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# Mechanisms, detections, and impacts of species redistributions under climate change

Nature Reviews Earth and Environment

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## Abstract

Shifts in species distributions are a common ecological response to climate change, with global temperature rise often hypothesized as the primary driver. However, the direction and rate of distribution shifts are highly variable across species, systems, and studies, complicating efforts to manage and anticipate biodiversity responses to anthropogenic change. In this review, we summarize approaches to documenting species range shifts, discuss why observed range shifts often do not match our expectations, and explore the impacts of species range shifts on nature and society. We use *BioShifts*, a global database of range shift observations, to show that while a majority of documented range shifts are directionally consistent with climate change, large variation remains, with many species not shifting, or shifting in directions opposite from temperature-based expectations. These lagging or expectation-contrary shifts might be explained by additional biotic or abiotic factors driving range shifts, including additional non-temperature climatic drivers, habitat characteristics, and species interactions, all of which are normally unconsidered in range shift documentations. We build the case for three suggested pathways for future research in the field: (i) increasing and connecting observational biological data, (ii) generalizing range shift patterns across systems, (iii) and predicting shifts at management-relevant timescales.

## Introduction

Species geographic ranges vary across the tree of life and are dynamic expressions of multiple factors. Abiotic conditions, such as temperature and light, are considered to set the bounds of a species' *potential range*: the set of areas where abiotic conditions do not exceed the physiological limits of population sustainability of the species<sup>1</sup>. Dispersal limitations, habitat availability, and biotic factors can further limit potential ranges into *realized ranges*: subsets of environmentally suitable areas where a species actually lives<sup>2-4</sup>. While ranges are often illustrated as single units, they are perhaps more usefully conceptualized as populations distributed across space that experience different levels of climatic stress<sup>5</sup>. As temperature

conditions broadly exhibit a large-scale gradient across the globe, species' ranges typically span from a "warm edge" (normally equatorward, downslope in elevation, or shallower in water) to a "cold edge" (normally poleward, upslope, or deeper in water), where conditions experienced by populations can vastly differ (Box 1). Although species might not be directly limited by temperature at either edge and might not be at equilibrium with their environment, populations in these regions will experience different levels of temperature stress and can have different or contrasting responses to temperature change<sup>6,7</sup>.

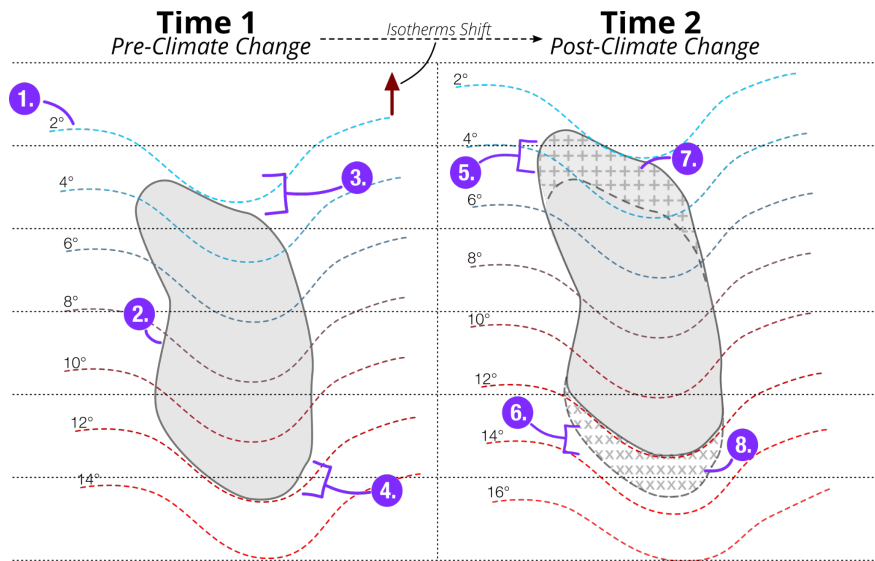
Anthropogenic climate change is causing global temperatures to warm on average, sending temperature isolines, or isotherms, shifting across Earth's surface, and altering conditions that organisms experience<sup>8</sup>. At warm edges of species ranges, where individuals are already living near their upper range-wide temperatures, climate warming is expected to cause populations to decrease in growth, reproduction, or survival, diminishing occupancy and contracting the range edge towards the center (i.e. local extinction at the trailing edge). By contrast, at cold edges, where individuals are living near thermal minima, climate warming can relax constraints on organisms (e.g., becoming warm enough for early-life development<sup>9</sup>), allowing for increased survival and persistence of populations and facilitating expansion of the range edge away from its center<sup>7,10</sup> (Box 1). Together, these changes lead to the expectation that species will shift their distributions towards previously cooler regions as global temperatures warm, leading to range shifts towards higher absolute latitudes, higher elevations in mountains, and deeper waters in oceans<sup>11,12</sup>.

Range shifts are now recognized as a common climate-driven phenomenon with varying impacts on ecosystems, economies, and people<sup>13,14</sup>, yet there is immense variation in the rate and directions of range shifts observed globally<sup>12,15-19</sup>. Although range-shifting is on one hand a mechanism by which species (and biodiversity) can persist through climate change, an increasingly unstable distribution of life challenges how we interact with, plan to manage, and conserve natural systems. Anticipating range shifts in species of particular ecological, economic, or health concern will be key to successfully adapting to climate change. Moreover, species redistributions and the human responses to them have been linked to a range of social equity imbalances<sup>20,21</sup>, underscoring understanding of species shifts as an important goal for a sustainable future. Better mechanistic understanding of processes driving and limiting range shifts will increase our ability to respond and learn from them.

In this review, we draw together knowledge of species redistribution processes, summarize the history and methods by which we have detected species' range shifts, and review mechanisms thought to underlie variation in observed rates and directions, from ecological and evolutionary factors to detection methods. We use *BioShifts*<sup>22</sup>, a global database including over 26,000 empirical estimates of latitudinal and elevational range shifts compiled from published

literature, to demonstrate general trends, knowledge gaps, and observation biases in range shift documentations. We briefly summarize the impacts of range shifts on natural and human systems as an update to a previous review<sup>13</sup>. We end with a case for areas for improvement in range shift detections and three exciting avenues for future research.

Box 1: Key terms



1. **Isotherm:** isolines connecting areas of equal temperature conditions across space, either at a given instance or as a summary of conditions over time (e.g., annual mean temperature).
2. **Range edge:** peripheries of a species' geographic distribution. Range edges (also called range margins, or limits) move across space in response to environmental change, and this process is termed "range shifting." Range edges can be difficult to define in space (see Box 2) and may not be set by current climate conditions, but denote the distributional limit for the species.
3. **Cold Edge:** the edge of a species distribution range located at the colder end of the temperature gradient, often the poleward or upslope edge.
4. **Warm Edge:** the edge of a species distribution range located at the warmer end of the temperature gradient, often the equatorward or downslope edge.
5. **Leading Edge:** of a shifting range, the edge experiencing expansions, thus "leading" a range shift. Under climate change, this is normally expected to be the cold edge of the species range, where abiotic constraints will ease with warming.
6. **Trailing Edge:** of a shifting range, the edge experiencing contractions, thus "trailing" a

range shift. Under climate change, this usually refers to the warm edge of the species range, where warming makes regions of the past range increasingly unsuitable for the species

**7. Range Expansion:** dispersal and establishment of populations in areas where individuals were not consistently present. Climate change is expected to cause expansions when areas beyond the cold limit warm above the suitable threshold for the species. Also commonly termed “range extension”.

**8. Range Contraction:** population declines or extirpations (i.e., local extinction processes) at the edge of a species range, causing the edge to contract towards the center. In climate change scenarios, contractions are expected to occur, for example, when environments at the warm edge of a species range warm past the upper temperature threshold of the species such that populations are no longer viable.

## Section 1 Observations of Climate-Driven Range Shifts

Connections between climate and species distributions have long been documented in the scientific literature<sup>23</sup>. Throughout the early-to-mid 1900s, changes in biogeographic ranges were observed in association with local periods of warming and cooling, extreme weather events, and land-use changes (many of these early studies reviewed in <sup>24</sup>). These early observations of range changes shed light onto when and where specific factors limit species ranges<sup>25</sup>. Decades later, the onset of increasingly rapid and consistent global warming (for example, at increased rates beginning in the early 1980s) provided a large-scale- if pseudo-replicated across earth - experiment in which to test the impacts of climate conditions on species redistributions in natural environments<sup>26</sup>.

The first contemporary observations of climate-driven range shifts were probably made in a non-scientific context, for example, by fur trappers, fishers, or people with close economic or cultural connections to species. In fact, in some cases, such information (e.g., fur trade figures, traditional ecological knowledge) has been used to reconstruct species' historical ranges in large-scale biogeography studies<sup>27-29</sup>. The first wave of scientific papers attributing range shifts to anthropogenic climate change occurred in the 1990s. These studies first observed changes in species distributions near range edges or shifts in thermal affinities among community members at static locations<sup>28,30,31</sup>, and eventually whole ranges shifting in response to climate change<sup>11</sup>. Since then, range shifts have been observed across many taxa and environments<sup>15,19,22,26</sup>, emerging as a widespread ecological response to climate change.

## 1.1 Measuring climate-driven range shifts

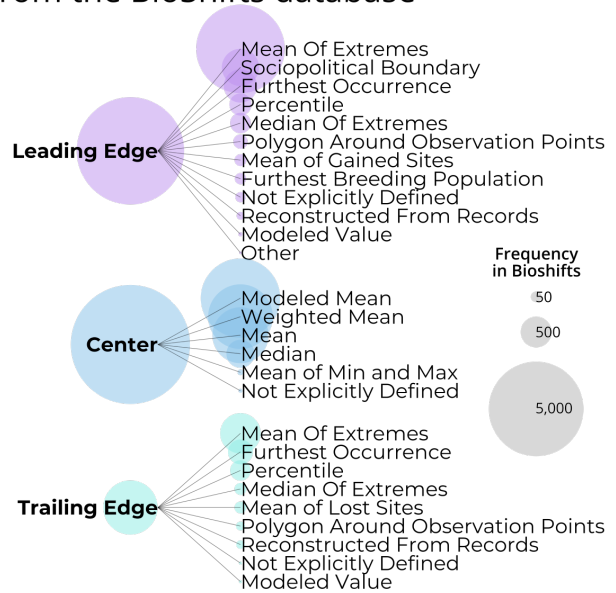
Estimating species distribution changes in response to climate change over time requires knowledge of where species currently are as well as where they once were, and ideally, climate variables over the relevant time period. In some exceptionally data-rich taxa and regions, this knowledge has been obtained by systematically monitoring occurrence and/or abundance of species with regular sampling at large spatial and temporal scales (e.g., National Oceanic and Atmospheric Administration fish trawls, used by <sup>32,33</sup>, Breeding Bird Surveys used by <sup>34</sup>, and the UK Butterfly Monitoring Scheme used by <sup>35</sup>).

When such high-resolution time series data are not available, species range movements can instead be inferred in other ways. When survey data are available in the present but not in the past, natural history records and museum collections can be used to reconstruct past species ranges to estimate distributional shifts<sup>36,37</sup>. When species range survey data are available in the past, conducting targeted re-surveys in the same regions years to decades later has been a relatively common method for assessing distribution changes<sup>38,39</sup>. When data are available over broad temporal, but not spatial scales, assessing change in biogeographic communities at fixed locations<sup>30,40</sup> can show relative abundance changes as “cross-sections” of shifting species ranges. Conversely, when data are available at broad spatial, but not temporal scales, comparing distributions of life stages of organisms at one point in time (e.g., seedlings versus adult trees<sup>41-43</sup>) can reveal distributional changes in new versus old growth. Finally, new techniques such as telemetry<sup>44</sup> and citizen science observations can help to detect range shifts in not-previously-conventional ways<sup>45,46</sup>. These different methods have allowed rapid documentation of biogeographic change across regions and systems, together identifying range shifts as a relatively ubiquitous “fingerprint” of climate change<sup>12,47</sup>, but variation among methods has caused difficulty in synthesizing and comparing studies globally.

Box 2: Defining Ranges in Space

Range shift studies have taken a practical yet varied approach to defining range limits and centers despite an extensive literature on how species ranges could be defined<sup>48-51</sup>, and these variations could influence downstream comparisons. Methods commonly used to define species ranges in biogeography research include mapping based on gridded occurrence records, creating convex polygons or linear extents along a transect from irregular observation points, and more recently, using species distribution models to infer distributions based on environmental parameters when observational data are limited or disparate (reviewed in <sup>52</sup>). Each of these methods are further affected by the definition of viable occurrences which are used as input data. For example, depending on the resolution of the underlying data, the edge of a species range might be defined as the furthest straying individual at any life stage, the mean among multiple extreme individual observations, a high percentile among all observations, or the furthest known reproductively viable population (see figure). In addition, depending on the location and spatial extent of the study, the “range edges” or “range centers” defined within the study do not always represent the range edge or center of the global distribution. These varied definitions may cause problems when comparing findings between studies or even between sampling periods within studies, and can have a greater effect on range edges (that are defined by a lack of observations) compared to range centers<sup>53</sup>.

### Latitudinal Range Section Definitions from the BioShifts database



Practicality often calls for different definitions of range edges and centers for different data types. If a study relies on data from only a few sampling locations over a large timescale, a range edge defined as the furthest sampling location where the species is found may be appropriate. Alternatively, if a study uses high-resolution data such as regularly sampled grid cells over a continental scale, the authors may define the range edge as the average position of some percentile of occupied cells. In over 16,000 latitudinal range shift estimates included in the BioShifts database<sup>22</sup>, a diversity of definitions have been used for each range section, with some tendency of consensual definitions across studies (see figure). While consistency in the definition within taxa or studies can still provide estimates of shifts within studies (e.g. the location of the 95% percentile of occurrences moved polewards), differences in definitions among studies can limit the interoperability of range shift data when combining them, for example if some range definitions are more responsive to climate change than others.

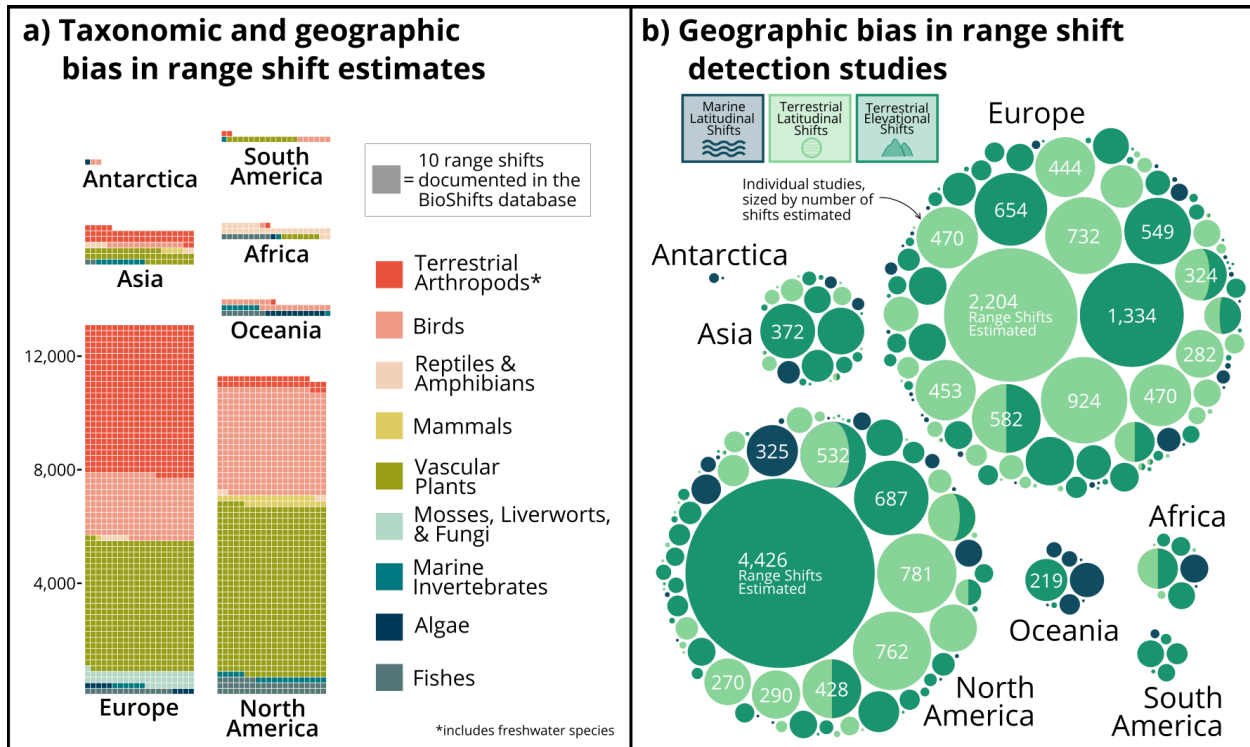


## 1.2 Where range shifts have been detected

Range shifts have been assessed across continents and ecosystems, with reported observations highly skewed geographically towards Europe and North America<sup>15,54</sup>. Indeed, among the over 26,000 latitudinal and elevational range shift estimates collated in the *BioShifts* database<sup>22</sup>, more studies appear to have been conducted and more species' ranges assessed per study in Europe and North America (Fig. 1a,b). We note, however, that the focus of this database on English-language papers could contribute to this bias<sup>55,56</sup>. Observations are also biased taxonomically, with most range shift observations documented among terrestrial arthropods (including freshwater), vascular plants, and birds (Fig. 1a). In fact, of all latitudinal and elevational range shifts included in the database, 84% were from these three taxonomic groups and measured in Europe or North America (Fig. 1a), lending a disproportionate amount of our knowledge of range shift directions and speeds to a limited set of species, mostly in the Global North.

In addition to spatial and taxonomic bias, the range shift estimation effort has been unequal across ecological realms. The vast majority of estimates have been made in terrestrial systems, with fewer than 5% of all shifts in the *BioShifts* database in marine systems (Fig 1b, 2). Because marine and terrestrial species interact differently with their environments, it is likely important to generalize within each realm rather than across them. It is further plausible that freshwater species could show different responses to climate change than their terrestrial counterparts, but the terrestrial/freshwater distinction can be difficult to make as many terrestrial species rely on freshwater environments for certain life stages or behaviors, but are not necessarily bound to them for movement; for this reason, all species that live all or part of their life cycle in freshwater are considered as terrestrial in the *BioShifts* database and throughout this review.

Within species ranges, range shift estimates are made far more rarely at warm range edges compared to cold edges or range centers (11%, 41% ,and 48% of all shift estimates, respectively) (Fig 2). This bias might limit our understanding of mechanisms, as the processes driving range changes are expected to differ between sections of a range<sup>7</sup>. Assessments of range shifts encompassing both range edges within single studies are exceptionally rare – accounting for only 2% of range shift estimates in a recent continental review in Australia<sup>57</sup> – highlighting that the vast majority of our observations are capturing only glimpses of full species-range responses to climate change.



**Figure 1: Geographical and Taxonomic Biases in Range Shift Detections.**

a) Taxonomic and geographical breakdown of latitudinal and elevational range shift estimates in the BioShifts database<sup>22</sup>. Each tile represents 10 empirically-estimated range shifts of a given taxonomic group, always rounded up. b) Geographic bias of range shift studies in the BioShifts database. Each circle represents one range shift estimation study; circle sizes and inset numbers represent the number of species ranges assessed in each study, and color represents the type of shift estimated (marine latitudinal, terrestrial latitudinal, and terrestrial elevational shifts). Note that one species may have multiple appearances in a study if the study assesses multiple parts of the species range, or estimates shifts over multiple time periods, and a study may be represented in multiple continents if the study area spans across them.

### 1.3 General findings on range shifts

The direction of collated latitudinal and elevational range shift estimates in the BioShifts database are remarkably variable. Within the database, most range shift estimates (59% of all estimates) were in the direction expected based on local temperature change (here defined as the direction of isotherm shifts over time in the study region). Still, a high proportion of shift estimates (35%) are in the opposite direction as expected (opposite the direction of local isotherm shifts; Fig. 2), and a portion (6%) of species were not found to shift at all. These tallies of raw change in range position over time do not take into account uncertainty or distance of range shifts, and make null shifts methodologically unlikely to detect; nevertheless, even in this coarse tally, the proportion of estimates matching the direction of temperature change is greater than those opposing in all realms and range sections (Fig. 2, up vs. down arrows).

Along both latitudinal and elevational gradients, shifts at the cold edge and range center are more often directionally consistent with climate expectations than shifts at the warm edge (Fig.

2). While there are fewer shift estimates at warm edges in general (Fig 2), and extinction processes are more difficult to detect<sup>58</sup>, the greater inconsistency with temperature shifts at warm edges could indicate that extirpation processes adhere less closely to temperature change than do range expansion processes (but see<sup>59</sup>), perhaps due to long life histories or compensatory processes<sup>60,61</sup> among other hypotheses (see Section 2).

Considering the magnitude of range shifts reveals further consistencies with climate warming. Despite wide variation between individual range shift magnitudes, previous syntheses have found that range shifts have occurred faster in regions with higher rates of climate warming<sup>16,17,62</sup>. Although there have been far fewer estimates of range shifts in marine species altogether and they are the least proportionally consistent with the directions expected from temperature change (Fig 2), a recent comparative study of range shift velocities that accounted for methodological variation and non-random taxonomic sampling found the velocity of range shifts to be higher in the ocean than on land, with marine species tracking isotherms more closely and moving more than five times faster than terrestrial ( $5.9 \pm 0.9$  km.yr<sup>-1</sup> for marine vs  $1.1 \pm 1.0$  km.yr<sup>-1</sup> for terrestrial) on average in the poleward direction<sup>15</sup>. These patterns might be related to the tighter thermal niche ‘filling’ of marine organisms<sup>63</sup>, the relative unavailability of microclimate refugia in marine habitats<sup>64</sup>, the relative lack of human-created barriers in the ocean<sup>65</sup>, and the faster climate velocities in marine habitats than on land<sup>8</sup>, and suggest mechanisms for slower or delayed range shifts on land (see Section 2).

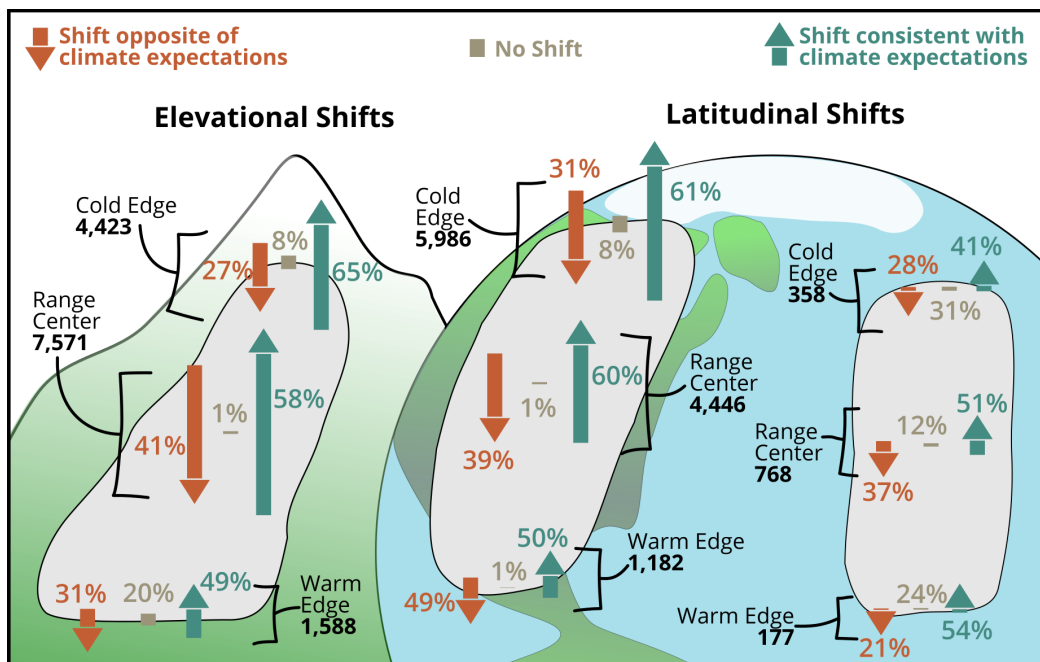


Figure 2: Proportion of elevational, terrestrial latitudinal, and marine latitudinal range shifts consistent with climate expectations (i.e., direction of isotherm shifts) in the BioShifts database. Green and orange arrows signify range shift observations (raw changes in range positions over time) in agreement and opposition (respectively) to the direction of isotherm shifts in the study area, and tan segments show number of observations that estimated no range shift. Bars (excluding arrow

heads) are sized by the total number of detections in each group. Note that this graphic only shows agreement between biological and climate shifts, but not the direction of the shift; (e.g., in some cases, climate change yields a downslope expectation for elevational shifts, but are portrayed as part of the upward arrow here if the detected biological shift matches the isotherm shift).

Despite these generalized global patterns of species redistributions, a significant portion of range shift estimations do not match the rate or even direction expected from temperature shifts alone<sup>15,18,54,66</sup>. The proportion of estimates consistent with the direction of temperature change across all realms is not overwhelmingly high (59%, Fig 2), and some range shift estimates vary in rate by an order of magnitude from their corresponding temperature shifts<sup>16,19</sup>. While some of these inconsistencies could be due to methodological limitations or random variation<sup>18</sup>, others might be due to ecological processes that affect species ranges over and above temperature. These non-intuitive responses could be especially valuable to improve our understanding of factors that limit and alter species distributions.

## Section 2 Why observations deviate from expectations

Several potential mechanisms have been proposed to explain why species ranges don't keep pace with changing isotherms, and why "naive" isotherm-tracking hypotheses may be insufficient for properly understanding species redistributions. These reasons can be summarized as (1) climate drivers other than (average) temperature, (2) non-climatic drivers of species ranges, and (3) low signal to noise in range shift detections. We unpack each of these below and review the literature on how these have been implicated in observed range edge responses.

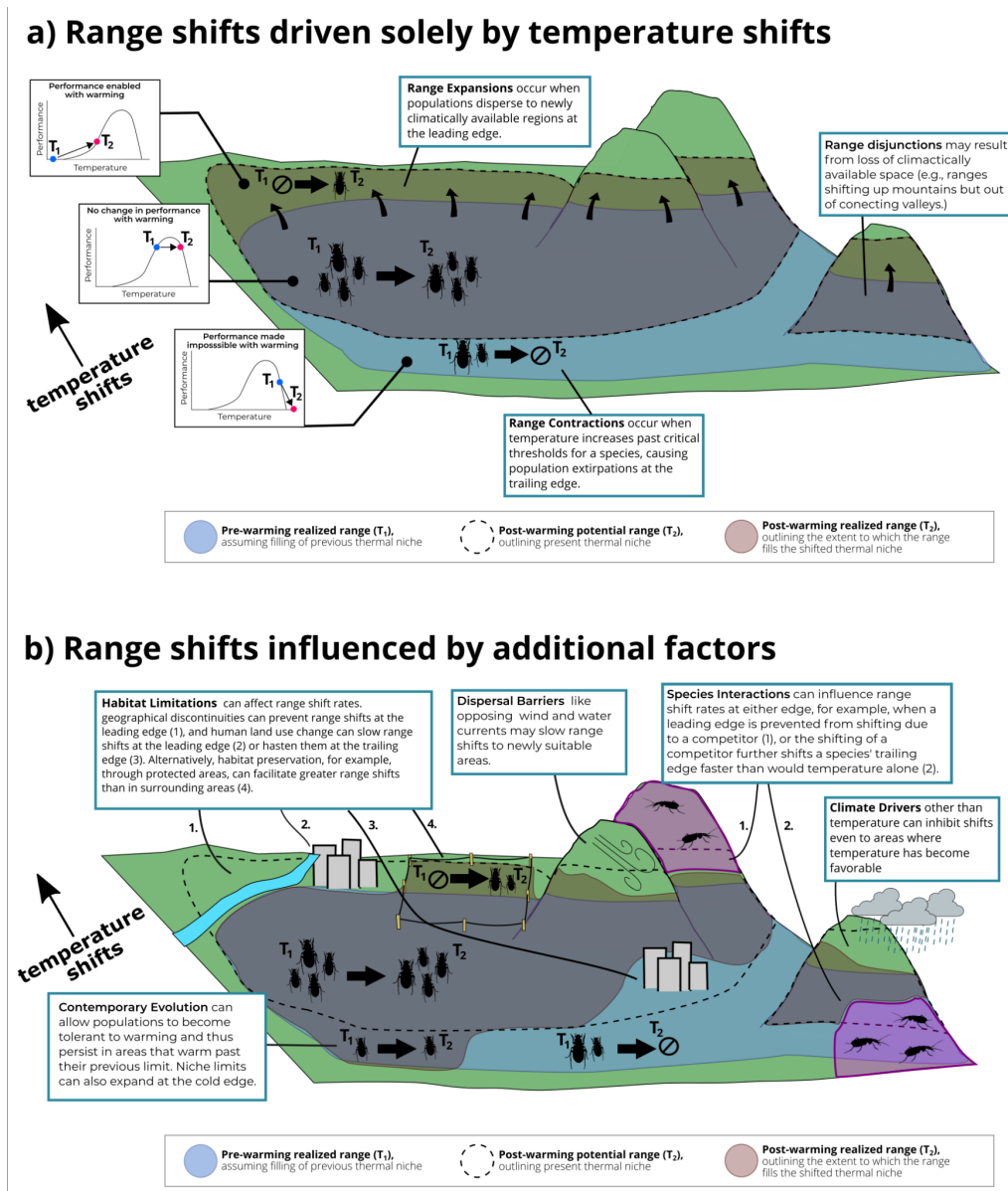


Figure 3: Schematic of factors driving range shifts. (a) processes of species range shifts if temperature is the only driver, and (b) additional factors that may deviate/diverge range shifts from temperature-based expectations. In both panels, blue shaded regions represent the species range under historical climate conditions ( $T_1$ ), and red shaded regions represent the species range under future, post-warming conditions ( $T_2$ ). Dotted outlines represent the post-warming ( $T_2$ ) thermal potential range, or regions where temperature is suitable for the species. Inset plots in panel A show changes in thermal performance of populations fixed in space between  $T_1$  and  $T_2$ . Features in panel B display various modifiers that can deviate/diverge range shifts from temperature-based expectations.

## 2.1 Climate drivers other than (average) temperature

There are multiple approaches to deriving expectations of the direction and velocity of species range shifts, and scale matters. In some cases, range shift expectations are derived from broad hypotheses based on global-scale temperature patterns, wherein species are expected to move towards higher latitudes, higher elevations, and deeper waters, without explicit consideration

of the actual climate gradient in the study region<sup>26,47</sup>. These global-scale expectations can misrepresent local-scale changes experienced by organisms, as microclimates and climate refugia can misalign local gradients with global gradients; in other words, local isotherms may not be shifting polewards or upslope<sup>17,67,68</sup>. Omission of local processes in favor of global-scale expectations can cause a higher proportion of detections to appear to defy expectations<sup>54</sup>. However, methods for including micro-scale changes are being developed<sup>69,70</sup>, and data to do so are increasingly available<sup>67,71,72</sup>. These advances can even allow for *a posteriori* reassessment of range shift studies<sup>73</sup>. For example, when local isotherm velocities were calculated for range shifts in the BioShifts database<sup>15</sup> following methods from<sup>8</sup>, about 2% of elevational study areas and 5% of latitudinal study areas had isotherm velocities in directions opposite of global gradients (that is, downslope or equatorwards). If species perfectly tracked temperature changes, situations like these would manifest as expectation-contrary shifts if only global gradients were used to form expectations.

Even at relevant spatial scales, temperature is not the only limiting climatic variable of species ranges. Different climate variables can show contrasting patterns of change through time<sup>74</sup>, so if a species' most limiting abiotic dimension is not temperature, that species can show shifts contrary to temperature-based expectations. For example, some species shifts have more closely tracked changes in precipitation or water balance than temperature, even when those environmental changes are directionally misaligned with temperature shifts<sup>75,76</sup>. In other cases, species range shifts have been more closely correlated with niche-tracking (over multiple abiotic dimensions) than isotherm-tracking alone<sup>77,78</sup>. Still, these non-temperature variables are rarely incorporated when forming expectations of climate-driven range shifts, and likely explain a portion of the temperature-contrary shifts seen in global estimates. Moreover, constraints imposed by abiotic gradients that are not changing with climate change can be important<sup>79</sup>. For example, day length may constrain photosynthetic processes of plants and corals from shifting across latitudes<sup>80,81</sup>, and atmospheric pressure and oxygen availability may constrain animals from shifting up elevations<sup>79,82</sup>. Interactions between variables with warming might also lead to expectation-contrary shifts, such as the link between temperature and oxygen demand driving oxygen-supply limitations downslope on warming mountains<sup>82</sup> or offshore in marine coastal systems<sup>83</sup>.

Even in cases where temperature is the primary driver of species' responses and the variable forming expectations, the chosen metric of temperature (e.g., annual mean, annual max, number of days over temperature threshold) may not best represent the limiting factor for the species. Temperature extremes, growing degree days, duration of summer, or temperature-related landscape variables such as spring snow cover might variably be more direct drivers of ecological responses to climate change<sup>84-87</sup>. Any of these variables can affect species differently

throughout their life histories, rendering average temperature a coarse predictor of species responses. Temperature anomalies that are not resolutely captured by average trends can also acutely affect species over and above long-term changes. For instance, marine heatwaves over the last decade have exacerbated poleward range shifts in shallow reef species in addition to gradual change through time<sup>88</sup>. Long-term temperature averages might therefore serve as a useful proxy to capture species responses to many correlated temperature variables in large-scale studies, but might not drive responses of individual species.

## 2.2 Non-climatic drivers of species ranges

Species can be excluded from portions of their climatically suitable niches for many reasons, and the extent to which species' ranges are in equilibrium with their environments can affect the predictability of their responses to climate change<sup>63,89</sup>. Limitations indirectly or fully unrelated to climate change can pose constraints on species' realized ranges (Fig 3), and result in ranges showing inertia or climate-change-contrary shifts. Here we organize these non-climatic range-limiting factors into four categories – habitat limitations, dispersal constraints, biotic interactions, and contemporary evolution – and briefly review evidence about how each alters leading or trailing range shift rates against temperature-based expectations.

### 2.2.1 Habitat Limitations

Habitat limitations caused by fragmentation, geographic barriers, and human impacts can either prevent or facilitate range shifts. Geographic barriers such as mountain ranges, valleys, and coastlines can present impasses for range-shifting species, regardless of climatic suitability beyond these barriers<sup>38</sup>. For species that are bound to geographically-constrained habitats such as rivers, coastlines, or high-altitudes (i.e. sky islands), landscape connectivity can be much more influential than climate in determining distribution ranges<sup>90</sup>, and can result in overall range reductions when ranges can contract at one end but cannot expand at the other<sup>59</sup>. When habitat availability does not align with latitudes, elevations, or climatic gradients over which range shifts are expected, species may be unable to keep pace with shifting isotherms (e.g., fish in an east-to-west river can't migrate north)<sup>91</sup> and thus might present as examples where species exhibit little or no range shifts in response to climate change.

Even when a habitat generally extends in the direction of climate velocity, habitat fragmentation and land use change can inhibit range expansions at the cold edge or amplify range contractions at the warm edge<sup>92-94</sup> (Fig. 3b). Human modifications like forest clearing can change the overall permeability of landscapes, which can slow or stop range shifts of forest species through cleared areas<sup>95,96</sup>; landscapes with higher conductance are most quickly shifted across<sup>97</sup>. Alternatively, conserving habitat through establishing protected areas can facilitate species range shifts compared to surrounding areas<sup>98</sup> (Fig. 3b). Of course, in cases where

species specialize in such human-modified landscapes (e.g., farmland-associated birds or mussels on man-made offshore structures), human modifications might represent increased connectivity and actually facilitate range shifts<sup>99,100</sup>. Some projections of climate-driven range shifts account for geographic barriers by including landscape connectivity in models or projecting range-shift corridors<sup>101,102</sup>, but such considerations are normally unaddressed in range shift detections and may present as unexplained lags or advances compared to climate tracking.

### 2.2.2 *Dispersal Constraints*

Climatically suitable areas may exist unobstructed by physical barriers, but remain inaccessible to species that lack a mode of dispersal to reach them, thus slowing range shifts from temperature-based expectations. Dispersal of sessile or slow-moving species such as benthic marine invertebrates and wind-dispersing plants relies on external directional forces (ocean currents or prevailing wind directions), and these forces may be misaligned with the direction of isotherm shifts (Fig. 3b). These misaligned dispersal processes can impede species from tracking changing environments, particularly at the leading edge<sup>103,104</sup>. Animal-assisted dispersal can also impede range shifts of seed-bearing plants as animal vectors do not always disperse in the direction of climate shifts<sup>105,106</sup>. Among actively dispersing organisms, like most terrestrial vertebrates, dispersal abilities can vastly differ, in some cases limiting species' ability to track environmental change. In addition, when there are few dispersers, Allee effects and inbreeding depression can limit the success of early arrivals, leading to lags between species responses and climate shifts<sup>107</sup>.

The role of dispersal ability is typically assessed using various proximal traits such as body size and reproductive mode<sup>108-111</sup>. Although strong relationships between these traits and range shift rates are not common, these expectation-contrary results could be a greater reflection of inadequate estimates of dispersal ability (in which proxies can perform poorly) than a true absence of effect<sup>112</sup>. For more on dispersal and species traits, see<sup>110,112</sup>.

### 2.2.3 *Biotic interactions*

Biotic interactions can affect a species' ability to redistribute under climate change and cause lags or unexpected range shifts relative to climate expectations. Species interactions are expected to affect leading and trailing range edges differently according to whether they are positive (e.g., food, mutualism, commensalism) or antagonistic (e.g., predation, parasitism, competition)<sup>113</sup>.

Positive interactions can result in reduced or delayed range shifts at either range edge. At the leading edge, a species may be unable to shift in response to climate change if its distribution is bound through an obligate positive interaction with another species (e.g. a specific habitat,



host, or food resource species) that is less able to expand in pace with isotherms. Such limitations have been demonstrated in butterflies shifting up mountain slopes being limited by distributions of host plants which are shifting more slowly<sup>114,115</sup>. At the trailing edge, positive interactions such as fungal mutualists on plant roots can broaden the environmental tolerance of the interacting species such that populations with mutualists contract more slowly than populations without in response to environmental change<sup>116-118</sup>. Positive interactions can also manifest as a direct alteration of climate conditions, such as when desert plants create microclimates for associated species; these can appear to alter the rate of climate responses, particularly when expectations are built on macro-level climate patterns that don't capture the microclimate conditions experienced by organisms (see Section 2.1).

Antagonistic interactions can lead to slower range shifts than expected. If a species has a trailing edge limited by antagonistic interactions (but not by climate), the trailing edge shift of the focal species could be driven by the speed of the leading edge shift of the antagonistic species, which, depending on climate-tracking ability of the antagonistic species and the time-course of the interaction, might be slower than climate<sup>119,120</sup>. The reverse is also possible, in which a species' leading edge is limited by an antagonistic species' trailing edge that is not (or is slowly) responding to climate change. Such is the case in intertidal habitats where mussels and barnacles that are shifting towards deeper, cooler waters, have their leading edge (the deeper edge) limited by presence of sea star predators<sup>121</sup>. But this scenario requires a non-temperature reason (in the case of sea stars, high-tide desiccation stress) for why the antagonistic species' trailing edge (the shallower edge) is fixed and not responding to warming.

In some cases, climate-consistent shifts of one species could lead to climate-contrary shifts of an interacting species. For example, if two competing species had overlapping ranges, but only one was sensitive and responded to temperature change, warming could lead to an expected range shift in one species, and an increase in abundance near the warm range edge in the other species where the competitor vacates<sup>122</sup>. This scenario, and many of those previously mentioned, hinges on differences in the climate responsiveness of interacting species, the frequency of which is plausibly high but generally unknown. Methods to model distributions of interacting species are becoming more common and might be able to disentangle some of these nuances. For more on multispecies modeling, see<sup>123-125</sup>.

While theory supports a number of mechanisms by which biotic interactions alter range shift rates compared to climate expectations<sup>126</sup>, they are difficult to observe. In the above examples, species-interaction-driven range shifts (or lack thereof) were identified through careful natural history observations and/or directed research. However, most large-scale range shift studies assess many species' ranges at once and typically lack context of species-specific climate

tolerances or community interaction webs. Without independent knowledge of species' interactions, the previously discussed examples would have presented as species responding in unexpected ways to climate change with the underlying mechanisms unrecognized. Thus, it is likely that unidentified biotic mechanisms underlie a portion of the expectation-contrary shifts that have been documented.

#### 2.2.4 Contemporary evolution

Contemporary evolution can affect the rate of species range shifts in response to climate change<sup>127</sup>, although a full summary of the theoretical directions and mechanisms is beyond the scope of this review. Briefly, evolution of dispersal ability can increase the rate of range expansions if previously unsuitable areas become suitable beyond the species range<sup>128,129</sup>, just as evolution of any trait that alters the role of range-limiting factors (desiccation resistance, species interactions, heat tolerance) can affect the response of ranges away from expectations<sup>130,131</sup>. The challenge to invoking trait or niche evolution during range shifts is explaining why these traits would evolve more readily during a range shift when they could have been under selection in previous climatically-stable periods<sup>132</sup>, i.e. ultimately understanding the limits to niche width evolution at all range edges. For more on evolution and range shifts, see <sup>127,133,134</sup>.

### 2.3 Low signal to noise in range shift detections

Methodological differences overall can greatly influence estimates of range shifts from empirical data. In fact, two recent syntheses of species range shifts made similar conclusions that methodological factors are better predictors of range shift rates than ecological traits or climate variables<sup>15,18</sup>. Because range shift detections often rely on sparse or opportunistically collected data, researchers often have little choice in methodology for individual studies. This range of methodologies adds noise that may impede our ability to detect meaningful signals of change or draw synthetic conclusions between systems<sup>18</sup>. Since species ranges are naturally variable from year to year<sup>7</sup>, and are themselves observed imperfectly<sup>37,53,58</sup>, low sampling frequency or spatial coverage can result in estimates that are misrepresentative of or even contrary to long-term trends<sup>32</sup>.

High noise in range shift estimates can be expected when the temporal extent of a study is small (i.e., a short total duration of observations). Even if the pace of climate change has been fast within this time frame, life-history constraints and stochasticity likely affect range edges in the short term, thus time can be required for robust changes to be detected at range edges. Indeed, both latitudinal and elevational shifts of range edges from the BioShifts database show patterns of high variability around the temperature-based expectation in short-duration studies; that variability diminishes towards zero (matching expectations) as study duration

increases (Fig. 4), suggesting that, at least among longer term studies, temperature is a main direct or indirect driver of range shifts. This trend is promising, but unfortunate, as reconstructing high-resolution biogeography information for the past is difficult. Nevertheless, it lends support to the value of reassessing documented range shifts in cases where sampling can be continued after an initial study is completed.

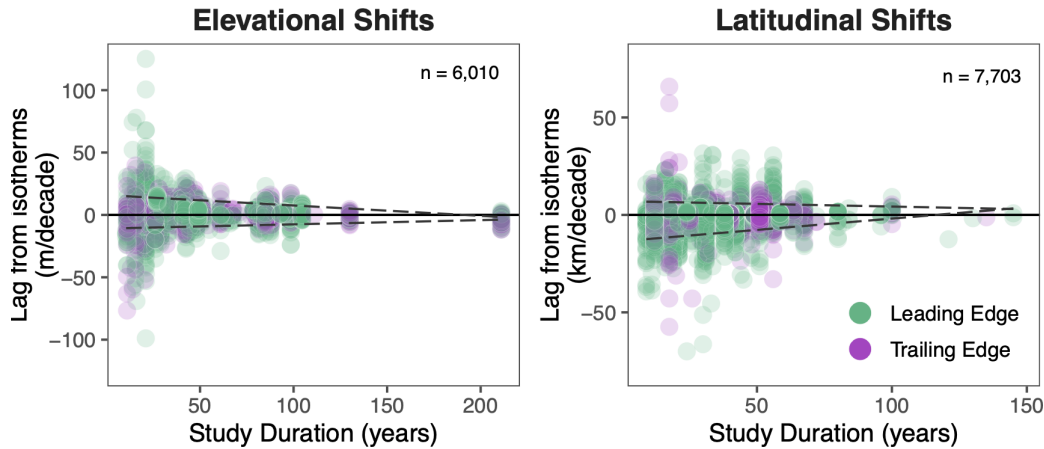


Figure 4. Lag between isotherm shifts and range shifts across study durations in the BioShifts database. Lag is calculated as shift velocity - isotherm velocity, where a perfectly isotherm-tracking shift would have a lag of zero. Purple dots signify range shifts estimates of trailing edges, green of leading edges for both elevational and latitudinal range shifts. Dashed lines show the 5th and 95th quantile regressions of all points in each plot.

Related to the role of time, estimates made from too few observations can carry both process and sampling error, affecting their accuracy. Range edges are particularly prone to low-accuracy shift estimates based on the likelihood of error of both types. Process error can greatly influence range edge identifications when stochastic events and idiosyncratic biological processes vary their positions from year to year (e.g., higher than normal wind dispersal in some years). Moreover, since edges normally contain lower population densities of focal species<sup>135</sup>, position estimates can be substantially affected by sampling effort, such that low sampling can add noise to already variable range edges<sup>53</sup>. While studies with many observations of range edge positions through time may be able to cut through this error to detect biological signal, those with sparse data are likely confounded by these issues to some extent.

Statistical limitations can further complicate range shift detections, and are often unaddressed in range shift detection studies<sup>136</sup>. For example, when range edge estimates are expected to be variable across observations (either because of natural range edge variability or observer error), the “regression towards the mean” effect can lead to an apparent range shift in which an estimated range edge is shifted towards the location of the true range edge (the expected sample mean), even in the absence of a true biological change<sup>137,138</sup>. In addition, because

sampling of species range position is done over a finite sampling domain (e.g. transects up mountains or across latitudes), range shifts that surpass the domain will necessarily be underestimated. Unless removed from the study, these “observation domain crossers” will lead to predictable correlations between the starting range edge relative to the domain edge and the magnitude of the detected shift<sup>137</sup>. Despite these potential sources of error, fewer than 2% of range shift detections are tested against null models<sup>136</sup>, resulting in an inability to distinguish whether range shift detections differ from range shifts due to chance alone.

Detecting range edge shifts based on the furthest occurrence of a species at only two points in time without comparison to a null model is one situation in which noise might particularly outweigh biological signal. Yet due to understandable limitations in data availability, scenarios like this are quite common; of the latitudinal range shifts in the BioShifts database, 10% of cold edge and 20% of warm edge estimates used furthest-occurrence detections to establish range edge positions (see Box 2), and in two recent syntheses of range shift estimates, 38 and 85% of range shift estimates (cold and warm edge, respectively) were made using two time-point data<sup>18,22</sup>. Various approaches can be taken to reduce the influence of these sources of noise when comparing range positions between few time periods or with sparse data<sup>37,139</sup>. Some common strategies include aggregating observations across multiple years to reduce the influence of natural variation and observer bias, accounting for sampling effort and detectability in occupancy models, and aggregating error-prone shifts across multiple species to form an understanding of community shift rate among noisy individual estimates. Future work should consider estimating error in range edge detections, including meta-analytic methods and null models that account for variation in precision among studies.

### Section 3 Impacts on natural and human systems

Range shifts and their cascading effects will lead to both positive and negative outcomes for species, ecosystems, and people. Range-shifting towards suitable habitats is, in itself, an adaptation that allows for persistence in the face of ongoing climate change. Therefore, climate-driven leading edge shifts have broadly positive effects for individual species and for maintaining biodiversity at large. Still, rapid changes in species ranges have led to corresponding needs for adaptation in natural and human systems that were established under more stable conditions. Among social-ecological coupled systems, range shifts are expected to have greater impact on those that lack the financial or political capacity to quickly adapt<sup>20,21</sup>, creating possible equity imbalances that should be addressed in future research.

Species shifting into new areas at their leading edges occupy a unique position in science, policy, and management. Although climate-induced shifts of species’ “native” ranges

fundamentally differ from the spread of invasive alien species, existing policies are not consistently or decidedly equipped to manage them. Due to the vast potential impacts of newly arriving species, understanding and predicting range shifts has been increasingly prioritized by governmental research agencies<sup>140-142</sup>, and their perception by resource managers has varied from new exploitable resources to dangerous invaders<sup>143,144</sup>. Here we provide a categorical overview and an update of major cascading effects of range-shifting species on ecosystems and people, focussing on impacts of range shifts that have already occurred rather than future projections, but direct interested readers to<sup>13</sup> for a more in-depth review.

### 3.1: Impacts on Natural Ecosystems

Redistributions of species can lead to changes in community composition and dynamics, or otherwise alter natural ecosystems, and leading edge shifts can have effects akin to those caused by non-native biological invasions<sup>14,120</sup>. When range shifts of multiple species occur in a region, the reshuffling can result in cold-adapted species being replaced by warm-adapted ones, referred to as 'thermophilization', thus altering the historical structure and function of the community<sup>145-149</sup>. Despite changes in distributions of individual species, the ecosystem as a whole might maintain function if species lost due to range shifts are functionally replaced by species entering, or if species change their functional contributions as communities change<sup>150</sup>. Range shifts can also lead to loss of specialist species in favor of generalists, potentially reducing biodiversity at regional scales<sup>151,152</sup>. The magnitude and rate of thermophilization can vary between taxonomic groups, biogeographic contexts, or species traits related to persistence and mobility, but changes in thermal affinities of communities tend to lag behind climate warming in general<sup>40,153</sup>, possibly leading to changes in the stability of communities as they become increasingly out of sync with their environments.

Some species range shifts can have disproportionate impacts on natural ecosystems, such as changes in habitat-forming foundation species. For example, the barren-forming urchin, *Centrostephanus rodgersii*, has exhibited a poleward expansion along the south-eastern coast of Australia in recent decades, leading to overgrazing of large areas of kelp forests and removing key habitat for kelp-associated species including those comprising major fisheries exports of the region<sup>154-156</sup>. Alternatively, global mangrove species have exhibited poleward expansions in recent decades<sup>157</sup> that could disproportionately change the composition of communities in areas in which they have established, given that mangroves provide essential habitat for a wide range of species<sup>158</sup>. Shifts of species that shape their environments can open niche spaces and promote shifts of other species, resulting in increased species richness or phase changes to new ecological communities<sup>149,159</sup>.

### 3.2 Impacts on Humans

Climate-mediated shifts in species distributions can have direct consequences on human communities, inclusive of economic and cultural systems with which they are connected. Shifting ranges of food species can lead to positive or negative outcomes for human communities, and require adaptation in order to begin harvesting and managing newly-arrived species, or transition away from reliance on outward-bound species. For example, distributional shifts of commercially important fisheries species have created opportunities to open commercial and recreational fisheries as new species arrive in some cases<sup>160</sup>, but reduced fishing employment<sup>161</sup>, and required increased travel for harvesting as target species shift in others<sup>162</sup>. Similarly, crop species have shifted ranges in recent decades, leading to economic opportunities in places that have become favorable, and necessity for adaptation in places that have become unfavorable<sup>163</sup>; crop pests and pathogens have also shifted, changing the spatial distribution of some food security threats<sup>164</sup>.

The effects of species redistributions on human cultural systems can be considerable. For indigenous communities, species range shifts can threaten abundance of culturally important resources<sup>160</sup>, access to traditional foods<sup>165</sup>, and traditional knowledge systems built around natural ecosystems<sup>20,165</sup>. Range shifts can also occur in species that are emblematic of the places where they were historically found<sup>166</sup>, potentially altering societal connections with local ecosystems.

Species range shifts can also present threats for human health. Documented range shifts of disease-vector species due to climate change have resulted in spatial changes to health risks for human communities. Malaria-vector mosquitoes in Africa have shifted upslope by about 6.5 m per year and poleward by about 4.7 km per year since the late 1800s<sup>167</sup>. Similar shifts of mosquitos and other disease-bearing species such as ticks and bats have been documented around the world<sup>168-170</sup> and are expected to continue in the future<sup>171,172</sup>. Ciguatera poisoning, caused by eating certain types of reef fish found typically in warm tropical water, has seen a geographical expansion of poisoning incidents since 2000, as warm-water fish shift polewards along the east Australian coast<sup>173</sup>. Public-health-relevant range shifts have direct implications, introducing regions and communities to risks for which they are historically not prepared and requiring preparation from healthcare systems to manage them. Meanwhile, range shifts of disease-bearing species could – in theory – relieve human populations from diseases that have historically been prevalent as trailing edges of their ranges contract upslope or away from the equator. Some such cases have been observed<sup>174</sup>, and others are predicted in coming decades<sup>171,175</sup>. In addition to direct range shifts of diseases and their established vectors, novel species interactions from range shifts are one factor leading to an increase in risk of zoonotic

spillover of pandemic-causing viruses, and a majority of these novel interactions to come in the next century might have already occurred<sup>176</sup>.

### 3.3 Impacts on resource management and conservation

Most conservation decision-making processes have been built around assumptions of relative stationarity – that is, assuming current ranges will persist into the future<sup>143</sup>. The global redistribution of species in response to climate change breaks this assumption, and management actions (including land acquisition, habitat management, and direct population management) will need to incorporate projected impacts of range shifts in order to achieve optimal or workable outcomes. Protected areas, for example, have been useful tools for preserving biodiversity, abundance, and assemblage structure within them<sup>177</sup>, but risk losing their effectiveness (depending on their stated goals) when species that inhabit them shift away and new species enter their boundaries<sup>178,179</sup>. In anticipation of species range shifts, conservation managers have needed to re-evaluate their goals and adapt their strategies in order to preserve biodiversity into the future.

One approach to management in light of anticipated range shifts is to supplement permanent protective measures with temporary efforts as needed, effectively increasing connectivity to sufficiently protect range-shifting species<sup>180</sup>. This strategy has been implemented in marine environments by adding temporary protective measures to increase connectivity between permanent sites or to protect new marginal populations<sup>181</sup>, adapting protected areas to shift over time in accordance with gradual shifting of species<sup>182</sup>, designing protected areas as stepping stones across climatic gradients<sup>183</sup>, and streaming low-latency (“real-time”) data to project species distributions and guide harvesting and management<sup>184,185</sup>. While less common in terrestrial settings, similar dynamic conservation goals have been achieved by implementing short-term conservation areas for migratory species through “rentals” of private land<sup>186,187</sup>. While the stated fundamental objectives of most conservation programs appear to be at odds with time-limited protected status, combining temporary conservation areas with traditional permanent protected areas might help to maximize conservation benefit with limited funds.

A related strategy is targeting establishment of new protective measures within “climate corridors” where species range shifts are likely to occur. For example, The Nature Conservancy (USA) recently implemented the Cumberland Forest Project<sup>188</sup> — one of its largest land acquisition projects to date — specifically intended to protect key “climate escape routes” for range-shifting species. Priority for range-shift corridors has also already been integrated in the biodiversity guidelines of the US Department of Agriculture’s National Agroforestry Center<sup>189</sup>.

Climate-driven range shifts have also spurred novel strategies in biodiversity conservation. In light of shifting climatic suitability, assisted migration has emerged as a conservation strategy wherein individuals are transplanted either within or outside of their current geographic range with the intention of situating them where they are more climatically adapted<sup>190</sup>. Although controversial<sup>191</sup>, some assisted range migration efforts have already begun<sup>192-195</sup>. To facilitate persistence at the warm edge, conservation efforts that protect genotypes pre-adapted to future conditions are particularly effective<sup>196</sup>. These efforts facilitate evolutionary rescue, a process likely to be particularly important to maintain biodiversity in the tropics<sup>197</sup>, whilst also bringing to light ethical considerations regarding where and for which species such efforts should be applied.

Given their importance to human systems, range shift projections have highlighted the need for transboundary management strategies as species shift across political or jurisdictional borders<sup>198</sup>. Transboundary conflicts have already arisen when commercially important species have shifted to neighboring jurisdictions<sup>199</sup>, and have been addressed as a priority in international resource management in the Anthropocene<sup>143,200</sup>. Needs for proper transboundary strategies will only become greater, given that models predict vast swaths of future habitat for many species to be in countries where those species are not currently found<sup>201-203</sup>, and many of these changes will disproportionately impact countries with high reliance on resource species and low capacity to adapt<sup>20</sup>. Without proactive management and transboundary agreements in place, species shifting from one historical jurisdiction to another may result in an incentivized depletion of the resource by the country the species is shifting away from that stands to lose future access.

### Box 3: Human Range Shifts

Shifting isotherms across Earth's surface are changing climate conditions experienced by humans, too. Despite our great powers of niche construction and climate buffering compared to many other species, human distribution for centuries has clustered in a surprisingly narrow envelope of climatic conditions<sup>204</sup>. Anthropogenic climate change is shifting this climatic envelope away from existing human population centers, especially those in tropical climates, and creating novel challenges, opportunities, and ethical considerations regarding "range shifts" of our own occupancy patterns and activities in a warming world<sup>205</sup>.

Range shifts of human activities due to climate warming have already begun, both at contracting warm margins and expanding cold margins. Warming temperatures over recent decades have already led to poleward and upslope shifts of agricultural activities, including latitudinal shifts of "breadbasket" and "rice bowl" crops across continents<sup>163</sup> and upslope shifts of mountain crops like coffee<sup>206,207</sup>. In the ocean, historical patterns of human ocean use have expanded concurrently with warming, with fishing fleets shifting polewards by almost 1



degree latitude per year<sup>208</sup> and trans-Arctic shipping routes having greatly expanded in navigability since the 1980s<sup>209</sup>. Warming conditions have also changed spatial patterns of scientific pursuit, resource extraction, and even recreation and tourism across latitude and elevation<sup>210-216</sup>. These changes to human behaviors may already be having downstream effects on natural environments, adding additional pressures to systems already facing stress from changing climates.

Whereas climate-driven range shifts of human activities have been documented, direct climate-related changes to human distributions are more difficult to attribute and predict, because many factors, including politics, wealth distribution, infrastructure, and cultural ties influence people's decisions and ability to migrate. Shifting human climate envelopes underscore the need for robust adaptation strategies when climate-tracking migration is not possible; recent models predict large areas of extreme climates, even surpassing human physiological tolerance thresholds, in the near future<sup>204,217</sup>. Moreover, these trends call attention to the global ethical considerations of shifting climate regimes, as many regions at the warm margin of the shifting human niche are those contributing the least to global climate change<sup>205</sup>.

## Section 4 Summary and Future Perspectives

In the above sections, we summarized evidence that species' range shifts are a ubiquitous response to climate warming, including where and how they have been documented, why they do not always match expectations, and the impacts they have had on nature and society. Despite considerable advances in understanding mechanisms by which species redistribute in response to climate change, there is vast room for progress in the field. Here we outline three key priority areas to advance how we understand and predict biodiversity redistribution and improve our ability to make sound management decisions about species 'on the move' and their associated impacts.

### 4.1 Increased effort in monitoring and harnessing of data

Existing monitoring programs have contributed greatly to observations of climate-driven range shifts, but are often limited to particular ecosystems, geographical areas, or taxa. While monitoring programs can be less tempting to prioritize for funding agencies because benefits largely accrue over longer time frames, increased support for these efforts will lead to greater ability to observe, attribute, and anticipate species responses to climate change<sup>218</sup>. Increased monitoring could be particularly valuable in systems or locations where current data are limited, or in which species ranges are already predicted to shift, to test and improve model prediction skill<sup>62,219</sup>. Furthermore, efforts to inter-connect disparate existing monitoring programs so they can be integrated, and include comparable and pertinent indicators of

biodiversity change (e.g., Essential Biodiversity Variables<sup>220</sup>), can help us to up-scale existing monitoring investments for inference at larger scales, such as whole-range biogeographical shifts<sup>221</sup>.

When systematically surveyed “gold standard” datasets aren’t available, range shift research could benefit from increased use of publicly available citizen- and community science data. Such volunteer-driven data are collected around the world and already account for over half of biodiversity occurrence records in the Global Biodiversity Information Facility (GBIF) database<sup>222</sup>. These records have already shown applications in biogeography research<sup>57,223–225</sup>, with ongoing citizen science monitoring programs having contributed greatly to our observations of range shifts within systems (e.g., Christmas Bird Count, used in<sup>34,226–228</sup>). Outstanding barriers to further integrating citizen science data into climate change biogeography research include the strong spatial and temporal biases of data collections, the statistical measures needed to account for unstructured data collection (but see<sup>229</sup>), and the validation of data from non-expert contributors (although robust post-hoc verification measures are possible, e.g.,<sup>223</sup>). Further research into how to control for these variables to best apply public data sources will open research pathways in the field.

#### 4.2 Understanding mechanisms to increase generalizability

Synthesis of range shift studies has offered valuable insight into general trends and variability in observed species range shifts, but better understanding of the sources of variability between studies and the influence of data biases are needed in order to generalize. Identifying organism or environment-specific factors that make range shifts likely will improve our ability to anticipate them in cases where observational data is limited.

Assessing the influence of species traits on range shifts, for example, should help to generalize the types of species most likely to shift at their leading and trailing edges. Intrinsic factors such as a species’ ability to move, its level of generalism, or its lifespan could influence its ability to shift in response to climate change, and theory suggests varying ways by which they should explain range shift rates<sup>10,112,230–232</sup>. Yet evidence to date suggests fairly weak or variable explanatory power of traits in relation to observed range shift patterns (reviewed in<sup>112</sup>), suggesting the methods and perhaps quality of data used to assess their influence have been lacking<sup>112</sup>. Further research into intrinsic sources of variation could benefit from simulations and theoretical models to understand the influence that traits might have on range shifts within biological communities<sup>233</sup>, combined with data synthesis to test theories against empirical data.

Another promising direction is generalizing how the spatial pathways of species shifts interact with properties of the landscape. For instance, global climate velocities can be used to identify

regions where range shifts might be expected<sup>234</sup>, global ocean and wind currents can identify areas where these forces will facilitate or impede shifts of passively-dispersing species<sup>103,104</sup>, and landscape *quality* maps can estimate potential routes through which range shifts are more likely to occur<sup>235</sup>. Such area-based approaches could aid in management efforts to facilitate climate-driven range shifts even in systems where species specific data are unavailable.

Once mechanisms have been identified that can explain variation in species' range shifts, a promising avenue will be to integrate these into mechanistic or process-based models that simulate the eco-evolutionary response of species in face of climate change<sup>236-238</sup>. Integrating variables such as dispersal, evolutionary potential, or demographic processes into models can improve model fits and extrapolations over correlative approaches<sup>239,240</sup>, and have the advantage of flexibility as key parameters can be estimated or imputed when species-specific data is unavailable<sup>241</sup>. Reliance on underlying mechanisms (such as species traits or landscape habitats) makes models of this type transferable to systems where statistical models may be limited by data scarcity. Moreover, mechanistic models can be used in simulation experiments to better identify specific drivers of range shifts with other factors being held constant. Process-based simulations can control for intrinsic and extrinsic factors affecting range shifts, as well as natural variation and detection error to assess the effects of potential drivers of range shifts<sup>197,242</sup>, and can even be used to assess effects of management interventions on species distributions<sup>243</sup>. The theoretical relationships that arise from simulation experiments can then inform needs to data collection that can circularly aid in improving *in situ* range shift observations.

### 4.3 Improving predictions at usable scales

While observing and detecting impacts of climate change is a necessary step in understanding processes, projections of range shifts into the future can inform mediation and management strategies to avoid or adapt to severe ecological impacts of climate change. In range shift research, projections are often made in the long-term (e.g., year 2100) using tools such as species distribution models or other correlative models of range position based on environmental variables; predicting range shifts in near-term, management-relevant timescales is much less common. This dearth of near-term predictions is one barrier to implementation of effective management strategies for species redistributions.

Near-term forecasting has grown in popularity and priority in recent years across subfields in ecology<sup>244,245</sup>. In some data-rich systems with direct applications, near-term forecasts of species distributions have already been implemented to support dynamic management strategies<sup>246-250</sup>. However, in most systems, such efforts have not been implemented. We suggest predictive efforts focus on systems in which predictions can occur in tandem with ongoing monitoring

systems to ensure that near-term predictions can be tested, falsified/validated, and improved as monitoring continues<sup>244</sup>. Focus on statistical tools that can accurately characterize and project uncertainty, as well as those that can integrate multiple processes from environmental suitability to landscape connectivity (see previous section) will be an important step in improving the predictive power of the field.

## Conclusion

Despite significant strides in our understanding of climate-driven species redistributions in recent decades, much remains to be understood and discovered in the field. Since the field began, observations of climate-driven range shifts have been made around the world<sup>22</sup>, revealing both clear trends in observed responses, and high variation due to observational, methodological and biological factors<sup>15,18,136</sup>. Given the recent growth of the field of climate change biogeography and the urgency to predict climate change responses globally, it seems projections, models, and theory have outpaced empirical observations in recent years, and our collective knowledge and abilities to predict stand to benefit from further efforts to augment empirical data for testing and validation. Expanding research efforts in the directions set out above will help us identify range shifts in the present, anticipate range shifts in the future, and use this knowledge to inform strategies for preserving biodiversity through climate change.

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