Trends in
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Review

Linking individual animal behavior to species range shifts under climate change

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Climate change has led animal species to shift their ranges to greater elevations, latitudes, and depths, tracking their preferred abiotic niche. However, there is extensive variation in these shifts, and some species have not shifted their ranges at all. Some of this variation arises because species' distributions not only align with the abiotic environment but are also shaped by biotic factors and movement. Through facilitating rapid adaptive responses to climate-mediated changes to abiotic, biotic, and movement factors, behavioral plasticity allows populations to survive environmental change by persisting in place, while also enabling successful establishment in novel habitats when shifting in space.

Highlights

There is extensive variation in species' range shifts in response to climate change, and existing models often fail to accurately predict and forecast these range shifts.

While range-shift models primarily focus on abiotic environmental factors, a species' range is also determined by biotic factors and movement.

As climate reshapes these factors, behavior is an important mechanism through which animals can respond to rapid changes in their habitat, and individual behavior scales up to shape species distributions.

Behavioral plasticity can be an important mediator of species range outcomes in changing environments, allowing animals to persist at the lagging, warm edge of their range, or shift their range at the leading, cool edge.

Challenges to understanding and predicting climate range shifts

Anthropogenic climate change is having profound effects on animal populations around the world [1,2]. As the abiotic environment changes, many species have shifted their distributions, through contractions on lagging or warm edges at low elevations and latitudes and shallower depths, or expansions along leading or cool edges at high elevations and latitudes and deeper depths [3–5]. These **range shifts** (see Glossary) occur when animals track their **fundamental niche**, or the range of abiotic conditions within which an organism can survive and reproduce [6,7]. However, there is significant inter- and intraspecific variation in the incidence of range shifts, with the magnitude and degree of synchrony in shifts on the leading and lagging edge causing range expansions, contractions, marches (in which both edges move symmetrically), or no change [8]. These outcomes are shaped by a species' ability to persist in place in its altered habitat or shift in space to a newly suitable habitat [9]. Disentangling this variation is crucial to understanding how animals and ecosystems are poised to be affected by climate change.

Increasingly, ecologists are considering not only the role of the abiotic environment but also the biotic environment and species **movement potential** in driving species distributions (i.e., the **biotic–abiotic–movement (BAM) framework**; Box 1, [10]). This framework posits that a species' realized distribution on the **landscape** is dependent on the availability of a sufficient assemblage of interacting species (biotic), appropriate physical habitat characteristics (abiotic), and the ability to access biotically and abiotically suitable habitat (**movement**). To better incorporate the biotic and movement factors into species range models, researchers have proposed measuring functional traits, or quantifiable characteristics of an organism that affect performance, and using them to predict which species persist in place or shift in space. These approaches, however, have done a poor job in explaining heterogeneity in range shifts [11,12]. There are myriad methodological and conceptual explanations for this weak relationship between traits and range shifts [13]. For one, many of the traits considered are discrete, readily quantified traits like body mass or dispersal syndrome, but more complex behavioral traits can play an underappreciated role.

Behavioral ecology is inherently concerned with how organisms make fitness-enhancing decisions in response to multiple facets of their environment, and serves as an effective lens

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Box 1. The biotic–abiotic–movement framework for understanding species distribution under climate change

A species range constitutes space with appropriate biotic and abiotic conditions that are physically accessible to an organism (Figure I, Z). Soberon and Peterson formalized this idea with the biotic–abiotic–movement (BAM) framework incorporating the biotic (B), abiotic (A), and movement (M) components underlying a species distribution [10].

Climatic factors, such as temperature and moisture, form the basis of the fundamental niche (Figure I, X) and thus species distributions. These abiotic features are the physical substrate in which organisms survive and reproduce, and are directly affected by climate change. This perspective underlies most **species distribution models** (**SDMs**), which pair climatic data with species occurrence data to estimate climatic characteristics of suitable habitat [81]. Various climate change scenarios can then be used to forecast future habitat suitability [82].

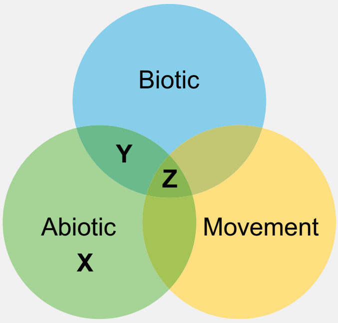

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Figure I. An outline of the biotic–abiotic–movement framework, conceptually illustrating the fundamental niche (X), the realized niche (Y), and a species true distribution on the landscape (Z) in relation to the abiotic, biotic, and movement drivers of distribution.

Appropriate abiotic conditions must also overlap with the biotic community that a species needs to survive, forming the realized niche (Y). Interspecific interactions are well established as a strong mediator of species' distribution [83–85]. Under climate change, one might expect species that have close positive relationships to shift their ranges synchronously if they have similar abiotic preferences [71], while antagonistic relationships such as predation and competition can constrain range shifts. Biotic considerations have been incorporated into SDMs by incorporating biotic layers, such as vegetation type or the presence of a strong interacting species, to improve accuracy [86], and with the development of joint species distribution models (JSDMs) to predict habitat suitability for multiple interacting species simultaneously [87]. We note that even SDMs that are solely based on abiotic climate variables are ultimately modeling the realized niche and implicitly accounting for biotic factors, given their use of actual occurrence data to parameterize models.

Locations with suitable abiotic and biotic conditions must also be accessible to become occupied via dispersal or colonization. If suitable habitat for an animal is blocked by an insurmountable barrier such as a mountain range or ocean, that habitat is not available. The movement component of the BAM framework describes the role of dispersal ability in facilitating or limiting habitat access, and incorporates the structural accessibility of the landscape itself, as well as species intrinsic movement potential. The movement component can be incorporated into SDMs through connectivity models, which use geographic data layers of environmental characteristics, such as vegetation type, hydrology, or human development, to predict animal movement through a landscape to suitable habitat localities. Climate connectivity extends this approach to analyze the ability of species to move through a landscape to track their fundamental niche under changing temperature and moisture regimes [17].

through which to better understand the mechanisms driving animal range shifts. **Behavioral plasticity** drives an individual's immediate responses to changes in local habitat (Box 2), and growing evidence suggests that animals respond behaviorally to climate-induced changes to their abiotic environments to maximize their fitness in novel conditions [14,15]. Organisms that exhibit greater degrees of behavioral plasticity are better equipped to cope with a changing climate than those that are more specialized [16]. Much of this work has occurred at the scale of individual animals and populations, but less is known about the implications of behavioral plasticity for global species distributions across space and time. As ecosystems and environments are rapidly changing in response to a myriad of stressors, a more mechanistic understanding of organismal responses to this change will better inform our models and predictions of species distributions and interactions.

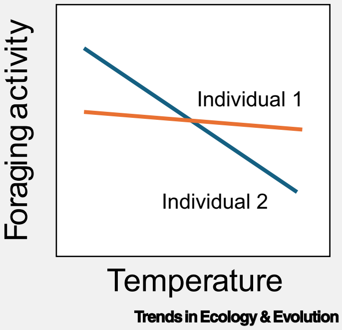
Here, we bridge behavioral ecology and biogeography to explore how individual animal behavior scales up to affect species distributions under climate change. We review evidence for how behavior influences, and is influenced by, climate-induced changes to movement potential and the abiotic and biotic environment. We generate hypotheses about how these behavioral mechanisms can drive species persistence or range shifts, and explore the implications for conserving animals under climate change.

Glossary

Behavioral buffering: behavioral changes that individuals make to minimize physiological stress in the local environment.
Behavioral plasticity: changes in an organism's behavior in response to changing environmental conditions.
Biotic–abiotic–movement (BAM) framework: a conceptual framework which posits that a species' realized distribution is determined by a combination of suitable abiotic, biotic, and movement conditions.
Connectivity: the degree to which a landscape facilitates the movement of organisms.
Ecological trap: a scenario in which, due to rapid environmental change, organisms make maladaptive assessments of habitat quality based on outdated cues.
Fundamental niche: the range of abiotic conditions in which an organism can carry out all essential functions, enabling population persistence.
Landscape: a geographically defined area encompassing physical land features, and the resident living ecosystems.
Movement: the change in the spatial location of an individual animal over time.
Movement potential: an individual's intrinsic physical ability to navigate a landscape (e.g., as described by dispersal kernel parameters or morphometric proxies).
Range shift: a change in the distributional limits of a species over time, often driven by large-scale environmental change.
Reaction norm: a pattern of phenotypic expression of a single genotype across a range of environments.
Social behavior: an individual animal's interactions with conspecifics.
Social learning: the transmission of information among conspecifics.
Species distribution models: a family of statistical models that seek to predict species distribution based on environmental data.

Box 2. Behavioral plasticity in rapidly changing environments

Phenotypic plasticity, the ability for a particular genotype to express a range of phenotypes across different environments, is an important driver of trait variation across individuals within species, populations, and generations. Behavioral plasticity in particular allows individuals to respond quickly to environmental changes. For example, many animals change their rate of foraging activity with temperature [88,89]. Figure I illustrates a **reaction norm**, which represents how changing environmental conditions can elicit variable responses among individuals.



A hypothetical reaction norm, displaying variable effects of temperature on foraging activity in two individuals.

Behavioral plasticity can be developmental or activational. Developmental plasticity describes the environment-mediated change in an individual's behavior over the course of their development [90,91]. This form of behavioral plasticity aligns with traditional understandings of phenotypic plasticity, and encompasses learning, as well as the developmental physiological and morphological changes required for and reinforced by certain behaviors. Activational or reversible plasticity, often called behavioral flexibility, describes the context-dependent response of pre-existing neural pathways based on an organism's sensory impression of its immediate environment [92,93]. These two forms of plasticity present important evolutionary tradeoffs when species are responding to change, with developmental plasticity usually producing better integrated, context-specific behaviors in response to change over longer time scales, while activational plasticity is more generalized and enables quicker responses to rapid change, but requires much larger and more costly neural investment to maintain [94].

When the environment deteriorates too quickly for populations to respond to selection, or under situations where dispersal is limited, plasticity becomes important for persistence. Adaptive behavioral plasticity, in the form of innovation, learning, and an affinity for novelty, can be advantageous in an altered or highly variable environment. Such plasticity will be greater for animals with more advanced cognition and sensory processes, which are better able to detect, interpret, and respond to cues, and for species that evolved in variable environments [95]. Plasticity in one behavioral trait may or may not predict plasticity in others, and rapid, complex environmental change may favor correlated plasticities that can equip an individual to respond to a variety of stressors. We expect these correlated plasticities where multiple cues in extreme or highly variable environments covary [96]. However, behavioral plasticity can also be maladaptive, as individuals using indirect cues of environmental conditions may make maladaptive assessments of their environment and adopt failing strategies, leading to ecological traps [97]. Human-induced rapid environmental change is predicted to produce ecological traps at a disproportionate rate, as the rapidly changing environment decouples cues from their fitness outcome [98]. Animals may more easily adapt to changing or novel environments if the altered condition is similar to conditions experienced in the species' evolutionary history [98].

Movement: the fundamental mechanism of range shifts

As movement is the fundamental mechanism of range shifts, predicting such shifts requires an understanding of its drivers. While movement decisions made at finer spatiotemporal scales (e.g., daily foraging) often do not affect long-term species range, these movements underpin movements larger than the scale of an individual's home range, such as dispersal and migration, which are key mechanisms of range shifts over larger spatiotemporal scales. The intrinsic movement potential of an organism is one important consideration, traditionally defined in terms of an individual's maximum or mean dispersal distance. One might assume that if an individual has the intrinsic dispersal capacity to physically access abiotically and biotically suitable habitat, then that species will colonize that habitat at a rate determined by its dispersal kernel and habitat structure. The importance of structural landscape **connectivity** in facilitating species range shifts under climate change has been well emphasized [17]. However, this perspective renders animal movement a deterministic or stochastic process, while movement is actually a behavioral process emerging from individual decisions about habitat use [18].

While the movement of sessile plants and fungi is shaped by the dispersal of propagules, animal cognition allows individuals to actively choose where to go. For animals, functional climate connectivity – the realized pattern of movement among suitable habitat patches as the climate changes – will therefore depend not only on the structural accessibility of habitats but also on the sum of many decisions underpinning an animal's movement [19,20]. Along with an individual animal's intrinsic movement potential, its willingness to explore novel habitat and the extent and timing of long-range movement decisions can affect whether it is able to reach accessible suitable habitat from its habitat of origin.

Dispersal into new areas may be associated with an individual's degree of boldness or exploratory behavior, correlated behavioral traits that encompass an individual's willingness to engage with novel or risky environments [21,22]. Bolder and more exploratory individuals tend to be better equipped to establish themselves in novel environments (e.g., urban environments, non-native ecosystems), and are more likely to be found at the leading edge of an expanding range [23–26]. More exploratory individuals should be more likely to seek out novel habitats under climate change, while timid and less exploratory individuals remain in place. Climate generalist Lodgepole chipmunk (*Tamias speciosus*) individuals tend to be more exploratory than its climate specialist cousin Alpine chipmunk (*Tamias alpinus*), which has experienced more significant elevational range contractions across its distribution compared to Lodgepole chipmunks [27]. Despite the theoretical underpinnings of this hypothesis, it remains to be robustly tested, and it is unclear whether invasion and urban colonization are appropriate analogs for range shifts.

Important animal movement events like migration and dispersal are often spurred by extrinsic environmental cues (e.g., changes in day length, precipitation, temperature). Climate change is poised to alter the timing and intensity of these cues, and animals will either have to adjust their timing of movement to ensure synchrony with critical resources or shift their movement in space to compensate, which in turn can change their distribution. An observed northward range shift in the Balearic shearwater (*Puffinus mauretanicus*), a pelagic seabird, was primarily driven by individual plasticity in migration destination in response to changes in sea surface temperature [28]. In many ecosystems, the timing and extent of seasonal rainfall has been changing, causing migratory ungulates to alter the timing of their migrations to align with peak availability of forage or shift their migration routes in space [29]. Leatherback sea turtles (*Dermochelys coriacea*) that are able to shift the locations of their nest sites are also projected to better buffer warming ocean temperatures [30]. Through their movement decisions, animals may persist in place by altering the timing of movement events or shift in space by altering the routes and destinations of these movement events.

The abiotic environment: tracking the fundamental niche

As climate change alters the abiotic environment, animals living at the limits of their physiological tolerance must adjust their behavior to maintain homeostasis if they are to persist in place. To buffer against the extensive physiological stress of climate change, many animals adjust local spatiotemporal activity to attenuate extreme fluctuations in temperature and/or moisture availability. Not only can some microhabitats provide thermal refugia, but the rate of temperature increase in the coolest microhabitats is often lower than in the overall macroenvironment [31,32]. Species that show a high degree of behavioral plasticity in microhabitat use should therefore be more likely to survive in their current habitat under climate change, limiting range shifts. North American Pika (*Ochotona princeps*), a high elevation specialist physiologically vulnerable to warming in its local environment, has persisted in warming habitats through flexibility in habitat use and thermoregulatory behavior [33]. In California desert communities, birds have been experiencing steeper population declines than mammals over the past century of climate change, in part due to mammals' greater ability to select microhabitat, thus limiting their exposure to harsh temperatures [34].

Animals cannot be active indefinitely, and structuring their diel activity allows them to effectively thermoregulate while optimizing their time spent foraging, finding mates, caring for offspring, and avoiding predators and competitors. Shifts to nocturnality under climate change allow animals to access resources (which may be increasingly limited under climate change) during times of day with reduced and more uniform temperatures [35,36]. For example, primarily diurnal white-lipped peccaries (*Tayussa pecari*) increase night-time activity in response to elevated daily temperatures [37]. By shifting their activity in time, animals have less need to shift activity in space. As a result, mammal species with more flexible diel activity patterns are less likely to exhibit range shifts in response to climate change than their strictly diurnal counterparts [38]. The climate generalist Lodgepole chipmunk (*Tamias speciosus*) displays more variability in diel activity patterns than the range contracting, climate specialist Alpine chipmunk (*Tamias alpinus*) [39].

When individuals are able to maintain their fundamental niche locally through behavioral shifts in microhabitat use and diel activity, they are more likely to persist in historic habitat, decreasing the potential of climate-induced range shifts on the lagging edge. However, the plasticity required to behaviorally buffer can also hinder adaptation by weakening the strength of selection on physiological traits [40,41]. Therefore, **behavioral buffering** can only be a viable strategy for species if changes in local environmental conditions do not exceed an organism's lethal physiological limits, or if buffering promotes persistence long enough for populations to respond to selection. Given many species' life histories, adaptation often cannot keep pace with the rapid rate of current climate change [42]. A global meta-analysis of lizards inferred that behavioral buffering will be insufficient to keep a substantial portion of lizard species from avoiding extinction under climate change [43], and empirical studies of *Sceloporus tristichus* lizards reveal that individuals are unable to select nest sites to buffer against warming [44]. In general, terrestrial ectotherms should face greater constraints to their ability to behaviorally buffer than endotherms. In marine systems, diel depth migration is often mediated by light rather than temperature, which may limit the ability of marine organisms to modify this behavior to buffer against changing temperatures. Studying animal habitat use alongside *in situ* measurements of microclimatic conditions will provide mechanistic insight into how climatic variation mediates species presence at multiple spatiotemporal scales. Many researchers are utilizing biophysical simulations that can incorporate behavioral responses to abiotic change in the environment to better understand how behavior mediates climate impacts [34]. Ultimately, behavioral dynamics must be linked to demography to determine the persistence potential of behavioral buffering strategies.

The biotic environment: intraspecific social dynamics

When considering the biotic factors that shape a species' distribution, researchers often focus on INTERspecific interactions. However, especially from the lens of behavior, an individual's INTRAspecific interactions with conspecifics can also shape their distribution. Animals exhibit a broad spectrum of **social behavior**, from solitary to obligately group-living cooperative breeders. Intraspecific social dynamics have the potential to have disparate effects on range dynamics, from enabling persistence in deteriorating habitats to facilitating or stymying colonization of new habitats.

Group living, through its myriad mutual benefits, can serve to buffer individuals from unpredictable and variable environments. Many animals live in stable groups of conspecifics, which facilitate antipredator defense, cooperative breeding, thermoregulation, or access to patchily distributed resources [45]. Intraspecific variation in social behavior is often related to variability in environmental conditions [46]. In birds, the evolution of family living is associated with increased environmental variability, and decreased risk of extinction in the face of rapid environmental change [47]. Gregarious caterpillars (Nymphalidae) in temperate environments are more likely to bask in the sun than solitary Nymphalid caterpillars, allowing them to better thermoregulate while potentially offsetting moisture loss [48]. In juvenile alpine marmots (*Marmota marmota*) decreased winter snow-depth leads to decreased year-to-year survival, in turn decreasing the number of helper adults further limiting survival [49]. As temperatures warm on a lagging range edge, groups can provide an important buffer potentially enabling persistence. Social behavior can also potentially enable colonization on the leading range edge. For example, in a range-expanding damselfly, *Ischnura elegans,* social aggregation serves to augment cold tolerance, enabling colonization of novel leading edge habitat [50]. Conversely, natal site fidelity – individuals remaining in or close to the place of their birth into adulthood – could act as a constraint on range shifts as individuals are unable or unwilling to break off from their group and disperse to novel habitat under climate change, falling into **ecological traps** [51].

Group living can allow for the development and transmission of behaviors within a population through **social learning**. Information can be transmitted either horizontally (within generations), or vertically (parents to offspring). Horizontal transmission in particular can yield novel behaviors and facilitate adaptive responses to change, as there is a wider pool of potential models from which an individual can learn, and information can move faster through a group [52,53]. Social learning can therefore serve as another buffer against climate change, increasing the likelihood of persistence on lagging range edges and expansions on leading edges, as individuals innovate strategies to survive under changing climates or establish themselves in novel habitats and share these innovations with their conspecifics [53]. Vertical transmission can also leverage the experience of older group members to enhance survival [54]. In whooping cranes (*Grus americana*), older experienced group members developed novel overwintering sites in response to climate change and then shared this knowledge with younger members of the flock [55].

Conversely, culturally transmitted information can also serve as a constraint to the development of innovative behavior that would facilitate persistence. Vertically transmitted information can be biased toward outdated environmental conditions, leading to maladaptive responses to rapidly changing environments [56]. Rather than facilitate plasticity and innovation, it can serve to canalize once-adaptive behaviors that are mismatched to current, altered conditions. In bottlenose dolphins (*Turciops truncatus*), culturally transmitted behavior of following human boats led to maladaptive outcomes as it increased the incidence of boat collisions and conflict [57]. Species with outdated or biased information would then be less likely to shift their ranges, despite climate change rendering that habitat unsuitable, or may continue to prefer increasingly scarce or unreliable but familiar resources, rather than switching to more abundant but novel resources.

The biotic environment: interspecific species interactions

Strong interspecific interactions may lead to a prediction of tightly coupled range shifts between interacting species, but behavioral plasticity (e.g., diet switching) can allow an animal to persist in place instead of following its primary resource. Individuals that lack the plasticity necessary to make use of novel trophic resources, or respond to novel biotic threats in their changing habitats, will be forced to move if an important resource becomes locally extinct or a novel consumer or competitor shifts into its range. These relationships complicate predictions of species distributions under climate change.

As climate change alters the quality, quantity, and distribution of available forage [58–61], herbivores can alter their diets in their current habitat [62,63] or seek out new habitat [11]. The ability to plastically modify foraging strategies and behavior based on environmental context will have direct consequences for species ranges, as organisms maintain historic range by switching to novel food sources, or shift their ranges as they follow a preferred food source. In a community of marine fishes in the Pacific (including Pomocentridae, Chaetonidae, and Kyphosidae), a species' degree of trophic generalization was the best predictor of its range extent [64]. In predator–prey interactions, a predator must not only be able to recognize and pursue novel prey to switch resources, but also counteract prey anti-predator defenses. The outcomes of novel matchups will depend on predator and prey capacity for innovation and flexibility, prior experience, and evolutionary history. Canada lynx (*Lynx canadensis*) have evolved specialized morphology and behavior to successfully hunt snowshoe hares (*Lepus americanus*) year-round, but as climate change leads to shallower winter snow depths, generalist coyotes (*Canis latrans*) expanding into more northern habitats are also starting to hunt hares, increasing overall predation pressure [65].

Species should be more susceptible to antagonistic interactions such as competition and predation on the edges of their range [66], potentially limiting expansions on the leading edge and hindering persistence on the lagging edge, although behavior can play an important role in mediating effects. In the last 30 years, the western bluebird (*Sialia mexicana*) has been expanding its range in the Pacific Northwest. Aggressive western bluebirds along the range-front displace resident mountain bluebirds (*Sialia currucoides*), allowing the western bluebird population to establish [67]. Range-shifting individuals can encounter locally adapted residents that are potentially better competitors, limiting their growth and survival in otherwise abiotically suitable habitats [68]. Therefore, individuals that can undergo rapid niche displacement through plasticity in foraging preferences, diel activity, and habitat use will be more likely to establish new ranges in the presence of a strong competitor. In the community-level analysis of Pacific reef fishes, niche displacement through diet shifts allowed range-expanding tropical species to coexist with resident temperate species [64].

Species interactions can also constrain the ability of an animal to behaviorally buffer in response to abiotic changes in climate. The acute risks posed by predation, for example, might outweigh the benefits of behavioral mitigation of longer-term effects of climate change. In warmer environments, crickets (*Gryllus lineaticeps*) tend to forage more often, but in the presence of black-widow spider predators (*Latrodectus hesperus*), they show no change in foraging rate regardless of temperature [69]. Similarly, African ungulates do not take advantage of cooler night-time temperatures to avoid increasing daytime heat under climate change, as they prioritize avoiding predation from nocturnal predators [70]. The constraints placed by species interactions can limit persistence on the lagging edge by pushing animals to seek out or avoid strong interactors in environments in which they otherwise would be able to persist through behaviorally ameliorating abiotic stress.

Integrating behavior into mechanistic predictions of species range shifts

By integrating these dimensions of behavioral variation in response to climate change, we can better understand and predict changes in a species' range (Figure 1). In particular, plasticity in behavior allows organisms to dynamically respond to novelty in their environment, enhancing survival in their current habitats through persisting in place or facilitating adaptive range shifts to novel suitable habitat through shifting in space. Along lagging edges of a species' range, which tend to encompass the warm, increasingly stressful range limits, behavioral buffering of abiotic stress should predominate, fostering persistence in place and forestalling range contraction. Along leading edges, the cooler range limits where once colder and stressful habitat is becoming more abiotically suitable, behavioral dynamics in the biotic and movement domain will predominate.

Behavioral plasticity will be an important determinant of species range shifts and persistence under climate change. For one, plasticity allows individuals to behaviorally buffer and persist in place at the lagging range edge. Species that can take advantage of a wider range of resources or modify their behavior to maintain their fundamental niche are poised to persist, in contrast to

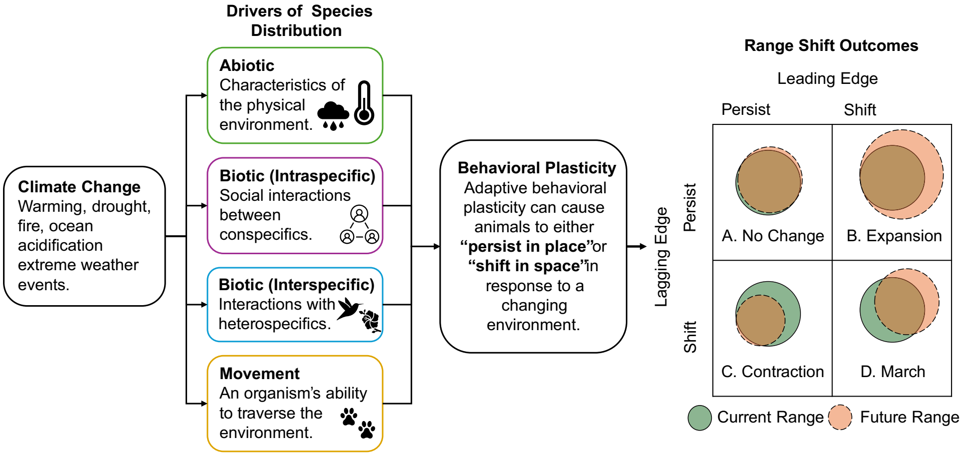


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Figure 1. A graphical framework describing the effects of climate change on species distribution. Climate change alters an animal species' abiotic, biotic, and movement environment, and the effects of these changes on species distribution are mediated by animal behavior. Behavioral plasticity allows animals to either persist in place or shift in space to adapt to rapid environmental change. Whether or not this plasticity operates on the leading and/or lagging edge of a species range can generate a diverse variety of outcomes under the same climate scenarios. We incorporate a portion of the range outcomes outlined in Lenoir and Svening [7]. (A) A species has the plasticity necessary to behaviorally buffer abiotic stress and persist in its current habitat along the lagging edge, but not to colonize newly available suitable habitat on the leading edge, leading to no change in the species' range. (B) A species has the plasticity to both persist on its lagging edge and shift on its leading edge, leading to a range expansion. (C) A species lacks the plasticity to persist on its lagging edge or shift on its leading edge, leading to a range contraction. (D) This species lacks the plasticity to behaviorally buffer along its lagging edge, but possesses the plasticity necessary to shift its range into newly available suitable habitat, resulting in a 'march', in which the species range extent does not change, but the center of the range marches up in latitude or elevation.

behaviorally inflexible species. In the short term, behaviorally inflexible species are more likely to shift their range, but these species may not necessarily be equipped to successfully establish in novel habitats that do not closely match their ancestral habitat in abiotic, biotic, and movement dimensions. Behaviorally plastic individuals are also more able to take advantage of novel biotic resources, and will be more successful establishing in novel habitats when shifting in space at the leading edge. Therefore, the ability to respond to a wide range of potentially adaptive cues broadens the range of suitable habitat available.

For species that exhibit intraspecific variation in behavioral plasticity, there can be different range outcomes depending on whether plastic individuals are concentrated on the leading versus lagging edge (Figure 2). The species interactions-abiotic stress hypothesis posits that abiotic considerations are most important at the abiotically stressful edge of a species range while species interactions are more important at the less stressful edge [66,71]. Traditionally, a species' warm range edge is considered the less stressful edge dominated by species interactions, while the cooler edge is the more stressful edge dominated by abiotic constraints. However, under climate change, warm (lagging) range edges are becoming more abiotically stressful, while cool (leading) edges are becoming less stressful, resulting in a reversing of this pattern. Therefore, we contend that adaptive behavioral plasticity on the lagging edge will facilitate persisting in place through mediating abiotic stress, while adaptive plasticity on the leading edge will be more important for mediating novel species interactions. However, the rapid nature of climate change can result in maladaptive plasticity as well, and as we see across the different components of BAM, there are new opportunities for organisms to fall into ecological traps. These maladaptive responses are often seen in cases of phenological mismatch, where changes

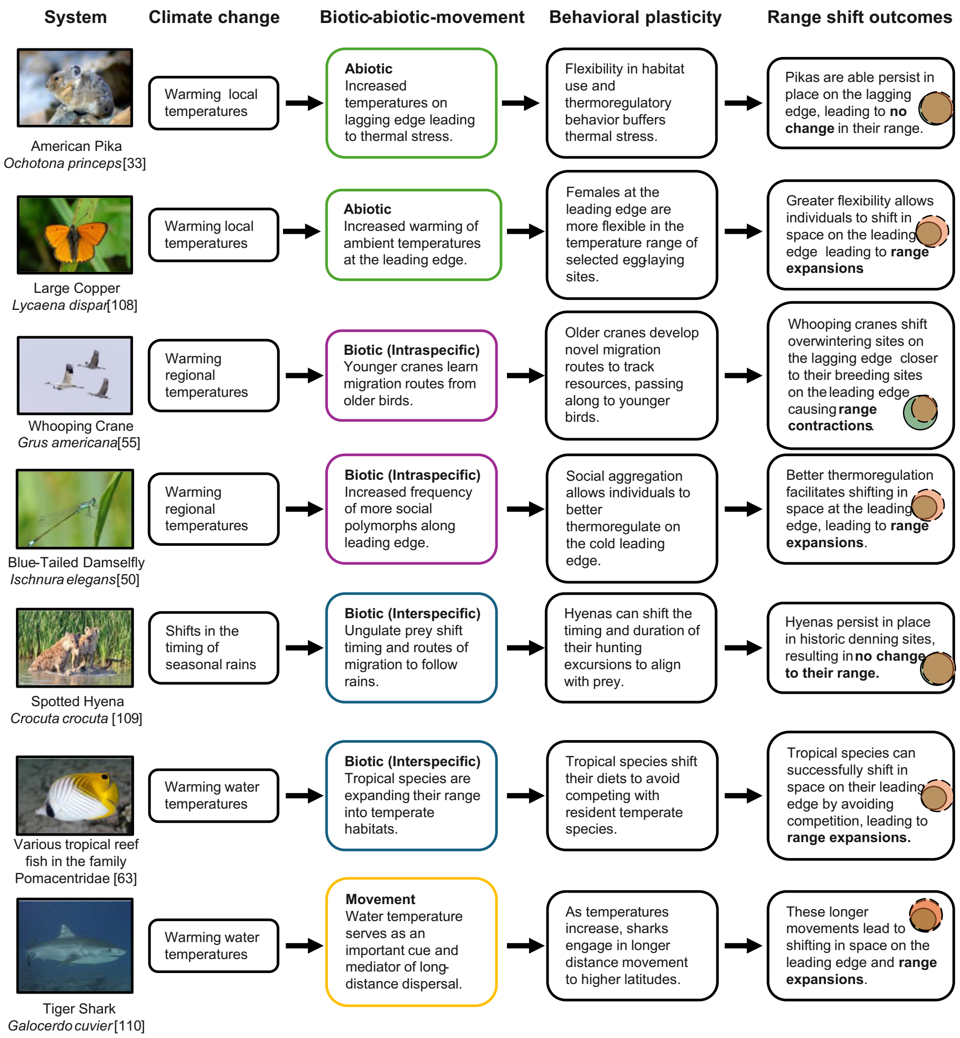

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Figure 2. A selection of case studies illustrating how behavioral plasticity mediates species distribution under climate change. For each case study, we use the framework outlined in Figure 1 to detail the pathway through which the effects of climate change on the environment, mediated through behavior, can lead to different range shift outcomes. For most cases, the predicted species range shifts have not been documented, but rather are derived from our hypotheses about the role of behavioral plasticity in mediating range shift outcomes. (See [33,50,55,63,108–110]). Photo attributions in order of appearance: K. Schneider https://creativecommons.org/licenses/by-nc/2.0/; xulescu_g, https://creativecommons.org/licenses/by-sa/2.0/; Diana Robinson https://creativecommons.org/licenses/by-nc-nd/2.0/; Thomas Bresson https://creativecommons.org/licenses/by/2.0/; Brian Ralphs https://creativecommons.org/licenses/by/2.0/; Francois Libert https://creativecommons.org/licenses/by-sa/2.0/; Kris Mikael Krister https://creativecommons.org/licenses/by-sa/2.0.

in the timing of seasonal events under climate change do not happen synchronously, decoupling environmental cues from seasonal resources on which organisms rely [72].

Concluding remarks

The ability to more accurately model and predict species' range shifts is an important tool for biodiversity conservation as the climate changes (Box 3). There are growing calls to conserve habitat with future range shifts in mind [73], and localities that can serve as climate refugia are considered critical for the survival of at-risk species [74]. However, the species distribution models we rely upon

Outstanding questions

Are species with high rates of behavioral plasticity less likely to exhibit climate-induced range contractions?

What are the demographic consequences of behavioral responses to climate change, and how do they influence species distributions?

Are behavioral traits that allow species to cope with climate change also conducive to coping with other forms of anthropogenic change, such as human disturbance and habitat modification?

Can modeling approaches that simulate real-time animal decision making and movement better predict species range dynamics?

How do behaviorally mediated range dynamics vary across different geographical scales, or between terrestrial and marine systems?

How might a more behavioral understanding of the drivers of species distribution inform the conservation of habitat and species under climate change?

What tradeoffs do animals face when behaviorally responding to climate change and human disturbance?

Box 3. How we can study behavioral mechanisms of range shifts under climate change

Using our framework, we propose a toolkit of approaches to empirically study behavioral mechanisms of climate-induced range shifts, and incorporate this framework into predictive models of species' ranges. Repeated, within-individual measures of behavior across environmental, spatial, and temporal gradients will be important to assess the ability of organisms to alter their behavior in response to rapid environmental change at range edges and interiors.

Abiotic

An animal's ability to behaviorally buffer is an important factor in their ability to persist in place under climate change. Understanding behavioral buffering entails measuring organismal physiological performance and spatiotemporal habitat use under a range of climate conditions, at a spatiotemporal scale relevant to the individual animal. Observations and measurements of an individual's microhabitat use and diel activity can be complemented by laboratory or field physiological assays [99], implantable biologgers [100], or portable weather sensors such as ibuttons [101].

Biotic (intraspecific)

An animal's social environment can mediate the effects of climate change on range shifts, but is challenging to measure. Researchers can collect behavioral observations from multiple uniquely identified individuals through direct observation of social interactions, or quantify spatial interactions with autonomous sensor data (e.g., proximity loggers or GPS trackers) [102]. Experimental studies of social learning can shed light on how adaptive or maladaptive climate responses spread through social groups, with spatial responses of particular relevance for range shifts [103].

Biotic (interspecific)

When possible, contextualizing studies of individual behavior in their local community can provide deeper insight. Whole-community surveys of species occurrence and habitat use using tools like camera traps can shed light on fine-scale spatiotemporal interactions among species, while individual diet analysis with DNA metabarcoding will help to quantify the strength, and nature of trophic relationships [104].

Movement

While surveys of species occurrence as a function of climate are relatively commonplace, direct measures of real-time movement through the landscape are more challenging to obtain. In particular, studies need to track individuals with enough resolution to capture dispersal events and map functional connectivity. Advancements in tracking technology such as GPS transponder collars [105], and satellite or drone imagery [106] are making these data more obtainable.

Modeling and predicting range dynamics

Importantly, studies should examine animal behavior and plasticity across elevations, latitudes, and depths. A study of behavior that captures variation across a species' range edge to interior, or compares the leading and lagging edges, can provide insight into how behavioral plasticity operates under different environmental constraints. As we seek to integrate our understanding of behavior and range dynamics, mechanistic agent-based models provide a unique opportunity to test how individuals with differing degrees of behavioral plasticity may influence range dynamics over short and long time scales. We can then compare these predictions to observed range shifts, as well as more traditional species distribution models [107], to determine what best aligns.

to identify suitable habitat often fail to predict species occurrence [75] or range shifts [13]. If we can identify refugia through the lens of species' behavioral responses to the abiotic, biotic and movement environment of an organism, we can better anticipate where species will persist in portions of their ancestral ranges under climate change [76]. A behavioral approach can also allow us to better parse the relative influence of climate and other forms of disturbance when predicting anthropogenic influences on species distributions because human disturbance and habitat modification are also having drastic effects on animal behavior [77,78] and species distributions [79]. In addition to reshaping ecological communities, this reordering of species could lead to novel human-wildlife interactions and amplify human-wildlife conflict [80]. Behavior, while not the only dimension influencing range dynamics, is a valuable component to a more robust, mechanistic understanding of the factors influencing species distribution under climate change (see Outstanding questions).

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Declaration of interests

No interests are declared.

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