts on ecosystems. For instance, 20% of the reported species are herbivores, including the three species with the most observed number of vagrants, and a poleward shift of these species presents a potential threat to kelp habitats. This study points to the potential impact that poleward shifts in marine species distributions can have on species interactions and communities, as a result of changing ocean temperatures and currents.

UPSLOPE DISTRIBUTION SHIFTS AND EXTINCTION

Because temperature decreases with increased elevation, warming in a mountainous region causes conditions previously found at lower elevations to move upslope toward higher elevations. This is the reason why many glaciers on high tropical mountains are rapidly melting, as warmer temperatures usually found at lower elevations are now found upslope (IPCC 2014; IPCC 2019). While climate-driven latitudinal and elevational shifts have been reported for numerous species in temperate regions, empirical evidence for such distributional changes are more rare for tropical species (Pecl et al. 2017). Yet, tropical species are considered more sensitive to temperature changes than temperate ones due to narrower climate niches (Perez et al. 2016). Furthermore, because tropical species' distributions are impacted more by elevational temperature gradients than by latitudinal gradients, it is likely that tropical species will shift uphill in response to warming (Colwell et al. 2008). Molina-Martínez et al. (2016) provide the first empirical study on the effects of climate change on Neotropical butterfly elevational distributions.

From 2010 to 2011, Molina-Martínez et al. (2016) surveyed eight sites in the Sierra de Juárez mountain range in Oaxaca, Mexico. These sites, previously surveyed in 1988, ranged in elevation from 117 m to 3000 m. Using fixed transects and traps, the researchers sampled from April to October, when adult butterflies are most active. In addition, they used historical temperature data collected from three meteorological stations to estimate temperature for each specific sampling site in 1988 and compared this to data obtained using data loggers during the sampling transects. The data showed



that temperatures had increased significantly across the entire area by an average of 1.3°C since 1988. This increase was even higher at sites below 1000 m, with an average increase of 1.8°C.

The authors found that since 1988, butterflies had increased their average elevational distribution across the entire gradient by an average of 145 m, with 65% of species showing an uphill shift. Species above 1000 m showed an even greater shift, with an average increase in elevational distribution of 308 m. In the latest survey, some species, such as *Pterourus pilumnus* and *Vanessa virginiensis*, were found only at the highest elevations. Because of the sensitivity of Lepidoptera to temperature, the researchers attribute this shift to climate change. If climate warming continues, potential suitable habitat may disappear, and these high elevation species could face extinction.

Below 1000 m, species also showed a significant elevational shift of an average 87 m upslope. However, the rate of change for these species did not keep pace with the rate of temperature increase. In addition, the researchers found that overall species richness had declined since 1988, particularly at sites below 2000 m. A number of species recorded in 1988 were not recorded in the 2010–2011 surveys, potentially indicating local population decline or extinction.

The study by Molina-Martínez et al. (2016) thus provides strong evidence that climate change is affecting montane communities. The dominant trend is that of upslope distribution shifts, with the potential for extinction in cases where the population is unable to move to higher elevation or adapt to new climatic conditions. Furthermore, the risks associated with climate change are compounded by other threats such as land-use change. Molina-Martínez et al. (2016) found that below 1000 m, there was a pronounced change in land use with an increase in agriculture and a corresponding decrease in rain forest. These shifts also impacted community structure; the latest survey showed an increase of up to 76% of generalist species in the low elevation area. As these species are well adapted to disturbed and open habitats, the researchers propose that this change in composition is indicative of local population declines and extinctions for species more susceptible to climate and land use changes. Land use changes could further impact species by reducing habitat connectivity, thereby limiting range shift potential.

DISEASE RISK

There is concern that rising temperatures and changed precipitation regimes may favor certain pathogens, thus triggering disease outbreaks (for review see Altizer et al. 2013 and Wu et al. 2016). Vector-borne diseases are particularly responsive to climate change, as climatic shifts can impact the abundance and distribution of both the pathogen and the vector. For instance, the range of the white-footed mouse, an important reservoir host of the pathogen *B. burgdorferi*, is expanding poleward, thus altering the geographical range of Lyme disease (Roy-Dufresne et al. 2013). The emergence and spread of vector-borne diseases into new areas can have severe consequences for human health and food security (see for instance Ryan et al. 2019 and Anderson et al. 2020) as well as susceptible native species.

Increasing temperatures are also likely to be associated with higher prevalence of malaria, a disease caused by *Plasmodium* parasites (Garamszegi 2010). The arrival of avian malaria (*Plasmodium relictum*) and the mosquito vector *Culex quinquefasciatus* to the Hawaiian Islands has had considerable impact on the distribution and abundance of many native Hawaiian birds over the century, resulting in range contractions and even extinction (Warner 1968; van Riper et al. 1986; Atkinson and Samuel 2010). Indeed, the Hawaiian Islands are already experiencing warming,



especially in the higher elevations that currently act as refuge from not only heat but from the transmission of disease as well (Giambelluca et al. 2008; Atkinson and LaPointe 2009). In their study, Atkinson et al. (2014) present empirical evidence for the association between avian malaria transmission and prevalence and changing climatic conditions in the Hawaiian Islands.

Atkinson et al. (2014) focused their study on Kaua'i's Alaka'i Plateau, a region characterized by montane rainforests and numerous endemic bird species. Using mist nets, they collected birds from three locations in the region over three periods: 1994–1997, 2007–2009, and 2012–2013, in both the summer and winter months. Birds were banded, measured, weighed, and blood samples were collected in order to detect the presence of parasites. The researchers then looked for associations and interactions between malaria infection, year, season, location, and native status of the bird, and compared the overall prevalence of malaria in birds from 1994–1997 and 2007–2013. They also determined changes in temperature from 1920–2007, using monthly temperature data from 18 weather stations as well as radiosonde temperature data. Finally, they measured long-term changes in precipitation and streamflow, using data from the National Oceanic and Oceanographic Administration and the United States Geological Survey surface-water data site. Both precipitation and streamflow are important for determining availability of habitat for mosquitoes.

The authors found that from 1994 to 2013, malaria prevalence more than doubled, from 8.6% to 19.6%. Increases were observed in most of the species sampled. The Puaiohi, or Kaua'i thrush (*Myadestes palmeri*), saw the largest increase at 22%, while the 'Anianiau honeycreeper (*Magumma parva*) only increased by 6%. The authors attribute these differences to potential variation in sample size, host defense behavior, host attractiveness, parasite resistance or tolerance, or other life history differences. Analyses of temperature changes showed that there was a 0.199°C increase per decade from 1960 to 2009. Precipitation and streamflow data indicated that the Plateau is becoming drier, but the availability of suitable mosquito breeding habitat has not changed over time. The authors suggest that because of declines in precipitation, high streamflow is occurring less frequently, thereby enabling mosquito larval habitats to persist for longer alongside streams. Persistence of these habitats may lead to increased abundance of mosquitoes on the Plateau, and therefore increased malaria transmission. Thus, the increase in malaria prevalence is associated with both increasing air temperature and shifting precipitation and streamflow patterns.

Atkinson et al. (2014) therefore illustrate that over the past two decades, avian malaria across the Alaka'i Plateau has significantly increased. These results support similar trends found in avian malaria increase at Hakalau Forest National Wildlife Refuge on the Island of Hawai'i (Freed et al. 2005; Freed and Cann 2013), though this study shows a much higher overall presence of malaria. Together, these findings are crucial for directing conservation efforts to protect native forest birds susceptible to the spread of avian malaria in Hawai'i under climate change.

PHENOLOGICAL CHANGES

Phenology is the study of biological life-cycles throughout the year. Examples of phenological events include egg-laying and migration in birds, flowering and fruiting in plants, and reproductive periods in frogs. Such events are often closely related to climate. For example, warming each spring initiates a flurry of biological activity, related to growth and reproduction for many species. Climate change can thus be expected to have an impact on phenology.

Bradley et al. (1999) analyzed a dataset comprising phenological events recorded over a 61-year



period at a site in Fairfield Township, Sauk County, southern Wisconsin in the USA. Phenological data were collected during two time intervals: 1936–1947 and 1976–1998. Interestingly, the first 11 years of data were recorded by famed ecologist and environmentalist Aldo Leopold, while the subsequent years were added by Leopold's daughter, Nina Leopold Bradley. Together they recorded 74 different phenological indicators, focusing especially on arrival dates for migratory birds and dates of first bloom of spring flowers. Examples of indicators recorded include arrival dates for geese (*Branta canadensis*), robin (*Turdus migratorius*), and meadowlark (*Sturnella magna*), and dates of first bloom for wild geranium (*Geranium maculatum*), forest phlox (*Phlox divaricata*), and marsh milkweed (*Asclepias incarnata*). Bradley et al. (1999) omitted 19 of the indicators from their study because there were too few records for statistical analysis, leaving 55 indicators that were investigated for long-term changes in the dates of events. All of these indicators occurred in the springtime (February-June).

Overall, 17 of the 55 indicators showed a statistically significant advance in springtime occurrence; in other words, during the period of study the event tended to occur earlier in the year. The data also showed that the timing of 20 indicators did not appear to change over the period of study, with dates of occurrence tending to stay roughly constant throughout the period of study. The remaining 18 indicators showed small responses, but none were statistically significant so these cases could not be classed as either responders or non-responders. Importantly, there were no cases with a statistically significant delay in springtime occurrence.

The earlier occurrence of spring events is an expected response to climate change: as the climate warms, higher temperatures arrive earlier and trigger life cycle events. The lack of any observed delays in phenology support the assertion that the trends in Wisconsin reflect twentieth century global climate warming. But why don't all indicators show a trend toward earlier occurrence? Many phenological events, such as bird migration and reproductive activity, are not regulated by climatic factors, but are instead related to other cues such as the number of hours of daylight per day (which is termed 'photoperiod'). We would therefore not expect these indicators to respond to changes in temperature and precipitation patterns.

One interesting conclusion of the Bradley et al. (1999) study is that some phenological indicators will respond to climate change, whilst others will not. Furthermore, the data show that species will respond by differing amounts. For example, geese were found to be arriving roughly half a day earlier per year, while forest phlox bloomed a quarter of a day earlier per year. Differing phenological responses can result in disruption of ecosystem interactions, such as birds failing to breed at the time of maximal food abundance (see, for example, Both et al. 2006 and McKinnon et al. 2012). This is called a phenological mismatch.

PHENOLOGICAL MISMATCHES

The impacts of climate change on phenology are likely to vary substantially among different taxa. As a result, differential phenological changes in species that closely interact, such as plants and pollinators, may cause them to become increasingly mismatched in timing (for review, see Renner and Zohner 2018).

Migratory species in particular are tied to the specific phenological changes of other taxa. Migratory birds, for instance, rely on the availability of resources at their stopover sites to provide fuel for migration, and at their eventual breeding grounds to feed offspring. Birds must match their stopovers, arrival, breeding, egg laying, and egg hatching upon the phenology of plants and insects



in order to maximize fitness (Marra et al. 2005). However, increasing temperatures earlier in the spring is driving an advance in the phenology of leaf growth and insect emergence (Renner and Zohner 2018). Many long-distance migrants, on the other hand, use photoperiod cues rather than environmental conditions like temperatures to signal the start of their migration (Dawson et al. 2001). Migratory birds must therefore shift the timing of their migration or else they may face a phenological mismatch with resources upon arrival at their breeding grounds.

Mayor et al. (2017) assessed the extent of phenological mismatch between migratory birds and vegetation in North America. Using citizen science data collected from eBird, they analyzed the arrival date for 48 passerine bird species over a 12-year period (2001–2012). For a proxy of food availability, they assessed “green-up” of vegetation using satellite imagery; green-up of vegetation has been shown to be strongly linked to insect emergence, a primary food source for passerine birds (Visser et al. 2012).

They found that between 2001 and 2012, green-up advanced an average of 0.372 days/year for all species. For 27 species, green-up significantly advanced by an average of 0.952 days/year. Species’ arrival dates also accelerated by an average of 0.426 days/year for all species, and significantly moved up for over half of the species by an average 0.669 days/year. The exceptions to this trend were a delay in green-up by 1.52 days/year for four species, and a delay in arrival by 0.370 days/year for a single species (*Contopus sordidulus*). Mayor et al. (2017) note that when green-up advanced in an area, there was often a corresponding change in species’ arrival.

The authors also measured phenological interval as the difference between a species’ arrival date and the date of green-up. Seven species showed a significantly positive increase in phenological interval, with green-up advancing faster than arrival by an average 0.630 days/year. For two species, there was a significantly negative increase in phenological interval, with green-up occurring progressively later than arrival date by an average 1.60 days/year. For all changes in phenological interval, however, green-up had a greater phenological shift than did arrival. Furthermore, Mayor et al. (2017) found that these trends differed by region, with species in the Eastern Temperate Forest showing a positive change in phenological interval, and species in Western Forests displaying a negative change.

This study shows that many migratory birds do have the capability of adjusting their arrival time to the changing phenology of vegetation. However, for a subset of species, this adjustment is already failing to keep up with changes in green-up. Furthermore, keeping pace with an advancing spring can still produce phenological mismatches for a migratory species. Lameris et al. (2018), for instance, showed that although the migratory barnacle goose has advanced its arrival date to its Arctic breeding grounds, it was unable to similarly advance its egg laying. As a result, it still experienced a phenological mismatch with resource availability, leading to a reduction in offspring survival (Lameris et al. 2018). It is therefore important to consider additional breeding and reproductive phenologies to better understand the impact that climate change will have on producing phenological mismatches.

CORAL BLEACHING

Coral reefs are one of the most biologically diverse ecosystems on Earth. Reefs support about 25% of all marine life, as well as a number of key ecosystem functions (NOAA 2019). A review by Brandl et al. (2019) highlights eight core ecosystem processes provided by coral reefs, including nutrient cycling, herbivory interactions, and CaCO_3 dynamics. In addition, coral reefs provide foods and services that are critical to people’s well-being. An estimated six million people depend on coral reef fisheries



for their livelihoods (Teh et al. 2013), and coral reefs are also valued for their aesthetics and spiritual importance (Cinner and Aswani 2007; Hicks et al. 2009).

Almost all corals live in a symbiotic relationship with zooxanthellae, a type of single celled algae that lives within the coral's tissues. Zooxanthellae photosynthesize, and in doing so produce compounds that are absorbed as a food source by the coral. Bleaching occurs when this coral-algae relationship breaks down, resulting in the loss of the zooxanthellae from coral tissues, and consequently a loss of color. Although corals can survive bleaching events, mortality tends to occur if the bleaching is prolonged. Bleaching can be caused by changes in salinity, intense solar radiation, exposure to air by low tides or low sea level, sedimentation, or chemical pollutants such as herbicides and oil (Reaser et al. 2000). In addition, the rate of ocean warming has more than doubled since 1993 (IPCC 2019), and observations have shown a significant correlation between bleaching events and high sea surface temperature (see Eakin et al. 2010, Krishnan et al. 2011, and Bindoff et al. 2019).

Large-scale coral bleaching events have increased in frequency in recent decades, and going forward, temperature anomalies capable of triggering severe bleaching events will also rapidly increase (Kleypas et al. 2021). It is predicted that most coral species will not be able to recover quickly enough to survive these changes (Kleypas et al. 2021). Reef resiliency is further impaired by two additional consequences of climate change: an increase in the intensity and frequency of storms and a decrease in the pH of seawater (termed "ocean acidification"). Frequent, intense storms like hurricanes and cyclones damage the physical structure of the reef, and ocean acidification slows coral growth and can weaken the calcium carbonate structure upon which the polyps live (Hoegh-Guldberg et al. 2017; NOAA 2021). In sum, these climate change stressors can cause compounding effects: coral weakened from ocean acidification or recent bleaching events may be more susceptible to the damaging effects of intense storms.

Coral reef ecologists use several techniques to study past bleaching events and model future bleaching scenarios. For example, after the Great Barrier Reef's mass bleaching event in 2015–2016, researchers conducted aerial surveys to assess the extent of bleaching at 1,156 individual reefs along the reef's 2,300 km length—the largest reef ecosystem in the world. Divers conducted detailed belt-transect underwater surveys via SCUBA to verify the accuracy of these aerial survey bleaching scores. The aerial and underwater bleaching data were then compared with satellite-derived sea surface temperature data and bleaching models, which showed a "tight" correlation between the level of local heat exposure and the severity of bleaching on individual reefs (Hughes et al. 2017).

Climate change is the greatest threat to coral reefs worldwide (GBRMPA 2019). At a global warming increase of 1.5°C, coral reefs are projected to decline by up to 30% of their former cover (IPBES 2019). As global warming progresses and sea surface temperatures increase, the potential for climate-driven mass bleaching and coral mortality during hot summers—regardless of El Niño events—is even more likely, and this shorter window of time between bleaching events makes it harder for corals to recover (Hughes et al. 2018). Corals and the ecosystems they support are therefore dependent upon the reduction of global greenhouse gas emissions and the management of local stressors (e.g., sedimentation, pollution) to bolster their resiliency. Maintaining healthy reef ecosystems will be critical for the local human populations that depend upon coral reefs for their food, livelihoods, and well-being (Burke et al. 2011).



META-ANALYSES

Many studies have described impacts of climate on biological systems. For example, in this synthesis we have seen how climate is affecting birds, butterflies, and plants in North America, reef fish in Australia, and corals around the world. However, most individual case studies such as these are limited to a particular region and/or a limited sample of taxa. Because species may be impacted by many different factors (for example, habitat destruction, introduced species, or nitrogen deposition), it is often difficult to demonstrate a strong influence of climate change in any particular study. Researchers have therefore examined results from a large number of individual studies using an approach called “meta-analysis,” which is a type of statistical method for exploring trends across multiple studies.

Pacifici et al. (2017) undertook a meta-analysis to better understand the impact that climate change has already had on birds and mammals, and the life-history traits that make species vulnerable to these changes. Since climate change is a global phenomenon, it is expected that certain traits will be consistent across different regions and taxa. Such traits include distribution, population size, phenology, behavior, genotype or phenotype. The authors conducted a literature search for studies between 1990 and 2015 that showed a change in climate in a specific area, and a corresponding climate-induced change (or lack of change) in a species’ trait. They used data from 70 studies on 120 mammal and 569 bird species. A species’ response was categorized into one of four types: “negative” if at least 50% of its populations had a decrease in population, range size, survival, reproduction, or body mass; “positive” if there was an increase in these traits or a change in phenology; “unchanged” if there was no response; or “mixed” if opposite responses were shown within a species. Pacifici et al. (2017) then determined the relationship between a species’ inherent and spatial traits, and their response to climate change.

The study found that of the 689 species analyzed, 38.3% of mammals and 20.9% of birds had shown a negative response to climate change. Negative responses were associated with a number of spatial traits. For both birds and mammals, species most at risk occurred in regions with large recent changes in temperature and low seasonality of rainfall. Negative responses in birds were also associated with species living at high altitudes, in areas with low seasonality of temperature, and high maximum temperature at breeding sites. Species that inhabit areas with low seasonality of temperature and precipitation generally have a narrower ecological niche, and thus are more vulnerable to climatic changes. In addition, species living at high altitudes are often more restricted in range, with less opportunity to move upslope to escape increasing temperatures.

For intrinsic traits, negative responses were associated with mammals with a narrower diet, and birds with low dispersal, long generation times, and limited altitudinal range. Mammals most at risk were primates, elephants, and marsupials.

Only two mammal orders had positive responses to climate change: rodents and insectivores. These orders include species with fast reproduction time and wide habitat generalization. Interestingly, most of the species in this category were also fossorial, or burrowing, which may allow them to limit exposure to temperature changes. On the other hand, the majority of bird orders did not have a negative response to climate change.

By quantifying the number of species that have been impacted by climate change, this study illustrates the wide-ranging impact that climate change has had over the last century. The authors



estimate that 47% of mammals and 23.4% of birds have had at least one population already negatively impacted by climate change. While many assessments of a species' vulnerability to climate change use modeling to project future risk under various climate change scenarios, it is important to consider the recent and current impacts of climate change on biodiversity. The findings demonstrate that climate change is a common force discernable in natural systems all around the world. Although, in individual cases, other threats may have a more overriding impact on species, climate change is an underlying force with the potential to directly (e.g., warmer seas causing coral bleaching) or indirectly (e.g., changing temperature and precipitation patterns promoting disease epidemics in birds) impact biodiversity.

CONCLUSIONS

Species have survived major climatic changes throughout their evolutionary history (Mayhew et al. 2008). However, the case studies presented in this synthesis suggest that contemporary anthropogenic climate change presents a significant threat to biodiversity. Furthermore, while the case studies provided here highlight the impacts of climate change to particular species or taxa, it is crucial to remember that natural systems comprise a complex web of interactions and feedbacks among species. As we saw in the Phenological Mismatch example, climate change impacts on a single species could have significant knock-on impacts on many other species, resulting in changes to the community as a whole (see Brown et al. 1997 for a case study example). The different ways and degrees to which different species respond to climate change will alter community interactions and ecosystem functioning in numerous and important ways (Pecl et al. 2017).

A key factor that differentiates contemporary climate change from past changes is that the impacts are combined with multiple other stressors, in particular habitat fragmentation. Natural systems in the twenty-first century exist on a planet that is dominated by humans, with over 75% of the ice-free land surface showing evidence of human modification (Ellis and Ramankutty 2008). The combined effects of rapid climate change and unprecedented habitat loss and fragmentation have the potential to greatly reduce global biodiversity (Mantyka-Pringle et al. 2012). Invasive species are another major driver of biodiversity loss. Under climate change, the distribution, abundance, and impact of invasive species are likely to be altered. Invasive species are often suggested to expand under climate change, as they are usually abundant, possess broader physiological niches, and inhabit a wider range of environments than other species (Hellmann et al. 2008). In particular, climate change is expected to impact invasive species by altering the mechanisms of their introduction, changing climatic constraints, varying species distributions, modifying their impact, and shifting management strategies and effectiveness (Hellmann et al. 2008).

Climate change thus presents an important challenge for conservation efforts. Ecosystems, and the biodiversity they hold, are of immense value to human society, providing many essential goods and services, including the recycling of waste, generation of soil fertility, pollination of crops, and regulation of climate (Millennium Ecosystem Assessment 2005; see also the NCEP module *Why is Biodiversity Important?* available from <https://ncep.amnh.org>). The effect of coral bleaching due to climate change on human populations through impacts on fish stocks and tourism has already been discussed earlier in the synthesis. However, climate change impacts food security in a wide variety of ways, as changes in temperature and rainfall limit crop productivity (Wheeler and von Braun 2013), and changes in weather impact availability, accessibility, and utilization of food systems (Gu et al. 2010). Tripathi et al. (2016) review the numerous ways in which climate change will reduce both the quality and quantity of major food sources across the world.



Predictions of continued rapid climate change over the coming century have prompted many attempts to estimate future impacts on biodiversity. Various methodological approaches have been taken to estimate future impacts, including the use of correlative and mechanistic species distribution models (Bradley et al. 2010; Kearney et al. 2010), dynamic vegetation models (Campbell et al. 2009), species-area relationships (Carnaval et al. 2009), IUCN status methods (Chevin et al. 2010), and dose-response relationships (Barnosky et al. 2011; for review see Bellard et al. 2012; see also the NCEP module *Species Distribution Modeling for Conservation Educators and Practitioners* available from <https://ncep.amnh.org>). In one high-profile study, Thomas et al. (2004) estimated that, on the basis of a mid-range climate warming scenario for 2050, 15–37% of species in their sample of over 1,000 study species would be on a trajectory toward extinction. Such predictions of extremely high extinction risk due to climate change have generated a great deal of debate among scientists, politicians, and the broader general public. Uncertainties inherent in the predictions, along with debate as to how (if at all) society should manage the threat, make this a controversial debate. Management options revolve around reducing climate change through reductions in atmospheric greenhouse gas concentrations, and developing dynamic approaches to contend with changing conditions, for example by incorporating potential shifts in species' distributions into the planning of new natural reserves (Williams et al. 2008).

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