Biogeographical Shifts and Climate Change

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Introduction

The notion that species occurrence is determined by local environmental conditions can be traced back over 2000 years to the early accounts of classical naturalists such as Pliny the Elder (AD 23-79). It was not until the onset of the 20th century, however, that ecologists began to describe the distribution of species in relation to environmental conditions, such as temperature and precipitation (water availability), and the concept of the ecological "niche," the role and position an organism has in its environment, emerged. This large body of knowledge developed rapidly and greatly advanced our understanding of how organisms are physiologically adapted to their environments, how they respond to changes in the environment, including climate, food, and competitors, and the effects on their populations. Emerging from this perspective was the idea of climatic niche tracking—the process by which species remain in their preferred climatic conditions over time by following, via local extinctions and colonizations, limiting variables through geographical space. Its fundamental expression is that of range contractions driven by the decline and extinction of local populations under unfavorable conditions, and expansions following dispersal and settlement into newly favorable sites.

Human influence on the climate system, through anthropogenic emissions of greenhouse gases, is well recognized and the existence of climate warming is unequivocal. Recent climatic changes have had widespread impacts on natural systems including shifts in the ranges (distributions) of terrestrial, freshwater, and marine organisms. Mounting scientific evidence now provides a clear picture of the causality between the contemporary range shifts and climate change. The overarching paradigm under warming is that of shifts toward cooler regions, resulting in range expansions into poleward, higher elevation (land), and deeper (ocean) regions. However, this expectation is challenged by the high variability in the direction and speed of observed distribution shifts both among and within species. Departures from expectations result from the complex interaction of climate change with species' physiology and life history as well as the myriad of other natural and anthropogenic factors amidst which climate change unfolds.

That anthropogenic climate change has, and will continue to, affect the distribution of species across land and ocean from basal primary producers to apex predators is undeniable. That these changes will result in the reshuffling of current biodiversity patterns traversing existing ecosystem boundaries seems also certain. To what extent, where, and when this will happen and the

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consequences for the structure and functioning of ecosystems remain largely unanswered, despite rapid important advances in the field. We anticipate the effects will be manifested beyond single-species and extend to impacts on ecosystem goods and services resulting in significant social and economic costs to human communities, for example, through the redistribution of fishery or pest species. We provide a general overview of these topics in the article below by highlighting current evidence from terrestrial, freshwater, and marine ecosystems. In defining range shifts, we refer to all areas a species occupies during stages of its life cycle. The periodical seasonal movements that occur in migratory species between breeding and foraging grounds and the influence of climate change on alteration of migratory routes, however important, are not considered further.

Species Ranges

All species have their own unique geographical distributions. Some species, referred to as range generalists or cosmopolitan species, occupy large swathes of space and are ubiquitous to many different type of environments. Others are range-restricted or endemic species occupying only small areas limited by particular geographical, environmental, or ecological factors. The factors defining the occurrence of species can be loosely organized into those describing (Soberón, 2007): (i) environmental conditions, including climate; (ii) resources needed for the species' survival; (iii) negative (competition, predation, parasitism) and positive (mutualism and commensalism) biotic interactions; and (iv) the capacity for movement or dispersal in space, thus conditioning the environments that species can access (Fig. 1). Humans are a major driving force capable of changing species distributions both directly (exploitation) and indirectly via the alteration of each of the former groups: transforming environmental conditions (e.g., climatic warming due to anthropogenic greenhouse gas emissions modifying resources (e.g., nutrient enrichment), changing the strength and type of competitions (e.g., introduction of invasive species), and facilitating (e.g., assisted migration of species) or impeding (e.g., habitat fragmentation) dispersal. Combinations of these factors result in species ranges that are highly dynamic in space and time, and it is often the case that where species are found (realized niche) is not the same as where they could potentially be found based on known requirements in terms of environmental conditions and resources (fundamental niche).

Ecophysiology and Range Dynamics Under Climate Change

Species must remain within certain critical limits where physiological activity is possible; this is defined as the species' tolerance breadth. How organisms fare within these limits is normally represented by performance curves describing the nonlinear

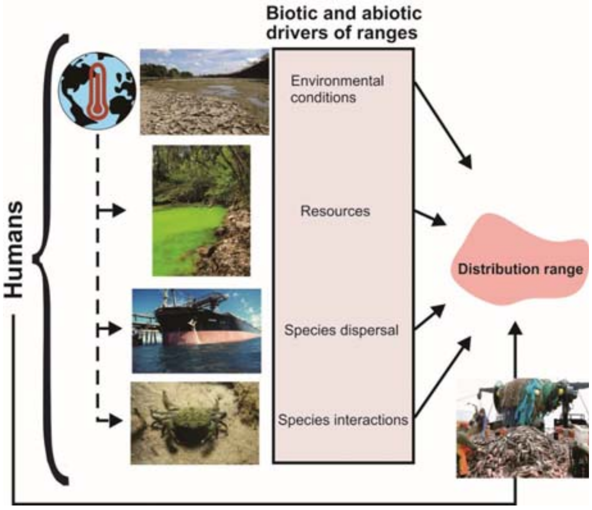

Fig. 1 Species's ranges are highly dynamic in space and time, driven by a combination of abiotic and biotic drivers defining the space that is effectively habitable for each species in any given period of time. Humans act as a major external force that can drastically change species' ranges both directly (through exploitation; photo by John Wallace, NOAA/NMFS/FRAMD) and indirectly by modifying any of the environmental drivers. For example, environmental conditions can be drastically modified by multiple human activities fragmenting habitats and modifying land use, such as river regulation for water abstraction and impoundment, and their interaction with climate change (top picture; extreme drought in the Garonne River at its passage through Toulouse, photo by Olybrius). Similarly, terrestrial runoff from agricultural fields and direct input of waste waters can have dramatic effects on nutrient levels and cycling in both freshwater and marine environments changing the availability of basal resources within ecosystems (eutrophication at a waste water outlet in the Potomac River, Washington D.C., photo by Alexandr Trubetskoy). Humans can also modify range dynamics by altering biotic processes such as species dispersion and interactions. Ballast water from ships (photo by CSIRO) is a major vector of human-assisted migration that has led the unintentional introduction and spread of many invasive marine species, such as the European green crab (*Carcinus maeans*; photo by CSIRO) into USA and Australian waters, which then compete with the resident species for space and resources and/or alter the physical environment. All photos included under public domain or Creative Commons license.

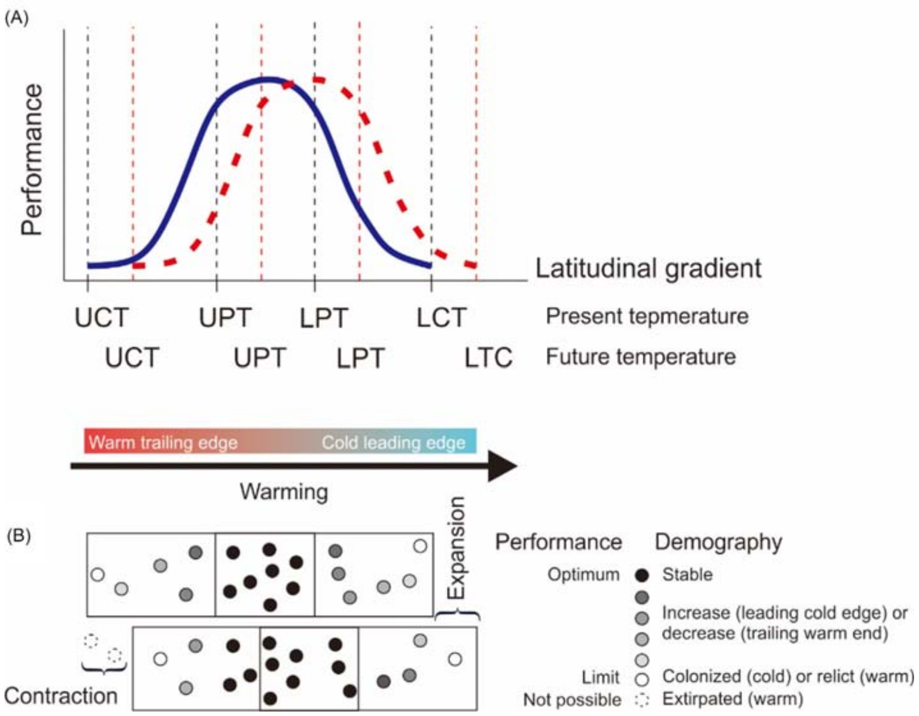

Fig. 2 Simplified representation of the relationship between physiological tolerance breadths and species range dynamics under climate change. (A) A thermal performance curve of a hypothetic ectotherm depicting its upper (warm; UCT) and lower (cold; LCT) critical thermal limits (beyond which physiological activity ceases), defining the thermal breadth of the species (UCT–LCT), and upper (UPT) and lower (LPT) pejus temperatures (from where performance starts to decline sharply; Pörtner et al., 2006). Under climate change, the location of the curve will shift in space following warming patterns (here depicted along a south-north latitudinal gradient for simplification). (B) The geographic distribution of the species comprising a number of populations scattered along the latitudinal gradient and limited in distribution by the physiological constraint imposed by ambient temperatures. Stable populations give way to gradually faster and slower degrees of population decline and increase, respectively, as we move from the thermal performance optima reached at the center of the distribution toward the warm trailing and cold leading edges, where existing local populations become extirpated (range contraction) and new populations established (range expansion) as temperatures surpass locally the upper and lower thermal critical limits under warming. The combination of both processes results in the overall shift of the species' distribution toward higher latitudes.

relationship between changes in some measure of performance (e.g., aerobic performance) and an environmental parameter (e.g., temperature). A common performance curve includes a performance optima, between the upper and lower pejus limits (Fig. 2A), signaling maximization of physiological rates and metabolic efficiency, and decreases first gradually then sharply toward both critical limits (Pörtner et al., 2006). The study of performance curves and the physiological mechanisms that define them is therefore instrumental to understanding the current distribution of species and for anticipating how they may respond to future climate change (Fig. 2).

Considerable research related to climate change has focused on the effects of temperature. The "climate variability" hypothesis states that species experiencing less variable ambient temperatures should have narrower thermal tolerance breadths, and therefore face a higher risk from anthropogenic warming. This appears to be of general application to ectotherms, so-called cold-blooded organisms (Sunday et al., 2012), whereas it is far less consistent in endotherms, for which the effect of warming in isolation may not represent a major future threat (Khaliq et al., 2014). Contrary to ectotherms, endotherms regulate body temperatures through metabolic heat production in response to changes in ambient temperatures. Within a certain temperature range (thermoneutral zone; TNZ), thermoregulation can be done at minimum energetic cost (basal metabolism). Outside the TNZ, metabolic energy increases rapidly and under prolonged exposures can impair other fundamental processes such as growth or reproduction affecting fitness. The breadth of the TNZ is thus directly linked with the capacity of a species to both occupy a wider or narrower range of thermal environments and buffer in situ against future changes in ambient temperatures. Other than physiological thermoregulation, recent studies also suggest some scope for behavioral and genetic adaptation, and phenotypic acclimatization to climate change in endotherms.

In the absence of physiological thermoregulation, metabolic rate in ectotherms is tightly linked to change in ambient temperatures (lack of TNZ), relaying on other forms of adaptation instead. Marine ectotherms (e.g., most fish) appear to be thermal range conformers, with minimum and maximum ambient temperatures at both cold and warm range boundaries closely matching their thermal tolerance limits (Sunday et al., 2012). This pattern is, however, not followed in terrestrial ectotherms (e.g., lizards), which tend to overfill their potential niches at poleward range boundaries (i.e., appear at higher latitudes that would be expected based solely on their lower thermal limit) and underfill at their equatorward boundaries. These patterns are undoubtedly related to the interplay of multiple factors including physiological (diapause or hibernation) and behavioral adaptations toward cold tolerance, other climate variables setting larger physiological constraints than those of temperature at warm trailing boundaries in terrestrial ectotherms (e.g., water availability), or the role of competitive exclusion being stronger at trailing range boundaries (Sunday et al., 2012). Regardless of the mechanism, this supports greater responsiveness and equally frequent range shifts at both poleward (expansions) and equatorward (contractions) range boundaries in marine ectotherms, whereas in terrestrial ectotherms contractions of equatorward range boundaries are lagging climate warming. Predictions of future range shifts on marine species based solely on the effect of temperature change should be then more accurate and less context-dependent than those of terrestrial species. A related implication is that the effect of climate warming on species' distribution shifts, being ecto- or endotherms, must be placed in context with where those changes in temperature fall within the thermal tolerance breadth of a species. Changes may be rapid or large but still remain well within its tolerance range having, from a physiological point of view, little impact on the species and causing no direct changes in the distribution of local populations (**Fig. 2B**), though these might still occur indirectly (e.g., changes in biotic interactions). This offers one possible reason for the lags in shift response to warming often observed in otherwise highly mobile taxa such as birds (Khaliq et al., 2014).

Species range dynamics are governed primarily by the two opposing processes of expansions and contractions (**Fig. 2B**). Range expansions refer to the new occupation of areas beyond a species' current range that become climatically available at some point in time. If we simplify climate change to the effect of warming, this essentially implies that ambient temperatures increase above the lower thermal limit of the species. However, other than temperature, the biotic and abiotic conditions at the colonizing location must be adequate for the species to settle and survive, while such localities outside its current range must be within reach of the dispersal capacity of the species. Where all these conditions are met, new populations will increase, consolidating the expansion of the range and, as ambient temperatures move within the pejus temperatures (**Fig. 2B**), becoming stable. At the other extreme, range contractions are triggered from within the existing range of a species as ambient temperatures start to move toward the upper thermal limit of the species. Initial declines in performance lead to population decrease and eventually, as temperatures move beyond the upper thermal limit, result in local extinctions contributing to range contraction.

Biogeography and Climate Change

Biogeography is the study of the distribution of species and ecological systems across the globe and through time. There are several well-documented spatial patterns in biodiversity, perhaps the broadest of which being the latitudinal gradient in the number of species per unit area or species richness. At the global scale, species richness generally tends to decrease from the equator to the poles. Tropical regions tend to have high species richness, especially rainforests on land and warm-water coral reefs in the oceans where high numbers of small-ranged flora and fauna occur. At the other latitudinal extreme, polar regions contain fewer species, which also tend to be range-restricted and adapted to life in low temperatures with long, dark winters, and high seasonal variability in food availability. This global paradigm is nonetheless not without exceptions, particularly when focusing on specific taxonomic groups or habitats. For example, taxonomic groups like cetaceans and pinnipeds exhibit peaks in richness at respectively mid- and high latitudes (Tittensor et al., 2010). Similarly, continental shelves and coastal waters tend to have high species richness with biodiversity concentrating at several tropical "hotspot" regions containing species-rich ecosystems such as coral reefs, seagrasses, and mangroves (e.g., the Indo-Pacific or the Caribbean). By contrast, the open ocean has lower number of species, though here sampling effort is much lower and specific habitats such as abyssal regions are strongly underrepresented, concentrating across broad mid-latitudinal bands in all oceans.

Though regionally freshwater species richness typically decreases with increasing latitude, the high diversity and endemism of freshwater ecosystems stem largely from the fact that fresh waters are embedded within a terrestrial landscape that limits dispersal within and among drainage basins. These factors underlie an interesting observation: at regional to global scales, most freshwater species occupy only a fraction of the localities where they might otherwise thrive. This constrained geography is at least partially responsible for the fantastic diversity of freshwater organisms seen around the world. Freshwater organisms, such as fishes, are subject to several biogeographic constraints that are unique to the aquatic realm. Their ability to move in response to climatic change is constrained by the dendritic arrangement of riverine ecosystems, as well as a variety of physiographic barriers. Consequently, large-scale natural range expansions of fishes are typically the result of rare opportunities associated with drainage rearrangement, temporary connections between drainages by freshwater plumes into oceans, and remote possibilities for random dispersal by "rains" and accidental movement by terrestrial organisms (Olden et al., 2010).

Global patterns of spatial turnover in the occurrence of species, that is, the gains and losses of species between locations, are necessary for understanding important ecological questions such as scale-dependent relationships in species richness. Studies conducted on different terrestrial taxonomic groups have focused on the relationship between turnover patterns and environmental gradients. Strong gradients tend to correspond to high species turnover, though evolutionary history, dispersal, and the geographic range sizes of the species are all important drivers (Buckley and Jetz, 2008).

Biogeographic patterns are also scale-dependent. At broad spatial scales, climate tends to play a large role in determining the distribution of species, biodiversity patterns, and the distribution of communities and biomes. For example, temperature has been identified as the only consistent cross-taxa predictor of global patterns of marine life, while temperature and precipitation, in conjunction with soil characteristics, drive broad-scale patterns of vegetation types as well as influence the distribution of individual plant species. Some physiographic regions have higher richness than others, and finer scale patterns of richness have been found to be associated with elevation, moisture, precipitation, and energy gradients on land, or with thermal fronts and dissolved oxygen in the ocean, as well as with distance from a mainland. At finer scales, however, patterns become increasingly dependent on the effect of other abiotic and biotic drivers, over and above the effect of climate, such as habitat availability and biotic interactions.

Climate as Major Driver of Biogeographic Shifts

Expectations for Climate-Driven Range Shifts

Many factors can influence species' responses to changes in the environment, including species' generation time, dispersal ability, physiological tolerances, habitat and food preferences, and the composition of existing or receiving communities in the case of range shifts. Nevertheless, the physiology of an organism with regard to limiting climatic variables, primarily temperature and precipitation (on land), still represents a main biogeographic driver, particularly in ectotherms. As environmental conditions move away from a population's optimum, organisms may compensate for those changes to avoid its extirpation. Several mutually nonexclusive adaptation strategies are available. These include embracing the environmental changes via physiological, behavioral, or morphological in situ adaptation, or avoiding them by shifting their phenology or geographic distribution to remain within optimal environmental conditions.

Climate change can make currently occupied habitats hostile for species survival, resulting in local population extinctions and range contractions, or make areas beyond the current margins of species distribution climatically available, thus facilitating the expansion of the species via dispersion and colonization. The process by which species shift in time or space to remain within their preferred environmental conditions is known as niche conservatism. It creates the simplest expectation for species responding to climate change by shifting their geographic distribution toward cooler environments under warming, that is, higher latitudes and greater elevation on land and deeper waters in the ocean. These overarching patterns have indeed been widely documented in marine, terrestrial, and freshwater biota albeit with large variability in response.

Stemming from the evidence above, climate landscape metrics quantifying different dimensions of spatiotemporal change in climatic conditions have been applied to generate expectations for the future redistribution of biodiversity patterns. For example, the velocity of climate change (Loarie et al., 2009), describing the speed and direction of geographic shifts of isotherms (lines of equal temperature) over time, has been used in different global analyses to highlight the pace of climate change that species should track to remain at the same climatic conditions in the future (Burrows et al., 2011), to reveal climatic connectivity patterns in relation to potential changes in species distributions (Burrows et al., 2014), and to project the future redistribution of global marine biodiversity (García Molinos et al., 2016).

Climate-Driven Range Shifts in the Anthropocene

Global climate has warmed by 0.74°C since preindustrial time, generally taken to be around 1750, with most of this warming occurring over the last 60 years. To put this in context, the Paris Agreement of the 21st Conference of Parties (COP21) to the United Nations Framework Convention on Climate Change (UNFCCC) pledges to avoid dangerous anthropogenic climate change, accepted at 2°C of warming by century's end, and to pursue efforts to limit the temperature increase to 1.5°C as a threshold associated to significantly lower risks and impacts from climate change. An anthropogenic signal in warming has now been detected on every continent and in every ocean, and widespread impacts around the world are evident.

Marine

Species range shifts in response to anthropogenic climate change have been observed from tropical seas to polar oceans (Parmesan and Yohe, 2003, Poloczanska et al., 2013). In the marine environment, climate-driven distribution shifts can be facilitated or limited by a range of other factors such as ocean currents and fishing pressure. Major ocean currents have been implicated in the observed range shifts of multiple plankton, fish, and invertebrates in south-west Pacific, north-east Atlantic, and the north Pacific. However, changing temperature remains a major driver of these shifts enabling larvae and juveniles to survive and thrive in new environments (García Molinos et al., 2017). Marine species occupy a three-dimensional environment and shifts in depth are also observed in response to warming, for example, where coastlines block latitudinal range expansions, where bottom-living species are moving over seabed topography, or where pelagic species retreat to cooler/warmer depths (see http://oceanadapt.rutgers.edu/regional_data/ for tracking over time of the changes in marine animals in US regions). For example, in the Gulf of Mexico where northern coastline limits poleward distribution shifts, fish and invertebrate assemblages have moved to deeper, cooler waters (Pinsky et al., 2013).

The North-East Atlantic is one of longest and best-studied marine regions that has undergone periods of warming and cooling over the 20th century with the most rapid warming occurring since 1980s. Rapid warming also occurred over the 1920–1940s, when temperatures and warming rates were comparable to today, with broad impacts that lasted some 30 years. Range expansions northward were recorded across plankton, fish, and marine mammals as a result of changes in wind fields, ocean currents, and/or the expansion of thermal habitats. Considerable concerns were raised within the scientific community regarding the stability of the ecosystem and the economic consequences. For example, cold-water fish such as cod and haddock declined or were replaced with less valuable warm-water species, accompanied by a reduction in fishing activity. However, with the subsequent cool period in the 1960s, distributions expanded southward once more and scientific discussion abated. With warming in recent decades, poleward distribution shifts are again observed across plankton, benthic invertebrates, and fish. For example, the range limit of the warm-water copepod (plankton) community in the north-east Atlantic shifted over 10 N (> 1000 km) since 1960s (Beaugrand et al., 2002). What should be noted is that warming in recent decades contains a strong anthropogenic signal, and the influence of anthropogenic forcing will underlie future natural fluctuations in temperature exacerbating warming rates in some periods.

Terrestrial

Many recent distribution shifts have been documented in terrestrial species (Parmesan and Yohe, 2003). For example, butterflies and birds have been observed moving poleward in Europe and in the western United States. Parmesan et al. (1999) explored changes in the poleward and equatorial ranges boundaries of butterflies. Of a sample of 35 European nonmigratory species, they found that 63% had moved poleward at rates of up to 24 km year, while only 3% had move toward the equator. A complementary analysis on 40 species focusing on the trailing lower latitudinal edge showed 22% having range contractions whereas only 5% expanded toward the equator. Thomas and Lennon (1999) documented shifts in bird species in Britain over a 20-year period. They found that species with southerly ranges moved north an average of 0.95 km year. In contrast, bird species with ranges limited to the northern portion of Britain showed no systematic contractions at their southern boundaries. However, latitudinal ranges often do not capture the real extent of ongoing shifts. Measuring range shifts on 360 degrees axes, Gillings et al. (2015) found that calculated poleward range expansions for 122 British breeding birds, 13.5 km over 20 years, were largely underestimated because they ignored common and larger north-west and north-east shifts.

Shifts in elevation have also been described concurrently with those in latitude in many terrestrial species. Many plants have been observed to have shifted their optimal elevation (elevation with the highest probability of presence) over the past century. In a study that examined elevational distributions of 171 plants species in Europe, Lenoir et al. (2008) documented an average rate of upward movement of 27 m per decade. These movements were greatest in grasses and species restricted to mountains. Elevational and latitudinal shifts in tree line have been observed on multiple other continents. There is also clear evidence that birds and mammals are shifting their ranges upward in elevation in ways that are consistent with recent changes in temperature. Moritz et al. (2008) resurveyed elevational transects in Yosemite National Park in the western United States that had originally been surveyed by Joseph Grinnell at the start of the 20th century. They found that half of the mammal species sampled had shifted their ranges upward in elevation—either with a contraction at the lower elevation edge of their range, an expansion at the upper elevation edge, or both. The majority of the remaining species showed no shift in their distributions.

Freshwater

Recent research points to the strong evolutionary and environmental determinants of freshwater fish thermal tolerances (Comte and Olden, 2017), thus supporting the fact that freshwater fish are already on the move in response to past climate change. Hickling et al. (2006) was the first to show a general elevational shift, averaging 13.1 m decade, for 15 species of British fishes. Comte and Grenouillet (2013) examined the distributional changes of 32 stream fish species in France and quantified potential time lags in species responses according to rates of isotherm shift in elevation and stream distance. Fish species displayed dispersal-driven expansions along the altitudinal gradient at their upper range limit (61.5 m decade); a response that exceeds the majority of past range shifts of terrestrial species (Parmesan and Yohe, 2003). Upstream movements were greater at the downstream limits (6.3 km decade) than at the upstream limits where a mean downstream shift across all species was observed (0.5 km decade). Similar to North American streams (Isaak and Rieman, 2013), climate change velocities in French streams indicated that isotherms shifted during the last decades about 41–74 m decade toward higher elevation, and about 1–17 km decade along the upstream–downstream gradient, as air temperature increased by 0.24 C decade. Therefore, despite being consistent with the geographic variation in climate change velocities, this study revealed that the majority of stream fish have not shifted at a pace sufficient to track changing climate, in particular at their range center where range shifts lag far behind expectation. Recent evidence suggests that responses of individual fish species vary considerably (also related to nonclimatic factors) and that range shifts are associated, in part, to species' traits. For example, the persistence of populations in climatically unsuitable areas was greater for short-lived species, whereas the extent of the lag behind climate change was greater for long-lived, restricted-range, and low-elevation species (Grenouillet and Comte, 2014). Moving forward, it is becoming clearer that understanding the extent to which phylogenetic constraints and adaptive evolutionary forces help define the physiological sensitivity of species is critical for anticipating climate-related impacts in aquatic environments.

Attribution to Anthropogenic Climate Change

Attributing anthropogenic climate change as the driver of shifting species distributions is challenging for many reasons including the capacities of organisms to adapt to local environments, that climate change is one of many drivers acting on species, the paucity of long biological time-series in most cases, and the mismatch between the spatial and temporal scales of biological and climatological measurements. One approach to overcome these limitations is metaanalysis, in which data from a large number of studies are analyzed together (e.g., Parmesan and Yohe, 2003; Poloczanska et al., 2013; García Molinos et al., 2017). If responses across many regions are shown to be generally in the same direction (e.g., poleward distribution shifts) then confidence in a global driver, climate change, is high.

Other approaches rely on intensive studies focused on single species or regions that may not be possible in many cases for the reasons outlined. One example where attribution to anthropogenic climate change has high confidence is the poleward shift of the sea urchin *Centrostephanus rodgersii* in south-east Australia. This urchin expanded its distribution from mainland Australia to Tasmania during the last 40 years where it consumes kelp beds with deleterious effects on local biodiversity and rock lobster fisheries (see https://www.youtube.com/watch?v¼t6nbR0te370). Multiple lines of evidence from anecdotal observations, long-term oceanographic and biological monitoring, laboratory and field experiments, genetic analyses, and ocean-atmosphere and ecological modeling studies point to the role of anthropogenic climate change.

Projecting Range Shifts Under Future Climate Change

Anticipating how, when, and where species will respond to projected changes in climate is critical to conservation planning and natural resource management. Projecting the future distribution of species is possible using models based on both direct (correlative) and indirect (mechanistic) attribution. Where the abiotic factors limiting the distribution of a species and its corresponding physiological tolerances are known, mechanistic relationships can be used to predict distributions based on future climate conditions independently from the actual distribution of the species (i.e., fundamental niche). In the absence of mechanistic information, correlative approaches statistically relate locations of known occurrence, and possibly known absences, for the species to environmental data to infer abiotic correlates of current species' ranges (i.e., realized niche).

Modeling Approaches: Balancing Realism and Complexity With Conservation Urgency

Niche concepts and theory, in the form of species distribution models (SDMs) or ecological niche models, have become central in efforts to understand how future environmental change may impact species and their habitats (Elith and Leathwick, 2009). Broadly, these models derive correlative relationships between current species distribution data and suites of environmental variables to forecast species distributions in space (e.g., in an alternate region) or time (e.g., under a climate change scenario). Where the predictor variables are exclusively or eminently climatic, these models are called climate niche or envelope models. Because of their relative simplicity and versatility, SDMs have been widely used to project the potential effect of future climates on both individual species ranges and global scale biodiversity patterns involving large numbers of species. However, they are subject to many well-known limitations and remain subject to criticism (see the next section).

Alternatively, mechanistic or process-based models linking physiological tolerances to environmental conditions, or even more sophisticated approaches incorporating demography, dispersal, or competitive interactions, have been applied at the level of individual species and populations from regional to local spatial scales. Emblematic, indicator, or commercially important species, for which sufficient knowledge and research funding are available, are often involved. For example, Xu et al. (2012) used a spatially explicit, dynamic forest landscape model coupled with an ecosystem process model to predict future changes in colonization and competition dynamics among 13 northern Minnesota tree species in response to climate change and different disturbance regimes (extraction and fire). Similarly, researchers have also forecast shifts and changes in biomes or vegetation types using different modeling approaches. Several studies have used simulation models such as dynamic global vegetation models to simulate responses of basic plant functional types to changes in climatic conditions and atmospheric carbon dioxide concentrations. These models simulate plant growth and competition as impacted by water and nutrient availability, temperature, light availability, and carbon dioxide concentrations. They can also take into account fire and other disturbances. In the ocean, Watson et al. (2015) developed a global size-based food web mechanistic model that incorporates plankton and fish dynamics accounting for trophic links and movement of fish species to predict the abundance and distribution of global fish biomass. This model is currently being tested for disentangling the contribution of anthropogenic forcing toward variability in commercial fish recruitment and population biomass.

Between both extremes, hybrid approaches are becoming increasingly common, where correlative and process-based models are coupled (e.g., dispersal, competition or disturbance, and population dynamics) to projected future changes in the distribution of species inferred from abiotic correlations. A good example is the dynamic bioclimate envelope model developed by Cheung et al. (2009). This model predicted changes in regional and global biodiversity of several hundreds of commercial marine fish and invertebrate species and related fishery catches under future climate change. This model has been used to inform climate change risk associated with fisheries in the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, https://www.ipcc.ch/report/ar5/wg2/). Enhancements to the model include the additional elements of species physiology, life history, distribution, and population dynamics.

Assumptions and Limitations of SDMs

Information on changes in distributions expected under climate or environmental change alone is useful for capturing general trends and assessing potential risk, with which to inform more detailed analyses or prioritize monitoring efforts. The simplicity of correlative SDMs comes nevertheless at the price of several important assumptions and limitations:

1. By focusing exclusively on abiotic correlates they ignore all the other multiple determinants of species distributions that are likely to interact with climate change in shaping distributions, especially at small local spatial scales. Biotic interactions can condition range shift responses to climate change in many different ways. An extreme example is that of specialized mutualists,

parasites, or predators limited in distribution to that of their partners or hosts. Similar range dependency can be expected for any species that depends on others for food or habitat, for example the many fish species that are strict coral-reef dwellers. Several experiments have also shown how thermal tolerances of different species can be modified, often narrowed, under both intra- and interspecific competition. On the other extreme, range expansions can also involve positive effects through enemy release or decreased competition potentially enhancing expansion rates in response to warming. Human activities can also interact with climate in defining distribution shifts. For example, recent evidence suggests that the shift in distribution of the Atlantic Cod (*Gadus morhua*) over the last 100 years in the North Sea is consequence of a combination of warming and fishing pressure (Engelhard et al., 2014).

2. They assume species geographic ranges are at equilibrium with the environment. This assumption implicitly creates the uncertainty in predicting distributions outside the range of conditions for which models are calibrated (i.e., future novel non-analogue environments).
3. They assume full occupation of future suitable habitats. However, colonization of new habitat becoming climatically available to a species is dependent on those areas being within the reach of the species either by its own (dispersal) or assisted (natural or anthropogenic) means. In the first case, dispersal capacity is dependent on multiple factors including dispersal mode and length of dispersive life stage (e.g., days vs months), demography (fecundity), and external directional forces, like winds or ocean currents, that are critical for species with limited or passive dispersal capacities and/or narrow dispersal temporal windows. Landscape connectivity is also a key factor in understanding dispersal routes and potential that can be effectively incorporated into SDMs (see http://maps.tnc.org/migrations-in-motion/#4/18.98/-78.00).
4. Accuracy of predictions is highly dependent on selection of a biologically meaningful set of environmental variables, since we are assuming those variables set the range limits of species. For example, sea surface temperature is by far the climate variable used most frequently for predicting range shifts in marine biota, yet temperatures in benthic habitats can differ substantially not only in magnitude but also in spatiotemporal patterns. Similarly, climate extremes can have far larger implications for physiological stress, hence range dynamics, than mean estimates, while effects of other climate change-related processes such as ocean acidification are largely unknown but likely to interact with warming.
5. Mechanisms mediating range shifts such as genetic adaptation and phenotypic plasticity are not accounted for (this is also a typical limitation of process-based models).

Given all these limitations, the use of different models is recommended for exploring uncertainty in projected distributions. Moreover, given uncertainties in climate projections, reporting on the sensitivity of SDMs to the inputs of different General Circulation Models and greenhouse gas emission scenarios is important.

Biodiversity Scenarios Under Future Climate Change

Given current trends in greenhouse gas emissions are currently tracking slightly above projections for the IPCC top-end emission scenario, the Representative Concentration Pathway (RCP) 8.5 (see https://www.skepticalscience.com/rcp.php for an introduction to RCPs), mid- to long-term risk assessment has mainly focused on futures involving global annual mean temperature anomalies of 2°C (~RCP4.5-6.0) or 4°C (~RCP8.5) above preindustrial levels by century's end (**Fig. 3**). However, the new global commitment of staying well below 2°C (~RCP2.6) and aiming at holding global warming below 1.5°C has refocused interest on estimating the benefits from achieving this new target (http://unfccc.int/paris_agreement/items/9485.php). In any case, the projected increase in global (sea) surface temperature is relatively insensitive to the emission path followed for the near future (~2030), though with differences in spatial trends, whereas differences in warming pathways intensify markedly over the course of the century (**Fig. 3**), which reflects on the magnitude and type of the anticipated biodiversity changes (see below). These contrasting differences between scenarios highlight the importance of the adoption of coherent and integrated measures toward reduction and stabilization of emissions by the international community.

Marine

Existing analysis on global marine biodiversity projections under future climate change anticipate an overarching pattern over the course of the century under all climate scenarios of widespread range expansions toward higher-latitude waters combined with high regional extirpation rates (García Molinos et al., 2016; Jones and Cheung, 2014). Projections under medium to high-end emission scenarios (RCP6.0-8.5) result in trends developing deeper and progressing further in time. For example, García Molinos et al. (2016) used a thermal niche model that includes climate connectivity to estimate changes in global patterns of marine biodiversity for over 12,000 species under emission scenarios RCP4.5 and 8.5 (https://vimeo.com/146125447). Range projections were driven by isotherm trajectories based on the magnitude and direction of local climate velocities (global climate velocity trajectories as kmz files are available for download at http://www.sams.ac.uk/michael-burrows), and physiological thermal limits inferred from the thermal variability existing within each species' range thus reflecting thermal niches. Biodiversity projections between the two RCPs are initially similar but diverge from mid-century when there is a transition from a prevailing global net gain to a net loss of biodiversity under RCP8.5. Under RCP8.5 expansions reach higher latitudes with net increases in species richness peaking at ~40–30°N/S, compared to the ~20°N/S of the mid-range scenario, while extirpations are more intense and spread over

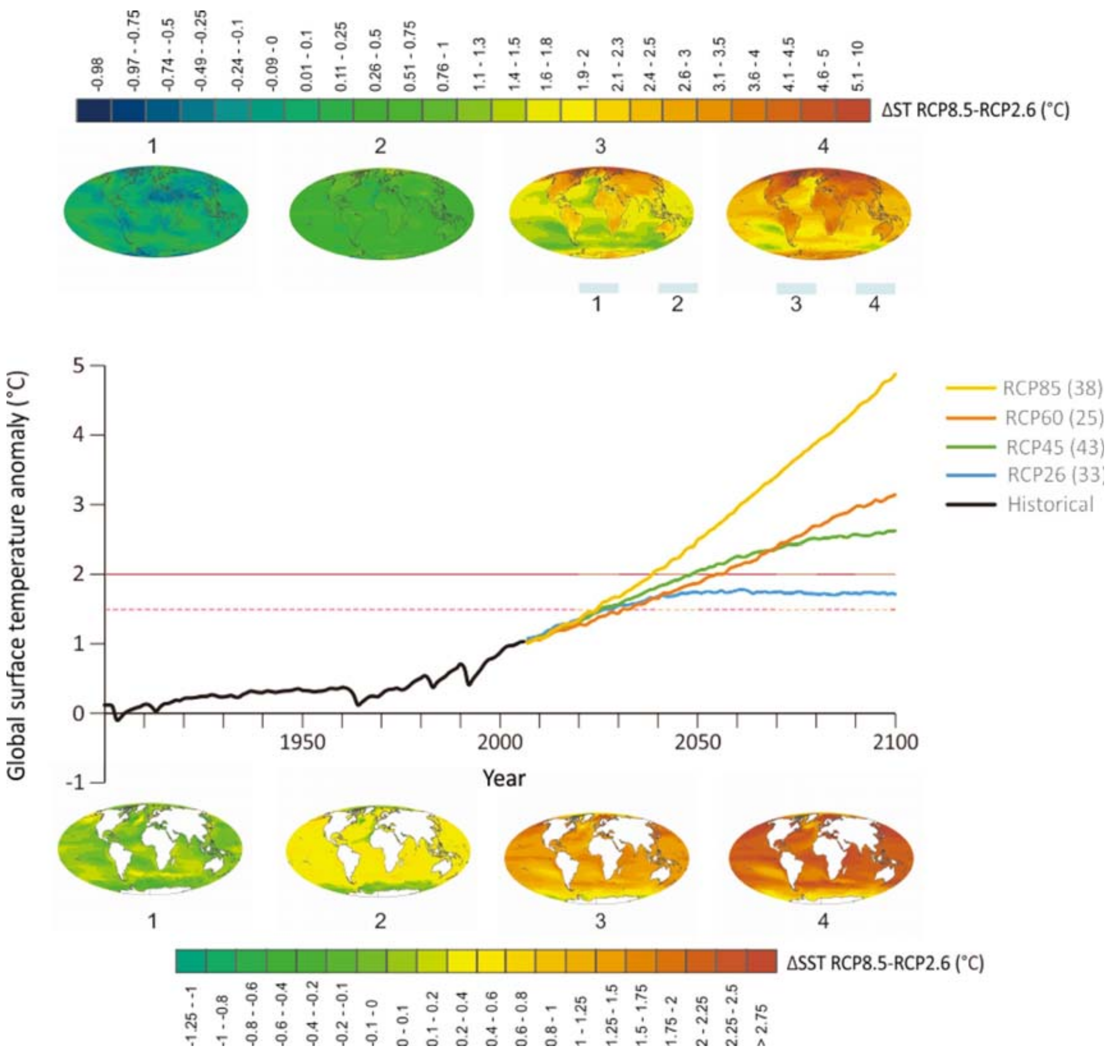

Fig. 3 Global temperature anomalies relative to the reference period 1880–1900 for atmospheric surface temperatures obtained from general circulation model mean ensembles (downloaded from https://climexp.knmi.nl/; number of models given in brackets) for each of the four IPCC AR5 RCP scenarios. An area-weighted scheme has been used to account for cell latitudinal area distortion. The global maps give differences in mean atmospheric (above) and sea surface (below) temperatures between the two extreme scenarios RCP8.5 and RCP2.6, averaged over different 10-year periods (*blue boxes* on the graph) throughout the century.

larger regions particularly in the tropics and semi-enclosed seas where movement toward higher-latitude cooler waters is blocked, such as the Persian Gulf or the Red Sea. Resulting changes in the composition of current marine assemblages are projected to be highest (> 0.5 dissimilarity under both scenarios though more widespread and intense under the RCP8.5) in the Arctic seas and northern Pacific, fueled by the arrival of species from lower latitudes, and throughout the tropics, particularly the Central Indo-Pacific, where most of the species extirpations are concentrated. These patterns of climate-induced species expansions and contractions and resulting changes in community structure are in overall agreement with those found in the modeling approach of Jones and Cheung (2014) which, based on a combination of three widely used SDMs, set average mid-century poleward latitudinal shift across 802 commercial fish and invertebrates of 15.5 and 25.6 km/decade for a low (RCP2.6) and high (RCP8.5) emission scenario. The profound rearrangement of marine biodiversity projected by the end of this century is also anticipated to enhance the global spatial homogenization of marine communities, particularly in temperate regions, where communities from currently distinct biomes will share an increasing number of species (García Molinos et al., 2016).

Terrestrial

The results of correlative SDMs have often been combined to generate projections of potential changes in species richness and turnover. Such projections have been made for plants and vertebrates on many continents. For example, depending on the climate change scenario considered, Thuiller et al. (2005) projected the potential loss of plant species richness across Europe to range from 27% to 42% by 2080 with some regions projected to experience as low as 2.5% and as high as 86%. The regions with the highest losses were projected to be around 45°N, and the regions with the lowest projected losses were at the highest and lowest latitudes in Europe. Related plant turnover rates were projected to range from 45% to 63%. Using a similar approach, Lawler et al. (2009) predicted the local loss of 11% and 17% of the vertebrate fauna (birds, mammals, and amphibians) across North and South America by 2071–2100 under, respectively, a low (B1) and mid-high (A2) emission scenario. The largest losses in fauna as a result of range contractions were predicted in Mexico, Central America, and the Andes Mountains where species loss could be as high as 50% under the mid-high scenario (A2). At the same time, large increases in species richness were also predicted for high-latitude regions and the Andes Mountains, with maximum gains reaching well over 100% under all scenarios. Assuming unlimited dispersal, rates of vertebrate turnover across North and South America were projected to be at least 25% for the lower and 38% for the mid-high emission scenarios. Confidence in these results was provided by agreement of 8 of the 10 climate models used to run the simulations. Under the same assumption of no dispersal constraints, and averaging across all climate change scenarios considered, Araújo et al. (2006) projected by 2050 an overall expansion of ranges across Europe for 31% of amphibians and 35% of reptiles and overall contractions (assuming no dispersal) for 69% of amphibians and 65% of reptiles. For amphibians, expansions were most concentrated at roughly 60°N, and contractions were concentrated between 40°and 50°N. For reptiles, patterns were more complex with both expansions and contractions forecasted to be concentrated between 36°and 53°N, but taking on very different patterns.

Freshwater

Despite their proportionally highest biodiversity and vulnerability to climate change, global studies projecting the effects of climate change on freshwater are still lacking. However, some understanding on the future effects of climate change on freshwater biodiversity can be obtained from the few existing regional studies. For example, Buisson et al. (2008) used presence–absence records in French river systems to predict the future (2080) distributions of 30 fish species under a moderate (B1 roughly equivalent to RCP4.5) and an extreme (A2 ≈RCP8.5) emission scenario. Their results suggest that cold water species would experience the greatest climate-induced reductions, whereas climate change would create new opportunities for some cool-water and warm-water fish species. As a result, the study anticipates a rapid reorganization of stream communities via strong local net increases in species richness and accelerated species turnover rates along the river network, with mean increases in richness and turnover across all sites of over 15% and 50%, respectively, for both scenarios. These effects were exacerbated under the more extreme climate scenario. Results of this study can be contrasted with those of Domisch et al. (2011) that modeled the impacts of climate change on the distribution of 38 benthic stream macroinvertebrates across the entire river network of a large catchment in Germany. They found average altitudinal shifts of 122 and 83 m by 2080 under the B2 (≈RCP6.0) and A2 scenarios, respectively. Same as with the fish projections, local extinctions were minimal under both scenarios, whereas ranges contracted primarily for headwater low-temperature species and expanded for mid- and low-reach warm-water species. These studies offer however only a partial regional vision. Similar analyses targeting nontemperate regions (e.g., tropical or arctic) are needed for gaining a more holistic perspective on the potential global effect of future climate change on global freshwater biodiversity.

Ecological and Socioeconomic Implications of Range Shifts

Ecological Implications

The immediate outcome of climate-driven distribution shifts is that of spatial changes in the abundance and/or composition of species. Species responses are highly variable among different taxonomic groups, thus increasing spatial mismatches between currently interacting species are expected to develop over time. This reshuffling of biodiversity and overlapping of ecosystem boundaries is anticipated to result initially in the spatial biotic homogenization of currently distinct communities, which could in turn lead to the eventual formation of non-analogue communities, and alter ecosystem dynamics and functioning.

The implications of these changes are still largely unknown but are related to the biological identity and ecological role of both new and extirpated species within an ecosystem. The degradation and loss of keystone and foundation species, such as reef-building corals from the combined effect of ocean warming and acidification, can significantly decrease the biodiversity and alter the structure and functioning of ecosystems, making them less resilient and more susceptible to regime shifts (e.g., changes from coral- to seaweed-dominated ecosystems). Changes in ecological networks and species interactions, particularly food webs and trophic interactions, are also of prime concern. For example, ocean warming and sea ice retreat are facilitating the arrival of large fish species with a generalist diet into arctic waters, such as cod or haddock. These species are rapidly restructuring arctic marine food webs by increasing connectance (adding trophic links) and reducing modularity through coupling pelagic and benthic habitats (Kortsch et al., 2015). On the other hand, extirpations of local biota can also restructure communities and result in cascading effects, particularly were specialized interactions are concerned (Cahill et al., 2013).

Changes in the composition and abundance of species resulting from climate-driven range shifts can also generate complex feedback mechanisms into the climate system. For example, in the Arctic, some of the best long-term documented responses to climate change correspond to the advance of boreal forested lines (trees and dwarf shrubs) into the tundra, with some estimated increases in cover at 1.2% per decade since the 1950s in the Alaskan Arctic (Sturm et al., 2001). Recent evidence suggests that this increase in woody plant coverage can trigger a number of related positive regional climate feedbacks thus accelerating ongoing warming (Loranty and Goetz, 2012). These include the mobilization into the atmosphere of soil-bound carbon from increased permafrost thaw by amplified Arctic warming via the microbial pathway, and the decrease in surface albedo and increase in evapotranspiration, leading to increase in atmospheric water vapor, resulting from higher vegetation canopy cover and productivity.

Natural Resources

Climate-induced changes in biodiversity may impact the availability of natural resources with implications for regional food supply and production. For example, wine grape production regions in Australia are located between 30 and 40°S in Mediterranean and cool-temperate climates. Wine producers are already buying land for vineyards further south as an adaptation option for anticipated warming temperatures.

It is projected that catch potentials of marine fish and invertebrates will increase 30–70% on average at high latitudes and decrease by up to 40% in tropical regions (Cheung et al., 2010). For example, the productivity of coral-reef fisheries, important for regional food securities, may decrease by 20% by 2050 due to direct species (fish and invertebrate) losses from warming and indirectly due to the climate-related degradation of coral reefs (Bell et al., 2013). Tropical regions contain not only high-density of human populations that are socioeconomically vulnerable to declines in fish but also rapidly growing populations that will increase pressures on marine resources. For example, tuna is valuable to small island states in the equatorial Pacific both as a source of food and revenue. Tuna are known to be sensitive to temperature and modeling studies project that the tuna stocks will be displaced eastward by warming, leading to gains for some small islands states and losses for others, particularly those in the western region of the equatorial Pacific (Bell et al., 2013).

Climate change is also expected to promote the spread of harmful invasive species. Using a cross-realm metaanalysis on the performance of 157 non-native and 204 cooccurring native species to varying climatic conditions, Sorte et al. (2013) found that performance in non-native species was more strongly enhanced than natives by increasing favorable conditions, which suggests higher risk of invasion at sites becoming climatically suitable under climate change. The analysis also revealed higher vulnerability to invasion by climate change in aquatic compared to terrestrial ecosystems. The arrival of new invasive species can pose serious risks not only to the biodiversity and functioning of local ecosystems but also in social and economic terms.

Conservation

Changes to the geographical distribution of species and resulting biodiversity patterns due to climate change can potentially compromise the effectiveness of the global network of protected areas in terms of the representativeness (species richness and composition), and connectivity of its constituent protected areas. For example, multiple modeling exercises predict that many existing protected areas are likely to lose suitable habitats for species of high conservation value, and that the range of these species will eventually move beyond their protected area boundaries under future climate change (Araújo, 2009). Spatial planning will need to adapt to the potential spread and loss of species and rearrangement of biodiversity patterns as a consequence of climate change. Adaptive spatial conservation approaches range from identifying and targeting areas anticipated to remain climatically suitable over a specific period of time and conservation corridors connecting them to current protected areas, to dynamic spatial prioritization strategies that combine selection and release of protected areas over time to meet conservation targets at minimum cost. The distinctions between invasive species and climate-driven expansions of native species are becoming nonetheless blurred, with implications for policy and regulation. Further, intense debate over adaptation strategies for threatened species such as assisted relocation (physically moving species to areas with suitable climate where the species does not currently occur), highlights the ethical and legislative challenges ahead. For example, the mountain pygmy possum, *Burramys parvus*, is found only in a single area of 4 km^2 of alpine habitat in southern Australia where it hibernates under snow. The area and duration of snow cover is declining rapidly, and it is argued that assisted relocation is the only viable option to ensure the long-term survival of this species. Evidence suggests that mountain pygmy possums were once found in forest habitat lower altitudes, therefore moving populations down the mountain, where more food is likely to be available year round and warmer winter temperatures may negate the need for hibernation under insulating snow may be viable. However, questions remain as to whether the populations could adapt to new food sources and avoid predation risk.

Human Health: Pathogens and Disease Spread Under Warming

Climate change is expected to increase the geographic range and burden of disease associated with temperature-sensitive pathogens and disease vectors such as *Vibrio* bacteria and harmful algal blooms (HABs) in the ocean and ticks and mosquitos on land. The links between disease outbreaks and climate change are not well known, but evidence of recent temperature-related distribution shifts in pathogens is emerging. A range of water-borne *Vibrio* bacteria cause gastrointestinal illnesses in humans (including cholera by *Vibrio cholerae*) through their direct ingestion or through consumption of contaminated fish and shellfish. The recent rise of *Vibrio* infections in northern European Seas have been linked to rapid warming of sea surface temperatures (https://www.carbonbrief.org/warming-atlantic-ocean-leads-to-rise-in-marine-bacteria). HABs of toxic algae are responsible for a variety of gastrointestinal and neurological illnesses in humans through consumption of contaminated fish and shellfish as well as the fatal poisoning of seabirds, porpoises, and other marine animals which have ingested the algae or contaminated fish and shellfish. HABs also appear to be becoming more frequent and more widespread and anecdotally changing patterns have been linked to climate change.

Expansions in the distribution of several pathogens or their vectors have been observed on land, including tick-borne encephalitis in Sweden, the ticks which carry Lyme disease in eastern Canada, and malaria in the western Kenyan highlands (Ostfeld and Brunner, 2015). As the climate warms, the expansion of mosquitos and ticks is expected to expand the risk of malaria, dengue fever, and other diseases to new regions where vigilance and health system response plans may be ill-prepared for new threats (McMichael, 2013). As well as the risks to human health, the economic and social costs can be locally high, for example, as fisheries are shut and aquaculture production is lost during *Vibrio* outbreaks. At present, around 3.8 billion people live in areas which are climatically suitable for the malaria mosquitos. By 2080, accounting for both climate change and population growth, this number could be as high as 8.9 billion.

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