Title: Adjusting the lens of invasion biology to understand risks of climate-driven range shifts

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Abstract:

As Earth's climate changes, species persist in part by shifting into new regions. Facilitating these range shifts is recognized as a key climate change adaptation strategy. However, some range-shifting species will displace other species and potentially alter community and ecosystem processes. Here, we use invasion ecology theory and knowledge to assess the potential impacts of range-shifting species. Although there are many differences between introduced and range-shifting species, impacts can occur via similar mechanisms, and the magnitude of impacts can be similar. By adopting an existing risk assessment framework, potential risks of range shifters can be assessed on the basis of traits associated with successful introductions. As existing ranges shift in response to climate change, we have a unique opportunity to develop plans for managing species' range shifts in real time by facilitating advantageous movements and discouraging those that are potentially problematic.

One-sentence Summary: Ecological impacts of range-shifting species could be predicted by leveraging our knowledge of invasion ecology and adapting existing risk assessments.

Main Text:

Climate change is increasingly affecting species and ecosystems across the globe, threatening biodiversity at both local and broad scales[1]. In response to unprecedented warming temperatures, species from virtually all taxa and ecosystems have undergone redistribution towards higher latitudes and elevations[2–6]. Because colonizing new habitats helps species persist both regionally and globally[7,8], range expansion is seen as overwhelmingly beneficial to biodiversity conservation[9]. However, with the exception of some problematic species[10] and considerations regarding transplants and assisted migration[11–13], few studies (although see [3]) have assessed the community and ecosystem impacts as species track their climate niche into new areas. The lack of studies on range shift impacts is remarkable given that the introduction and spread of new species is often viewed by ecologists through the lens of invasion biology, where the primary concern is the potential for negative impacts on the recipient community. This dichotomy underscores the importance of considering ecological impacts of range-shifting species in terms of both the benefits to their persistence, as well as the potential costs to recipient communities, and subsequently ecosystem processes.

There are important ecological differences between introduced and range-shifting species that may result in different levels of risk associated with each group. For example, synthesis work considering a broad range of introduced species suggests that 10 to 50% become invasive and have negative impacts[14–16]. In contrast, empirical analyses indicate that native species are much less likely to be problematic when shifting to nearby recipient communities[16]. Despite the

overall lower expected risks from range shifting species, being able to predict which particular species are likely to have a large impact is critical for conservation of the recipient community. Invasion ecology, therefore, provides insight for considering these interactions and assessing risk on a species by species basis.

The movement of populations in response to climate change is in many ways similar to the invasion of introduced species, in that it creates the potential for novel species interactions[17]. Both introduced and range-shifting species (see Table 1 for definitions) have been shown to negatively impact recipient communities by consuming, parasitizing, or competing with native species that lack the ability or defenses to overcome them[3,10]. However, range shifters frequently share an evolutionary history with some species in the recipient community and will not be completely novel, decreasing their potential for harmful impacts due to established niches and community roles[18]. By mapping concepts from invasion biology onto range shifts, we hope to clarify the conditions under which invasion ecology may help to identify conservation-related risks. As more species shift in response to climate change, methods for assessing potential impacts on recipient communities, and thus prioritizing which species to facilitate, become more valuable. Here, we leverage our understanding of biological invasions to describe a framework for assessing the likelihood and degree to which a range-shifting species could impact recipient communities.
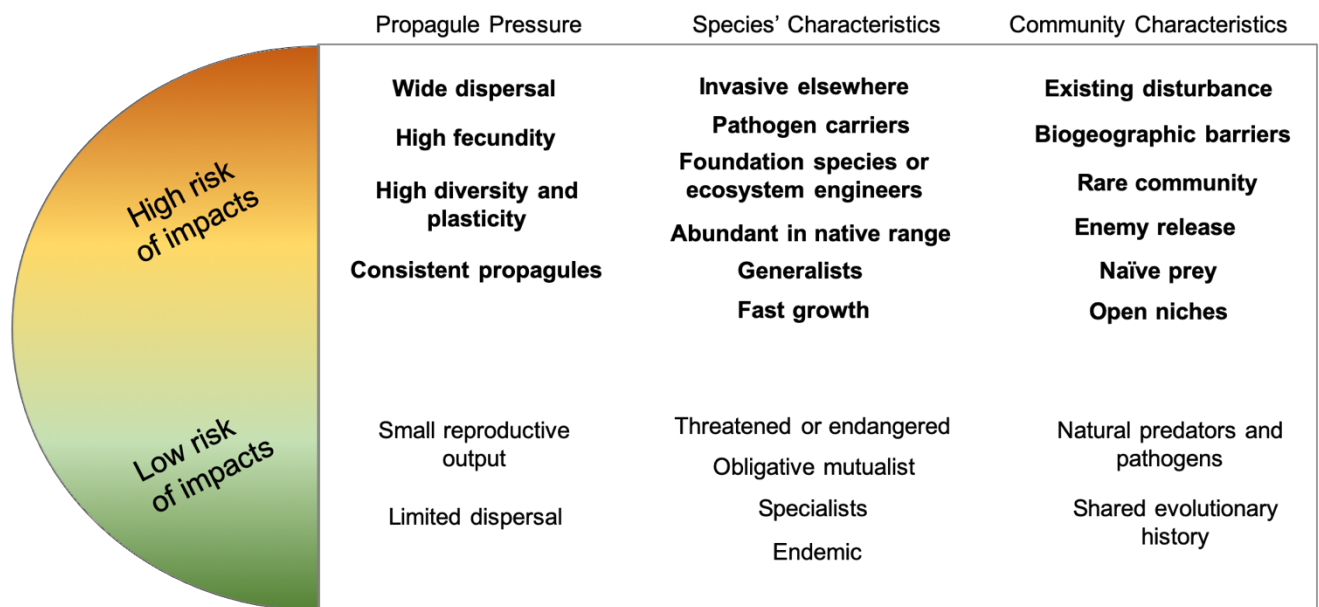
Table 1. Definitions of terms as used in this manuscript.	
Range shifter/range-shifting species	A species that changes its range to track its environmental niche under climate change. This paper focuses on species that expand (or relocate) their ranges beyond historical native ranges into nearby communities.

Introduced species	A species transported to a new ecosystem by humans, whether intentionally or unintentionally (not including range shifts as a result of anthropogenic climate change).
Invasive species	An introduced species that causes negative ecological, economic or environmental impacts.
Impact (ecological/environmental)	A measurable change in pattern or process at any level of ecological complexity (i.e. species, communities, ecosystems).
Recipient community	The community to which an introduced or range-shifting species arrives.
Donor community	The community from which an introduced or range-shifting species originates.
Establishment	The process by which a founding population increases in size and becomes self-sustaining.
Spread	The process by which a species' range expands into new locations at an increasing distance from the original area of establishment.

Applying an Invasion Ecology Framework to Range-shifting Species

Invasion ecologists have invested considerable effort into developing rubrics for predicting which introduced species are likely to become problematic. These risk assessments are based on how invasive species' traits combine with community vulnerability to influence the likelihood of establishment, spread, and negative impacts. Researchers have tested many

hypotheses about mechanisms that cause introduced species to become invasive [19]. Catford et al.[20] proposed a framework that broadly categorized these hypotheses into groups involving propagule pressure, abiotic characteristics of the recipient community, and biotic characteristics of both the recipient community and introduced species. Many but not all of the factors influencing invasion success, as identified in the Catford et al. framework, might also translate to impacts of range-shifting species. Here we use this framework to help assess the potential impacts of range-shifting species and identify species and communities of concern (Figure 1).

	Propagule Pressure	Species' Characteristics	Community Characteristics
High risk of impacts	**Wide dispersal** **High fecundity** **High diversity and plasticity** **Consistent propagules**	**Invasive elsewhere** **Pathogen carriers** **Foundation species or ecosystem engineers** **Abundant in native range** **Generalists** **Fast growth**	**Existing disturbance** **Biogeographic barriers** **Rare community** **Enemy release** **Naïve prey** **Open niches**
Low risk of impacts	Small reproductive output Limited dispersal	Threatened or endangered Obligative mutualist Specialists Endemic	Natural predators and pathogens Shared evolutionary history

Figure 1. Risk assessments for biological introductions focus on three main components: the introduction of propagules, the abiotic environment, and the biotic interactions that lead to the successful establishment and spread of species. Many overlaps are found between range shifters and introduced species (in bold) that can indicate whether a species is likely to be high-risk (warm colors). Identifying range-shifting species with these traits can inform potential management strategies.

Propagule Pressure

Propagule or dispersal pressure is critical to establishment success of any introduced species[21,22]. Most biological invasions experience a lag period between the initial introduction and the time they become invasive. This lag can last from 3-140 years in plants and from 10-38 years in birds[23], in some cases due to a lack of genetic diversity from founder effects because of introduced species' small populations. Increased propagule pressure can reduce these lags by increasing genetic diversity and adaptability of spreading populations[24,25], which could facilitate the movement of range-shifters with a larger native gene pool.. Additionally, propagules and dispersals of range-shifters are likely to have been arriving sporadically into the recipient community, at least at locations near the shifting species' range margin, for a long time. Thus, the existence of nearby source populations could reduce time lags and increase the rate of population growth and range expansion, especially for species that are dominant and prolific propagule producers (Figure 1). For example, marine organisms are expanding an order of magnitude faster than terrestrial species, likely due to higher rates of propagule production and higher connectivity between systems, which limits the barriers to widespread dispersal[3,26].

Abiotic Effects on Impacts

Introduced species can establish in new communities when they have a competitive advantage or they occupy an empty niche; for example, anthropogenic disturbances can provide a window of opportunity for non-natives[27]. As the climate continues to change, recipient communities are likely to experience more frequent and acute abiotic stresses, which may lead to decreased populations and extirpations across taxa and ecosystems[4,28]. This may enable the establishment of range shifters as they track their optimal climates. For example, shorter winters

and higher minimum temperatures are allowing many range-shifting insect pests (such as spruce and pine beetles) to colonize forests that were previously outside their range[29–31], leading to profound impacts on these ecosystems[32]. As these fast-growing insect pests shift into novel forest communities, drought conditions increase trees' vulnerability, exacerbating pests' impacts [33,34].

Similarly, some of the most problematic introduced woody species host nitrogen-fixing microorganisms in their roots, thus allowing them to outcompete native species. *Myrica fava* in Hawaii, *Lupinus arboreus* in California grasslands, and *Acacia* spp. in South Africa are examples of highly invasive shrubs and trees that benefit from greater access to nitrogen in nitrogen-poor soils[35]. Black locust, *Robinia pseudoacacia*, is a fast-growing nitrogen-fixing native tree of southeastern North America that is currently undergoing a climate-mediated range shift[36]. As black locust moves north of its current range in response to climate change[37], it is likely to have a competitive advantage over native vegetation, especially in nitrogen-deficient soils. Early identification of abiotic characteristics that promote invasions can be useful for identifying similar traits in range shifting species.

Biotic Characteristics

As with invasion, biotic characteristics of shifting species and recipient communities influence potential impacts (Figure 1). Traits that make introduced species successful (e.g., high fecundity, fast growth, generalists versus specialists, ecosystem engineers, etc.) will also facilitate the spread of range shifters[38–42]. However, because of the differences in shared evolutionary history with species in the recipient community, impacts on the recipient community are likely to differ[43]. Introduced species often benefit from interacting with new

species (naïve prey)[44] and leaving old enemies behind (enemy release)[18], and the magnitude of impacts depends on the strength of interactions, either via differences in abundance or per capita effects[45]. In contrast, species undergoing passive range shifts settle in adjacent communities, which are likely to have some overlap of species composition and history of interactions with the donor communities[3,46]. Such overlaps may limit species' abilities to track climate change as biotic barriers to expansion are likely to be higher [47,48].

There is, however, evidence that range-shifting species can also experience enemy release[49,50], especially when a range shift occurs over a long distance or crosses a biogeographic boundary that previously limited dispersal[51]. Furthermore, the probability that a range-shifting species will experience release from natural enemies and encounter naïve species in the recipient community is higher at ecotone edges where dissimilar adjacent communities meet[52]. For example, the movement of tropical fish species to temperate communities has been facilitated by weaker chemical defenses in temperate algal species. In the southeastern Mediterranean Sea, the expansion of tropical herbivores led to a 60% loss in benthic biomass, a 40% decrease in species richness, [53] and ultimately, a shift from a temperate reef system to one that more closely resembles adjacent tropical communities. Such "tropicalization" of marine systems has become widespread as a result of range-shifting species[54,55]. When such control mechanisms are absent, impacts of range shifts can occur at a magnitude equivalent to that of invasions[3].

By applying an invasion ecology framework to species that are undergoing range shifts, we can predict that range shifters are less likely to impact recipient communities if they have coexisted with species in the recipient community. As with introduced species, the strongest impacts will likely be seen in communities with high concentrations of specialist species[56],

populations with low genetic variability[7], species that are already threatened by exploitation[57], or species with low population sizes[58]. However, communities with traits that confer high biotic resistance, such as high rates of predation or herbivory, high diversity, or strong competitive interactions[59], will be most resistant to impacts of range shifters[60].

**Impacts of range-shifting species can parallel invasions**

Impacts of range shifters have been reported across taxa and ecosystems[61]; however, many have been overlooked in the climate change literature. In marine systems, for example, range-shifting and introduced species can cause community-level effects of the same direction and magnitude, but these impacts have been studied in fewer than 10% of documented marine range shifts[3]. Here, we present examples that illustrate how impacts of range-shifting species could have been predicted by applying an invasive species risk assessment framework based on the traits and associated impacts reviewed above.

When Range Shifters Experience Enemy Release

Range shifters encountering new species can have significant impacts on recipient communities through changes to biotic processes, such as predation, competition, and the transmission of new parasites or pathogens. In North American forests, the southern flying squirrel (*Glaucomys sabrinus*) is displacing the smaller northern flying squirrel (*G. volans*) as the southern species expands in response to increasing temperatures[62]. In addition to being superior competitors, southern flying squirrels are carriers of an intestinal parasite that is deadly to northern flying squirrels[63,64]. These interactions can also have cascading effects on other range

shifters, leading to a "squeeze" for species that cannot undergo range shifts. In the same forests, white-tailed deer and their associated parasites are also expanding northward in response to climate change[65]. Due to increased parasites as well as thermal stress, moose, which are boreal specialists, are ultimately predicted to be extirpated from sites along the southern edge of their range[66]. However, at the northern end of the moose's range in Alaska, deciduous forest is expanding. This has led to the establishment of moose, which outcompete native caribou[67] (Figure 2). Similar to introduced species, some range shifters will cause localized extinctions, and risk assessments can help identify these species prior to their impacts.

Figure 2. Range shifters can negatively impact recipient communities. For example, as white-tailed deer expand their range (stripes) northward in response to climate change, moose at the southern edge of their range (stippling) are experiencing greater rates of parasitism and are projected to undergo population declines[66]. In contrast moose populations at the northern range edge are increasing and outcompeting caribou[67]. Ranges based on USGS GAP data.
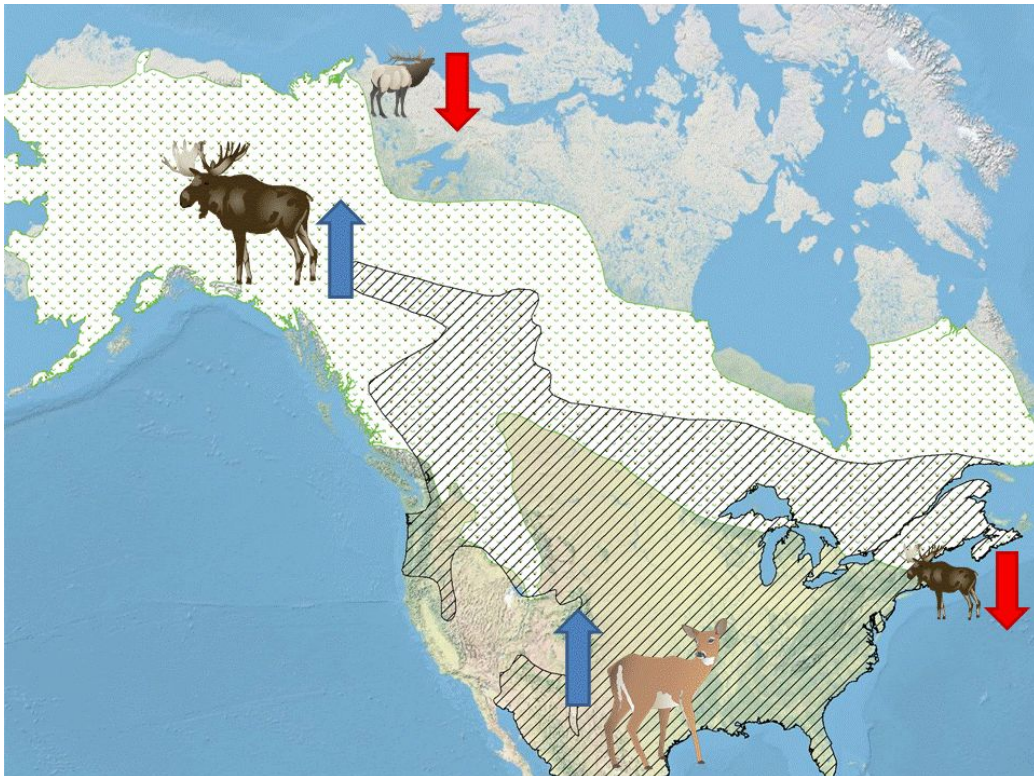
Invasive traits in range-shifting species

As with species that become invasive, range shifters with certain traits are more likely to have larger impacts. For example, many expanding trees are conifers, which have biological traits that make them good colonizers. Most notably, pines can have relatively fast growth, are resistant to environmental stresses, and develop monospecific stands that provide high propagule pressure[68]. Many dominant species are also generalists, which are able to utilize a variety of different resources. In marine systems, ocean warming has allowed the long-spine sea urchin *Centrostephanus rodgersii,* previously limited by juvenile growth, to redistribute poleward from mainland Australia to Tasmania[69]. This urchin consumes a wide range of marine macroalgae, leading to significant declines in kelp forest habitat[70]. Additionally, the long-spine urchin, a generalist herbivore, consumes many of the same prey species as the blacklip abalone, a specialist; the reduction in resource availability has led to decreased abundance, fitness, and survival among abalone populations[71].

Community changes by range shifters can alter ecosystem states

The abundance, role, and trophic level of a species in its donor community can be indicative of its success in a recipient community[45,72]. Effects on populations and communities can ultimately scale up to alter ecosystem states and processes.

As trees colonize new areas, changes in ecosystem functioning may include increases in aboveground and belowground biomass and altered nutrient cycling through changes in litter decomposition, processes that can lead to a complete replacement of the recipient community[73]. For example, climate-related shifts of tree lines have been described in many parts of the

world[6,74,75], and grasses are expanding in the tropics as fire frequency increases[76]. The ecosystem impacts of these changes have been less explored than those that occur after invasions by introduced trees and grasses. Community and ecosystem effects have been observed in aquatic and marine systems, as well. For example, herbivory by the long-spine sea urchin *Centrostephanus rodgersii* has resulted in the collapse of kelp forests, leading to decreased biodiversity, a simplified food web, and low primary productivity[77].

Another ecosystem shift occurring in tropical and subtropical regions is the poleward expansion of mangroves into salt marshes[66]. In Florida, mangrove forests have doubled their area of distribution at the northern end of their historical range due to reduced frequency of cold-weather extremes[67]. Both mangrove trees and salt marsh grasses are foundation species in their respective ecosystems and play an important role in structuring communities by providing habitat and altering nutrient cycling[78]. Because mangroves have greater aboveground biomass and, therefore, structural complexity than native salt marsh vegetation, their expansion has broad implications for coastal wetland ecosystems. The establishment of introduced mangroves in sandflats has increased the concentration of fine sediments and organic matter, leading to a higher abundance and diversity of non-native macrofaunal[79]. The lack of defenses of temperate species to tropical herbivores[80,81], general patterns of increased nutrient content with latitude[82], and increased disease due to increased herbivory[83,84] may accelerate the tropicalization of these temperate wetland regions under future climate change. Previous research on the impacts of biological invasions on ecosystem properties and processes has shown that these impacts are highly context-dependent, as the magnitude and direction can vary both within and between types of impacts depending on taxa and ecosystems[85]. Identifying species that are likely to act as

ecosystem engineers or have other characteristics associated with high risk (Figure 1) is therefore a priority.

Balancing conservation with risk

Conservation options for promoting persistence (and preventing extinction) of species threatened by climate change include increasing habitat connectivity to facilitate species movement and actively moving species, i.e., assisted migration[11,12]. In the context of assisted migration to facilitate climate change adaptation, conservation organizations, e.g., International Union for the Conservation of Nature (IUCN)[86], are already considering invasion risk. However, increasing habitat connectivity to facilitate the movement of range-shifting species is generally considered an unmitigated good with little regard to the full range of impacts on the recipient community.

Rather than encouraging the movement of all species, we suggest using a risk-benefit analysis framework to assess the level of risk that a range-shifting might pose. In some contexts, increasing habitat connectivity might best be based on analyses of donor and recipient communities with a focus on providing connectivity for low risk, nearby natives (Figure 1). Although there are inherent value judgements in assigning worth to species, we suggest that management should generally 1) facilitate range shifts that promote ecosystem services and biodiversity[87] and 2) discourage range shifts of species with the potential to negatively impact sensitive or rare communities and ecosystems[88]. In some cases, the analyses will be straightforward. For example, species that are both locally and regionally uncommon may pose little risk to recipient communities (Figure 1) and would benefit from opportunities to shift their

ranges. However, this is unlikely to be true for species that have large impacts on their native

communities. Keystone predators (which have a disproportionate impact relative to their

abundance) and foundation species (species that facilitate diversity by providing habitat and

modifying the environment) may lead to management conundrums, as such species may pose

great risk to recipient communities, but could facilitate the colonization of other, more desirable

range-shifting species with which they interact[89].

Even range-shifting species with small impacts in their donor communities can have large

impacts in recipient communities because of novel interactions with species in the community.

For example, if range-shifters occupy formerly open niches and possess functional traits that are

qualitatively different from native species, range-shifters are likely not only to colonize

successfully but also to cause major impacts to the community and ecosystem. A single invasion

can be devastating to a community[90], and risk assessments are a useful and often-applied tool for

identifying species of concern. Therefore, like those who warn about the dangers of assisted

migration[91], we propose that before facilitating range shifts, the potential ecological, economic

and social impacts associated with these management actions should be considered[87]. There are

many impact assessment tools that can be used to evaluate the potential impacts of introduced

species[92]. Notably, the Environmental Impact for Classification of Alien Taxa (EICAT)

framework is a standardized, objective, and transparent approach adopted by the IUCN in 2016

that identifies the mechanisms through which introduced taxa can impact recipient

communities[72,86]. Although this assessment was developed for introduced species, the

mechanisms of impact outlined in EICAT apply to the interactions between range shifters and

recipient communities as well. Identified mechanisms primarily fall into the biotic characteristics

of the Catford et al.[20] framework and consist of competition, herbivory and predation (including

parasites and pathogens), hybridization, poisoning/toxicity, biofouling, herbivory, ability to alter

the ecosystem, and interactions with other non-native species. These mechanisms are scored

based on their magnitude of impact to the recipient community, with scores ranging from

minimal (i.e., reductions in fitness) to *major* (i.e., local extinctions), which can lead to novel

communities (Figure 3).
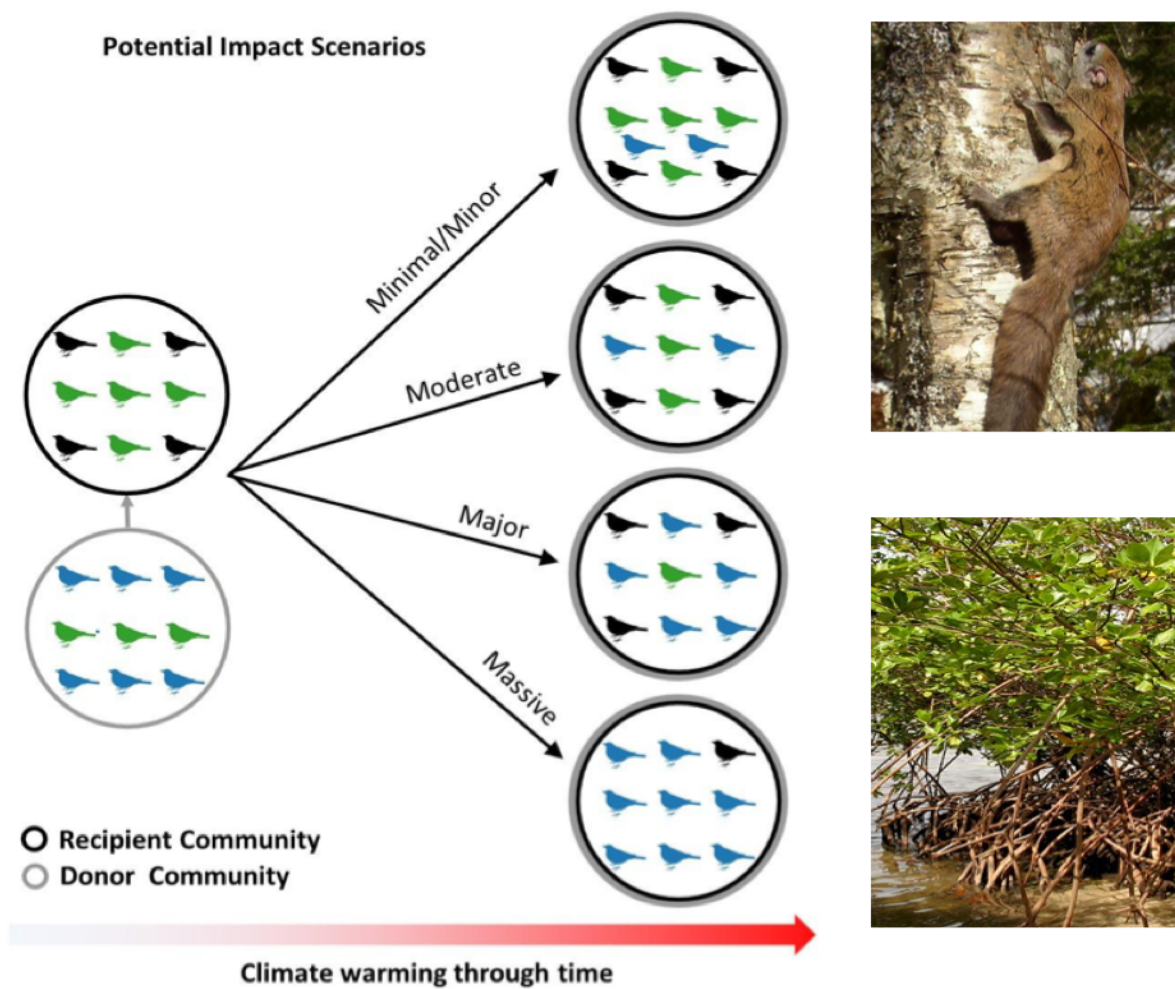
Figure 3. As climate change alters environmental conditions, range shifts can lead to new species interactions and changes to community structures depending on the magnitude of associated impacts. For example, as individuals from a nearby donor community (blue birds in grey circle) shift into a novel recipient community (green and black birds in black circle) in response to climate change, they may have minimal impact (few blue birds in a community of primarily green and black birds), up to a massive impact where the shifting species predominates. Similar impacts can be seen in the cases of southern flying squirrels driving out northern flying squirrels (moderate due to effects on populations) to tropicalization (massive, irreversible shifts in ecosystems). Images obtained from the U.S. National Park Service.

We suggest applying EICAT to rank and prioritize range-shifting species based on their potential impacts on recipient communities and to develop monitoring or control plans to limit those impacts. For example, communities receiving range-shifting species with the lowest potential to experience negative impacts (*minimal*, *minor*, and *moderate*) are likely to benefit most from passive management, such as monitoring. Such range shifts could maintain or even increase community diversity and allow for persistence of populations under increasingly stressful environmental conditions. Although *minor* and *moderate* impacts lead to reductions of fitness in individuals or declines in population abundances, respectively, the recipient community structure and functioning are preserved. Future communities may not be analogous to existing recipient community, but shifts are likely to have a net positive impact on global biodiversity.

Range-shifting species with *major* or *massive* impacts, however, may need to be actively managed, whether through facilitating or restricting movement, as their impacts could alter community structure and composition and cause local extinctions in the recipient community.

While such changes, by definition within the EICAT framework, are reversible for species with major impacts, those with *massive* impacts are likely to cause irreversible changes as the community passes a threshold from which it can no longer recover. In the cases of species with *major* or *massive* impacts, early detection and rapid response is vital to preserve future options and serious consideration should be given to whether the benefits of promoting the persistence of the range-shifting species or populations justify the impacts on the recipient communities. Based on approaches traditionally used to manage invasive species, we recommend the following specific strategies for range-shifting species:

1) **Involve stakeholders early:** Work closely with natural resource managers, conservation practitioners, and decision-makers at every step of the process, including to identify priority ecological and cultural species[93,94] and important ecological services[5].

2) **Identify management priorities for range-shifting species and recipient communities:** What is the conservation status of the range-shifting species? How important is the range shift for its persistence? How unique is the recipient ecosystem? How important are its constituent species and associated services for stakeholders? Supporting range shifts for species of conservation concern will remain a key climate change adaptation tactic for conservation practitioners and natural resource managers.

3) **Incorporate species distribution model forecasts:** Use the best available data and models to anticipate the movement of range shifters and identify high priority conservation areas, hotspots of biodiversity[95], and hotspots of high impacts[96,97]. Additionally, triaging which species are most likely to persist under projected climatic conditions can inform where resources can be most effectively allocated. Regularly revise management proposals to

incorporate updates to these forecasts.

4) **Use tools to assess invasion risk:** Consider the parallels between traits common in successful introduced invasives[19] (Figure 1) and potential impacts (EICAT[72]) to identify high- and low-risk range-shifting species.

5) **Monitor changes in recipient communities:** Monitor for shifts in abundance of target species and the arrival of new species, especially following disturbance and extreme climatic events[21].

Challenges and Potential Limitations

Important knowledge gaps related to range-shifting species must be addressed to better understand the impacts that these species may have while also promoting persistence of species as their climate zones move. While range shifts have been documented for hundreds of species across all taxa and ecosystems[3–5], they can be difficult to detect, as the historical ranges for many species are unknown or imprecise and our understanding of a "native range" is not well defined[98]. This is especially true for systems that are not as well studied, such as deep-water marine systems that are difficult to access. The impacts of range shifters, which may accrue more slowly than impacts of introduced species, have received less attention and our ability to predict future outcomes is limited. For example, range-shifting species could undergo hybridization, experience toxicity, or evolve or adapt, but understanding the potential interactions with new environments is needed to address these possible outcomes. Addressing these knowledge gaps will require working across broad stakeholder groups to leverage and continue existing monitoring programs and incorporate non-traditional resources, such as local and traditional

ecological knowledge[99].

Predicting potential shifts is further complicated by our limited understanding of the biotic and abiotic limits to species' ranges. Predicting which species are likely to undergo shifts requires a knowledge of organismal physiology and thermal limits. Additionally, while temperature is a primary driver of distribution patterns[100,101], biotic resistance also plays a critical role[46]. To detect species interactions and community impacts, manipulative *in situ* experiments are likely necessary and should be a focus for climate change researchers. However, these experiments are often too time-consuming or expensive to provide a comprehensive global understanding of impacts, but a lack of experimental studies should not preclude using general risk assessment frameworks (Figure 1) and knowledge from invasion biology to inform decision making. Additionally, such assessments can be used by practitioners, providing an accessible resource for those making management decisions.

Finally, we must acknowledge that anthropogenic climate change is likely to restructure communities on a broad scale and at a rate rarely experienced before the Anthropocene[102,103]. At the same time, as range shifters are altering recipient communities, those communities themselves are responding to climate change, and disentangling the causes and effects of these drivers will be a continuing challenge.

Conclusions

Although the consequences of range shifts vary from beneficial to catastrophic for recipient communities, risk assessments of the impacts of species movements in the context of climate change have focused almost entirely on assisted migration[7,25,85]. As species shift to track

a changing climate, we have a unique opportunity to facilitate advantageous, and discourage potentially problematic, movement of species in real time. However, both researchers and managers will likely need to adopt a more fluid and dynamic view of what constitutes a community, as differences in species' responses could result in communities with no current analog.[104,105], Communities are unlikely to shift as a whole, and partial shifts will disrupt species interaction networks and lead to trophic mismatces [106]. Rather than developing new strategies to evaluate the potential impacts of range-shifting species, we suggest leveraging invasion ecology theory and risk assessment tools (e.g., EICAT) to quantify the magnitude of the potential impacts of range-shifting species and define specific conservation goals in response. This will allow us to most effectively maintain biodiversity and ecosystem functioning in a changing climate.

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